



## Research article

Macro and mesofauna soil food webs in two temperate grasslands: responses to forestation with *Eucalyptus*María Leticia Sabatté<sup>a,b,\*</sup>, Marcelo Juan Massobrio<sup>b</sup>, Mariano Tomás Cassani<sup>b</sup>, Fernando Roberto Momo<sup>c</sup><sup>a</sup> Universidad Nacional de Luján, Laboratorio de Ecología, Rutas 5 y 7, B6700ZAB, Luján, Argentina<sup>b</sup> Cátedra de Manejo y Conservación de Suelos. Facultad de Agronomía, Universidad de Buenos Aires, Av. San Martín 4453 C1417DSE, Buenos Aires, Argentina<sup>c</sup> Instituto de Ciencias, Universidad Nacional de General Sarmiento, Juan M. Gutiérrez 1150, B1613GSX, Los Polvorines, Argentina

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## ABSTRACT

We studied the effects of land use change from grassland to *Eucalyptus* spp. plantation on macro and mesofauna soil food webs in two sites in the Rolling Pampas. We expected to find differences in the parameters that characterize the structure of soil food webs, as the implantation of *Eucalyptus* implies changes in the characteristics of the resources and the microhabitat conditions. We also expected to find differences in the communities in terms of diversity, abundance, and species present. The treatments were: grasslands; 10-year-old *Eucalyptus* plantations and 20-year-old *Eucalyptus* plantations. Seasonal samplings were performed for the extraction of soil fauna in winter, spring, summer and autumn. For the analysis of food webs, we worked with “trophic species”: groups of organisms that have the same prey and the same predators. A total of 25 food webs were laid out using bibliographical information of feeding habits from the identified taxa. From each food web, we obtained a predator overlap graph, in which the consumers that share the same source or prey are linked by an arrow. In addition, the Shannon-Wiener index was calculated. We found that trophic species densities were different among the treatments: communities from grassland and the younger plantations were dominated by earthworms and other secondary decomposers, while the community in the older plantation showed a greater contribution of primary decomposers (Shyphyla, Isopoda and Diplopoda). No significant differences between treatments were found in the parameters that characterize the structure of soil food webs, i.e. connections number, number of trophic species nor connectivity. However, the diversity of the community was lower in the youngest plantations than in the other treatments, and it shows evidence of compartmentalization in the predator overlap graphs. Our findings suggest that the meso and macrofauna communities in the 10-years-old plantations represent a transition between the communities from grasslands and the oldest plantations. We conclude that the effects of forestation with *Eucalyptus* on soil fauna communities are evident through changes in functional groups rather than changes in the parameters that characterize the structure of soil food webs.

## 1. Introduction

At a global level, the implantation of forest species in new areas is taking place at a rate of 5 million hectares per year (FAO, 2019). In Argentina, the rate of forestation has increased progressively over the last 30 years and the implanted forests currently cover an area of 1,120,411 ha (MAGyP, 2019). These forestations are fundamentally implanted with fast-growing exotic species, mainly *Eucalyptus* spp. and *Pinus* spp. In the Rolling Pampas region, Argentina, planted forests are on sites formerly occupied by grasslands. The consequences of this land use change from

native grassland to fast-growing exotic plantations are poorly understood. The effects of *Eucalyptus* spp. implantation on soil physical and chemical properties have been the subject of some studies (Mathers et al., 2003; Laclau et al., 2010) and its impacts on the microbial community have also been investigated (Sicardi et al., 2004; Murugan et al., 2014). However, there is no evidence of how forestation with *Eucalyptus* spp. will affect macro- and mesofauna soil food webs. The importance of studying soil food webs, their patterns and their changes lay in their relationship with the ecological processes on soils and its ecosystem

