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Uncultivated margins are source of soil microbial diversity in an agricultural landscape

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ABSTRACT

Agricultural intensification simplified environments, reduced their diversity, and hindered their ecosystem processes. Permanently vegetated areas (uncultivated margins) embedded in the cultivated matrix play a critical role in maintaining diversity and soil properties, and so mitigate the negative impact of intensification. We performed two studies aimed at evaluating the role of uncultivated margins on soil heterotrophic bacteria. In the first study, we sampled soybean fields and herbaceous and woody margins in three locations along a 100-kilometer transect. In a second study, in one location we sampled uncultivated margins and perpendicular 50-meter transects from each margin towards the centre of its adjacent soybean field. As control, we sampled similar transects in soybean fields that had cropped fields as margins. In both studies, we characterized the catabolic profiles and diversity of the heterotrophic bacterial community and soil properties. Soil microbial communities of uncultivated margins differed in composition and were more diverse than the cropped matrix. In turn, these differences positively correlated with soil pH. Woody margins also influenced the soil microbial composition, diversity and soil pH of neighbouring cultivated fields. In contrast, herbaceous margins did not influence their cultivated neighbours. These results broaden our understanding of soil heterotrophic bacterial community in agro-ecosystems and its implications for ecosystem functioning.

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1. Introduction

Agricultural intensification fragmented, simplified and homogenized the landscape of the most productive lands of the world. This process involved an increasing use of inputs (e.g. fertilizers, pesticides) and the specialization in a few annual crops. As a result, agroecosystems produced more food, but lost some of their capacity to provide other services (Foley et al., 2005). In the Rolling Pampa region, mixed farming systems combining extensive animal husbandry with annual crops were largely replaced by continuous cropping (Baldi et al., 2006). As a consequence, food provision increased, but biodiversity (de la Fuente et al., 2006; Bilenca et al., 2007) and carbon sequestration decreased (Caride et al., 2012; Viglizzo et al., 2011).

Uncultivated elements (margins) embedded in the agricultural landscape increase spatial heterogeneity, provide habitat for many species (Burel et al., 1998; Tscharntke et al., 2005), and preserve ecosystem functions (Klein et al., 2003; Follain et al., 2007). In the Rolling Pampa, uncultivated margins are either herbaceous or woody and sustain diverse communities of plants, small mammal and arthropods that spill over adjacent cropped areas (Bilenca et al., 2007; de la Fuente et al., 2010; Poggio et al., 2010, 2013; Molina et al., 2014). Margins dominated by woody species are particularly complex and diverse, harbour a diverse herbaceous understory, and are more the result of an invasion process than a planned design (Ghersa et al., 2002). Their greater plant diversity and temporal cover seemed to boost larger soil carbon contents and litter (D'Acunto et al., 2014), which could also influence soil microbial diversity.

Landscape context (i.e. agricultural mosaic) and crop management critically affect soil properties and the composition and diversity of soil biota. At the landscape scale, the heterogeneity of land use (e.g. crops, pastures, woodlands, grasslands) alter carbon cycling and the organisms involved in this process (Liao and Boutton, 2008; Castro et al., 2010). Moreover, greater litter production and plant diversity are associated with more diverse soil microbial communities (Zak et al., 2003). Because plant species differ in histochemical composition, changes in plant diversity and composition might indirectly alter the composition and function of heterotrophic microbial communities (Zak et al., 2003). However, the impact of uncultivated margins in the Rolling Pampa types on soil microbial communities has not been evaluated yet. At the field

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scale, management decisions such as tillage system, crop sequence, fertilization and pest management, largely control both primary production and eventually the litter incorporated into soil (Follett, 2001). Ultimately, these practices alter soil biota by changing plant litter amount and quality, soil pH and nutrient availability (Zak et al., 2003; Fierer and Jackson, 2006; Lauber et al., 2008, 2009; Gomez and Garland, 2012).

Here we investigated to what extent the changes previously observed in soil properties of uncultivated margins and cultivated fields (D'Acunto et al., 2014) correspond to changes in heterotrophic soil microorganisms. First, we sampled the composition and functional diversity of the heterotrophic soil bacterial community and other soil properties in herbaceous and woody margins and in soybean fields, the most frequent land use. We sampled them in three locations along a northeast-southwest 100-km transect in the Rolling Pampa. Second, in one of the three locations, we identified uncultivated margins adjacent to fields cropped with soybean. In each of this 'margin-soybean' pairs, we sampled the margin and the first 50 m-interface with the soybean fields. We also sampled a third 'margin-soybean' pair as control, consisting of cropped fields (cultivated with maize or soybean) and the interface with the corresponding adjacent soybean field. Based on the properties of woody margins described above, we expected them to have the largest bacterial diversity and soil carbon stocks. We also expected woody margins to have the greatest effect on composition and functional diversity of soil bacterial community of neighbouring soybean fields as a consequence of the litter spill over previously detected (D'Acunto et al., 2014).