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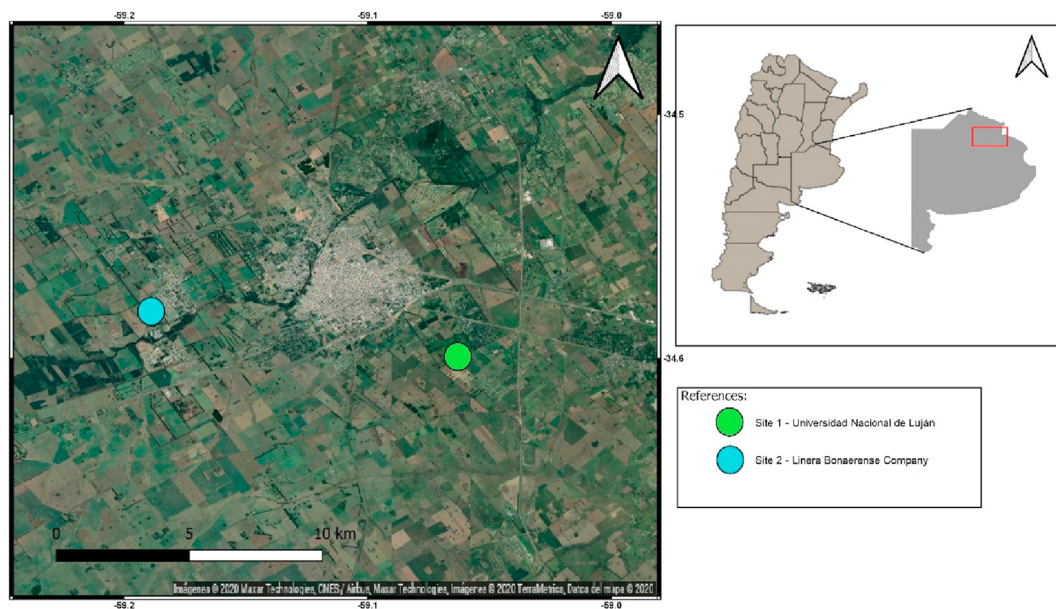


Figure 1. Map of study area showing the location of the study sites, in Buenos Aires province, Argentina.

services, such as the organic matter decomposition, the nutrients cycle and the water dynamics.

Soil food webs involve a great diversity of organisms that depend directly or indirectly on detritus, a reservoir of dead organic matter with different levels of decomposition, which forms the basis of soil food webs. Indeed, soil food webs are considered as “donor systems” (Pimm, 2002) for not being directly based on energy provided by photosynthesis, but instead being based on the complex organic matter decomposition provided by other compartments. There is evidence that food web structure is related to resource availability (i.e. bottom up forces) which is in turn linked to detrital inputs to soil (Cole et al., 2008; Doblás-Miranda et al., 2009; Scheu, 2002). According to theoretical studies, food web complexity is expected to drive the ecosystem functions and stability (Odum, 1953; MacArthur, 1955; Elton, 1958; De Angelis, 1975), although the mechanisms determining the trophic network structure are poorly understood. In addition, agricultural practices and other human

activities can shift the community's structure and dynamics from fungal-based to bacterial-based energy channel, affecting the stability of the food webs (Moore et al., 2005). In terrestrial ecosystems, most of the primary production enters the soil through dead plants in grasslands; through leaves, roots and wood in forests, and through crop residue in agricultural fields (Coleman et al., 2004). In the particular case of forestation in grasslands, the partial replacement of herbaceous vegetation with woody vegetation implies a change in the quality of the plant litter provided to the system (Zhang et al., 2008), in the vertical distribution of the resources, in the microclimatic conditions, and in the refuge offered for the soil fauna on the ground and the surface.

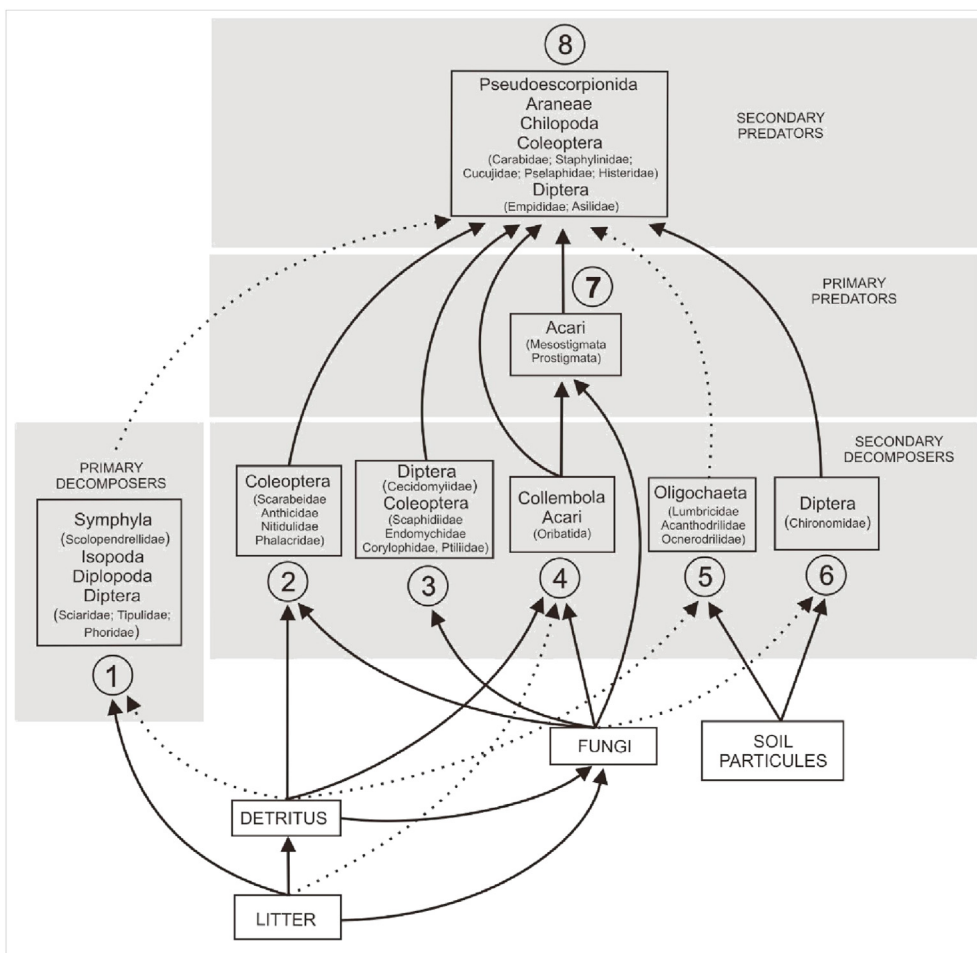
From an ecological theory perspective, the forestation of grassland can be considered as an anthropogenic disturbance. Disturbances can be characterized by their frequency, duration, size or spatial extent, and their intensity or severity, and they usually have characteristic temporal and spatial scales (Holling et al., 1994). Forestation is clearly what

Table 1. Soil properties in the studied sites at Lujan River basin, Buenos Aires, Argentina.