2. Materials and methods

2.1. Description of the study area and landscape elements

The study was carried out between 2011 and 2012 in the central Rolling Pampa which extends from 32°S to 34°S and 60°W to 61°W (Argentina). Climate is temperate sub-humid, without a marked dry season. Mean annual rainfall is ~1000 mm and mean annual temperature is 17 °C. Soils are Argiudolls, characterized by a subsurface horizon with clay accumulation (Soriano et al., 1991). Since the 1990s, reduced tillage, genetically modified crops, and higher soybean prices led to a strong agricultural intensification process (Viglizzo et al., 2011). Sown perennial pastures and natural grasslands were extensively cultivated and nowadays continuous cropping dominates the landscape. Most fencerows have been removed to enlarge and simplify the cropped area. Therefore, in the current landscape, spontaneous vegetation occur only as small, scattered fragments of semi-natural vegetation in grazing paddocks, wire-fencerows and roadside verges (Viglizzo et al., 2011).

Current landscape is characterized by three main elements: cultivated fields with soybean, representing the most frequent situation, and two uncultivated margin types dominated by spontaneous herbaceous vegetation (hereafter herbaceous margins) or woody vegetation (hereafter woody margins). These uncultivated margins represent between 1 and 2% of the landscape (Ghersa et al., 2002). 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 (de la Fuente et al., 2010; 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 also have an herbaceous understory. The most abundant tree species are *Broussonetia papyrifera*, *Fraxinus* spp., *Gleditsia triacanthos*, *Ligustrum* sp., *Melia azedarach* and *Morus alba*, and the most abundant species of the understory are *Ammi majus*, *Bromus catharticus*, *Chenopodium album* and *Tagetes minuta*. Woody margins are not directly sprayed with herbicides, but they may receive drift from neighbouring crops. In contrast, herbaceous margins are usually sprayed with herbicides to reduce weeding. The cropped matrix encompasses fields of approximately 50 ha, most of them cultivated with soybean as single year crop or as a wheat–soybean double crop (Andrade et al., 2015). Crops are sprayed with systemic and contact pesticides during spring and summer, until harvest, in early autumn (Ferraro et al., 2003).

2.2. Sampling design and analysis

Firstly, we characterized the composition and functional diversity of the heterotrophic bacterial community and soil properties in herbaceous and woody uncultivated margins and in soybean fields. They were located in three areas along a northeast-southwest 100-km transect: San Pedro (33°47′S; 60°00′W), Pergamino (33°55′S; 60°23′W) and Junín (34°23′S; 60°48′W). Secondly, in a separate experiment only performed in Pergamino, we evaluated the influence of uncultivated margins on the composition and functional diversity of the heterotrophic bacterial community of adjacent field cropped with soybean.

2.2.1. Uncultivated margins and cropped matrix

In each location, we randomly selected 5 replicates for each uncultivated margin type (herbaceous and woody) and 2 replicates for the cropped matrix, represented by soybeans fields. In the spring (November, 2011), we sampled soil at each replicate and determined total and labile carbon, total nitrogen, pH, respiration rates, and the composition and functional diversity of the heterotrophic bacterial community.

In order to determine the functional composition and diversity (richness and evenness) of the heterotrophic bacterial community, in each replicate we sampled 5 soil cores of the top 10 cm and mixed them into a single composite sample. Soil samples were kept in the refrigerator (4 °C) until laboratory analyses. We used sterile micro plates that contained 96 wells with one of 17 carbon sources: amino acids (alanine, arginine, histidine, and proline), organic acids (benzoic acid, salicylic acid and pyruvic acid), a carboxylic acid (itaconic acid), carbohydrates (cellobiose, fructose, dextrose, lactose, mannitol, rhamnose and xylose), a fatty acid (Tween 80) and an alcohol (glycerol), and a blank with sterile distilled water (Garland and Mills, 1991 adapted by Di Salvo and García de Salamone, 2012). Each well received 50 μl of a standard basal media, 50 μl of tetrazolium violet, which develops colour under CO_2 production, and a soil aliquot of 50 μl from 10^{-4} soil suspensions. Incubations were at 25 °C for a maximum of 96 h. Well colour development was measured at 24, 48 and 72 h (only 48-h measurements are shown), as absorbance at 590 nm (Multiskan EX spectrophotometer®). The average well colour development of the 17 carbon sources of each sample was calculated. Then it was used to transform individual well values to eliminate variation in colour development caused by different cell densities (Garland, 1997). Functional diversity was calculated using the Shannon–Weaver index (H) which combines richness and evenness in the distribution of metabolic activity. Briefly, this index is calculated as the sum of the product of the optical density recorded at each carbon source and its own log for the 17 carbon sources used. We used an optical density of 0.25 as a threshold of a positive response (Garland, 1997). Catabolic richness is the number of different carbon sources that were used by the bacterial community (i.e. equivalent to species richness in the soil), and was calculated by counting all the positive optical density readings.

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