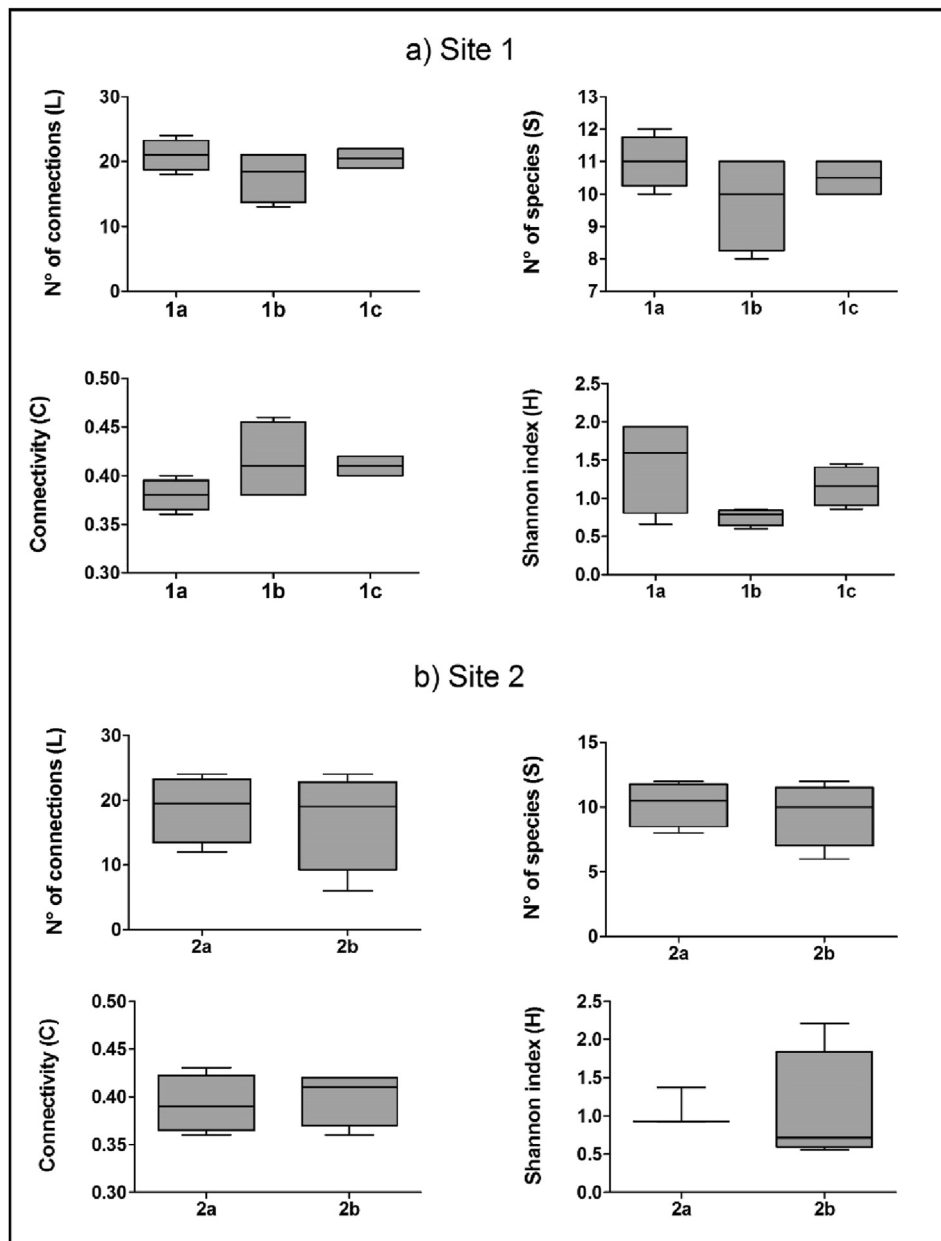
|              | Site 1    |  |  | Site 2    |  |
|--------------|-----------|--|--|-----------|--|
|              | Grassland | 10-year-old <i>Eucalyptus</i> plantation | 20-year-old <i>Eucalyptus</i> plantation | Grassland | 10-year-old <i>Eucalyptus</i> plantation |
| <b>Clay:</b> |           |  |  |           |  |
| <2μ          | 18.6      | 19.0                                     | 18.5                                     | 21.6      | 19.5                                     |
| <b>Silt:</b> |           |  |  |           |  |
| 2-20μ        | 31.2      | 33.6                                     | 29.2                                     | 28.1      | 30.6                                     |
| 2-50μ        | 63.0      | 64.2                                     | 57.1                                     | 57.7      | 61.2                                     |
| <b>Sand:</b> |           |  |  |           |  |
| 50-74μ       | 10.6      | 8.7                                      | 10.9                                     | 10.3      | 8.2                                      |
| 74-100μ      | 4.4       | 3.7                                      | 5.6                                      | 5.9       | 5.4                                      |
| 100-250μ     | 1.8       | 2.9                                      | 5.7                                      | 2.4       | 3.9                                      |
| 250-500μ     | 1.2       | 1.0                                      | 1.4                                      | 1.3       | 1.0                                      |
| 0.5–1 mm     | 0.3       | 0.3                                      | 0.6                                      | 0.6       | 0.7                                      |
| 1–2 mm       | 0.1       | 0.2                                      | 0.2                                      | 0.2       | 0.2                                      |
| MO %         | 3.65      | 4.67                                     | 4.15                                     | 4.53      | 4.00                                     |
| CO %         | 2.12      | 2.71                                     | 2.41                                     | 2.63      | 2.32                                     |
| P asim       | 4.5       | 17.4                                     | 4.6                                      | 2.3       | 10.8                                     |
| K meq %      | 1.2       | 1.3                                      | 1.3                                      | 1.8       | 1.2                                      |
| CIC          | 23.9      | 25.1                                     | 24.5                                     | 26.9      | 25.7                                     |

**Table 2.** Classification of soil fauna into trophic species and its reference number (node). Trophic species were defined using bibliographical information referring to the feeding habits of the identified taxa in the grasslands and the *Eucalyptus* plantations in the studied sites.

| Trophic species and its reference number (Node) | Taxa  | Food source  | Predators        |
|---|---|--|------------------|
| 1 – Macrofauna decomposers.                     | Symphyla (Scolopendrellidae); Isopoda; Diplopoda; Diptera (Sciaridae).  | Litter. Detritus as a complementary source.                                      | Species 8.       |
| 2 – Coleoptera detritivores and fungivores.     | Coleoptera (Scarabeidae, Cryptophagidae, Anthicidae, Phalacridae).  | Detritus and fungi.  | Species 8.       |
| 3 – Diptera and coleoptera fungivores.          | Diptera (Cecidomyiidae); Coleoptera (Scaphidiidae, Endomychidae, Corylophidae, Ptiliidae).  | Fungi.   | Species 8.       |
| 4 – Mesofauna decomposers.                      | Collembola; Acari (Oribatida).  | Mainly detritus and associated microorganisms. Litter as a complementary source. | Species 7 and 8. |
| 5 – Oligochaeta.                                | Oligochaeta ( <i>A. caliginosa</i> , <i>A. rosea</i> , <i>A. trapezoides</i> , <i>M. dubius</i> , <i>M. phosphoreus</i> , <i>O. tyrtaeum</i> , <i>B. parvus</i> , <i>Eukerria</i> sp.). | Soil particles and detritus.   | Species 8.       |
| 6 – Diptera microphage.                         | Diptera (Chironomidae).   | Soil particles and associated microorganisms.                                    | Species 8.       |
| 7 – Mesofauna predators.                        | Acari (Mesostigmata, Prostigmata).  | Mainly Collembola and Acari (Oribatida). Fungi as complementary resource.        | Species 8.       |
| 8 – Macrofauna predators.                       | Arachnida (Araneae); Chilopoda; Diptera (Empididae, Asilidae); Pseudoescorpionida; Coleoptera (Carabidae, Staphylinidae, Cucujidae, Pselaphidae, Histeridae).                           | Other arthropods and Oligochaeta (Species 1 through 7).                          | -                |



**Figure 2.** Soil food web based on litter and detritus for the soils in the grasslands and *Eucalyptus* plantations of the studied sites. The numbers represent trophic species. The arrows represent the connections or the feeding relations among species: complete arrows indicate the connections of higher intensity (main food sources) and dotted arrows indicate those of least intensity (complementary food sources).



**Figure 3.** Medium, quartiles, and extreme values for the variables: number of connections (L), number of trophic species (S), connectivity (C), and Shannon index (H) of the trophic webs of the studied treatments in Sites 1 (1a: Grassland; 1b: 10-year-old *Eucalyptus* plantation; 1c: 20-year-old *Eucalyptus* plantation) and Site 2 (2a: Grassland; 2b: 10-year-old *Eucalyptus* plantation).

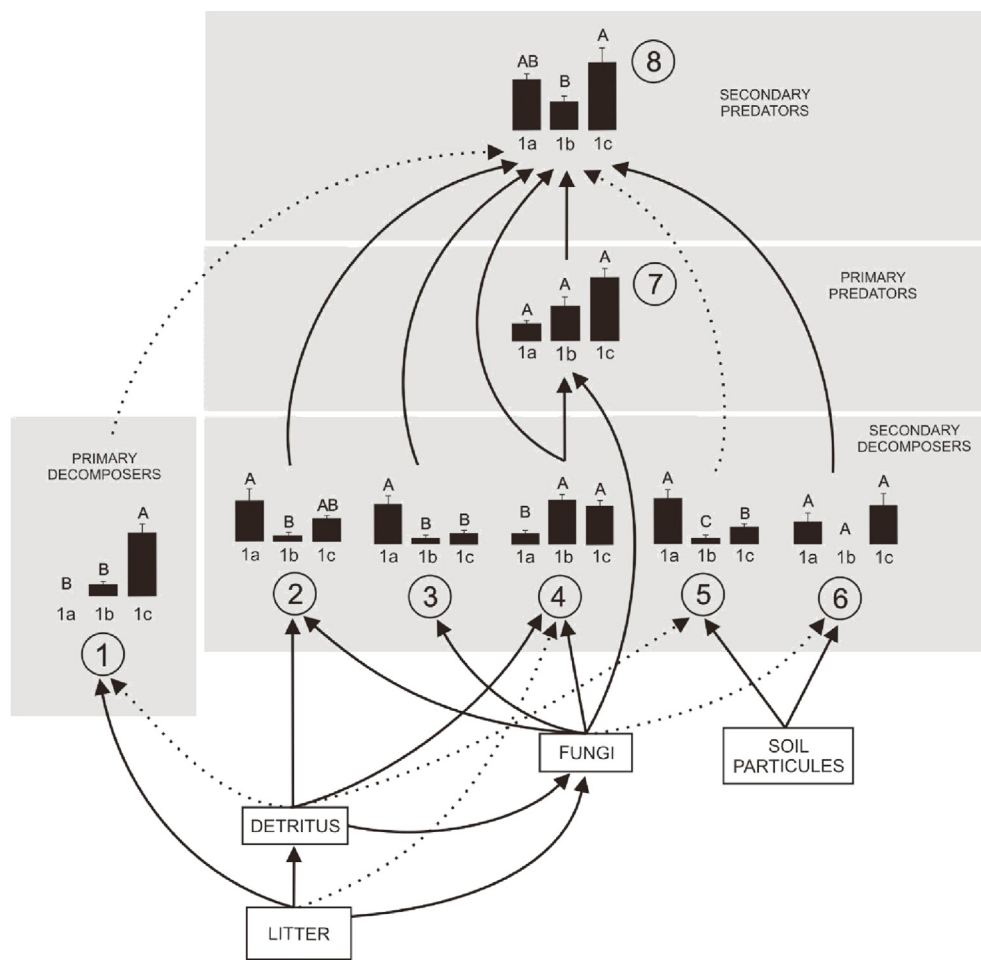
Bengtsson (2002) calls a “press disturbance”, i.e. a chronic stress agent that is generally anthropogenic in origin. Therefore, it is reasonable to assume that forestation causes changes in soil food webs since it changes the amount of energy that reaches the base of these webs. Moreover, it could be expected that the change in the characteristics of the resources at the base of the food webs in these soils, will be translated into differences in the structure of the food webs and the species present.

The aim of this work was to describe the macro and mesofauna soil food webs in *Eucalyptus* spp. plantations of different ages, in two sites in the Rolling Pampas. Our hypothesis was that meso and macrofauna communities will be different between *Eucalyptus* plantations and grassland in terms of diversity, abundance, and species presence. We also expected to find differences in the parameters that characterize the structure of soil food webs, i.e. the number of connections, number of species, and connectivity.

## 2. Materials and methods

### 2.1. Study area

The study area was in a small basin that belongs to the middle basin of the Lujan River in the Rolling Pampas sub-region of Argentina. The climate is humid temperate with an average temperature of 16.4 °C and an average precipitation of 938 mm, with maximum rainfalls during the summer. This study was conducted in two *Eucalyptus* plantations located in the Universidad Nacional de Luján, Site 1 (34,58 S and 59,08 W), and the Linera Bonaerense Company, Site 2 (34,58 S and 59,18 W) (Figure 1). In Site 1, three treatments were proposed: grasslands without significant use for at least 20 years (1a); plantation of *Eucalyptus* spp. from 1996 (1b) and plantation of *Eucalyptus* spp. from 1986 (1c). In Site 2, two treatments were considered: a grassland without significant use for at least 20



**Figure 4.** Soil food web based on litter and detritus for the treatments in Site 1. 1a: Grassland; 1b: 10-year-old *Eucalyptus* plantation; 1c: 20-year-old *Eucalyptus* plantation. The numbers represent trophic species, as in Figure 1. The arrows represent the connections or the feeding relations among species: the complete arrows indicate the connections of higher intensity (main food sources) and the dotted arrows indicate those of lesser intensity (complementary food sources). The vertical bars represent the standardized mean density ( $n = 12$ )  $\pm$  standard error of the trophic species with regards to the maximum density value reached by each species during the year. Different letters indicate significant differences between treatments for each the trophic species ( $p < 0.01$ ).

years (2a) and a plantation of *Eucalyptus* spp. from 1992 (2b). The *Eucalyptus* trees were all 6-months-old at the time of planting. Therefore, the plantation age and the site are variables, both combined in five different situations. The soils are Typic Argiudolls in both sites (INTA 1974). Three composite pooled soil samples were taken in each treatment for the soil physical and chemical determinations. Organic matter content was determined by the method of Walkley and Black (1934), and extractable phosphorus was measured by the method of Bray and Kurtz (1945). The cation-exchange capacity (CEC) was measured at pH 7 with ammonium acetate by extraction with potassium chloride (Norman and Chapman, 1965). Exchangeable  $K^+$  was measured using flame photometry. Particle size distribution was measured using the Robinson pipette method for the clay and silt fractions and by sieving for the sand fractions (SCS, 1972).

**2.2. Sampling measurements and calculations**

Seasonal samplings were performed for the extraction of soil macro- and mesofauna in winter (August of 2004), spring (November of 2004), summer (February of 2005), and autumn (April of 2005). Samples were taken along three parallel transects spaced 50 m apart. Three samples of 20 cm x 20 cm x 25 cm were taken at 5 m along each transect. In short, nine samples were taken from each treatment each time (Southwood and Henderson, 2000; Manly, 2001). Earthworms and other macrofauna organisms were extracted from all the samples by hand sorting. Mesofauna was extracted using the flotation technique with magnesium sulfate described by Jackson and Raw (1974). Organisms were fixed in alcohol (70%) and identified at different taxonomic levels using keys (Balogh and

Balogh, 1988, 1990, 1992a, 1992b; Borror et al., 1989; Dindal, 1990; Bernava Laborde, 2009). The number of individuals per sample was referred to the area and expressed as density (individual. $m^{-2}$ ).

For the analysis of food webs, we worked with “trophic species”: groups of organisms that have the same prey and the same predators. So, each trophic species constitutes a specific component in the matter and energy cycles, being therefore able to represent a group of biological species, a single biological species, or a determined state in the cycle of life of one or many biological species. Trophic species were defined using bibliographical information referring to the feeding habits of the identified taxa. Considering this information, the food resources mentioned in the bibliography as main food sources were separated for each taxa from those resources identified as occasional food sources.

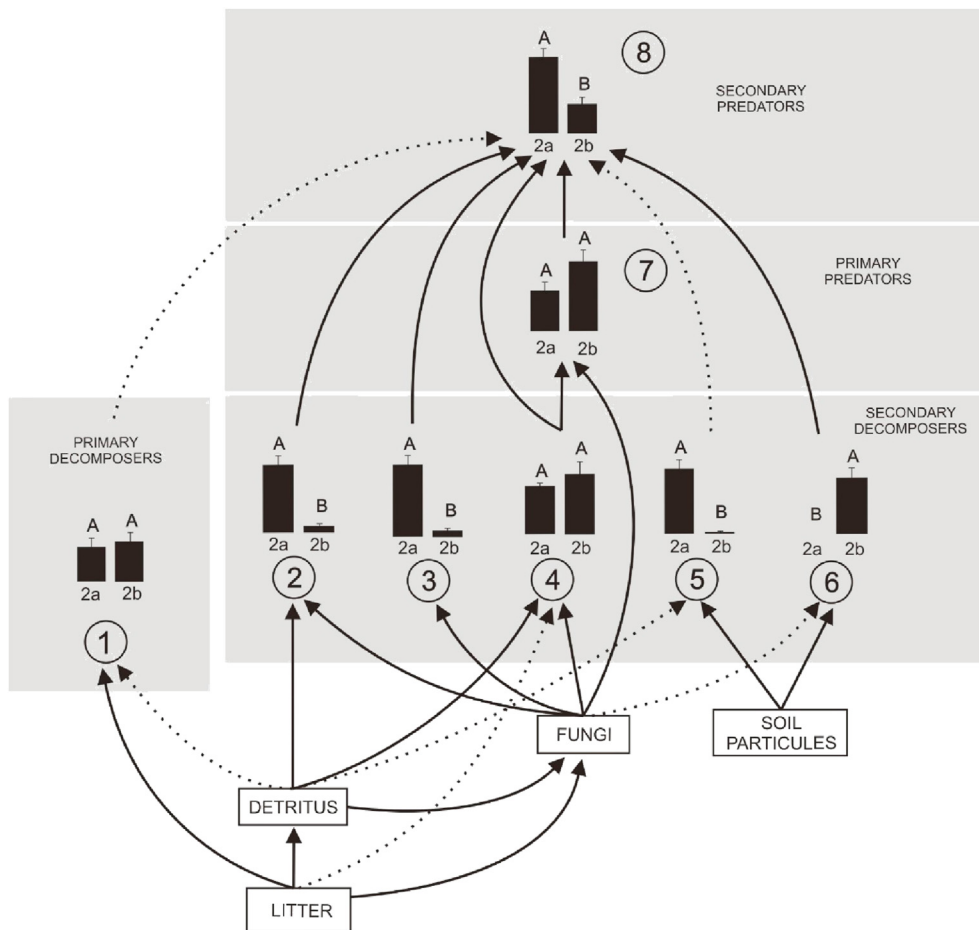
With this bibliographical information we also discriminate between trophic levels, considering that primary and secondary decomposers form a continuum of species feeding on litter to those feeding predominantly on microorganisms (Scheu and Falca, 2000; Scheu, 2002). Therefore, species that feed predominantly on litter were considered primary decomposers while those species that feed predominantly on detritus and microorganisms were considered secondary decomposers.

For each treatment, five food webs were laid out: one for each season of the year and an annual food web, built from the average of the seasonal data. Each of the resulting 25 food webs was described by the number of trophic species ( $S$ ), the total number of connections ( $L$ ), and the connectivity ( $C$ ) calculated as (Pimm et al., 1991):

$$C = L \cdot 2 / (S \cdot (S - 1))$$

The density (individual. $m^{-2}$ ) of each trophic species was also calcu-





**Figure 5.** Soil food web based on litter and detritus for the treatments in Site 2. 2a: Grassland; 2b: 10-year-old *Eucalyptus* plantation. The numbers represent trophic species, as in Figure 1. The arrows represent the connections or the feeding relations among species: the complete arrows indicate the connections of higher intensity (main food sources) and the dotted arrows indicate those of lesser intensity (complementary food sources). The vertical bars represent the standardized mean density ( $n = 12$ )  $\pm$  standard error of the trophic species with regards to the maximum density value reached by each species during the year. Different letters indicate significant differences between treatments for each the trophic species ( $p < 0.01$ ).

lated for each treatment and season. In order to better show the results, we calculated the standardized mean density for each trophic species in each treatment (1a; 1b; 1c; 2a; 2b) as:

$$SMDn\ m = 100 \cdot AMDn / MDn\ m$$

*SMDn m*: Standardized mean density of species *n* in site *m*.

*AMDn*: Annual mean density of species *n*.

*MDn m*: Maximum density of species *n* in site *m*.

Annual mean densities were calculated using data from the four seasons sampled during the year. The maximum density corresponded to the maximum value of density observed during the year for each species in each site.

In addition, from each of the 25-food web, we obtained a predator overlap graph, in which the consumers that share the same source or prey are linked by an arrow (Pimm, 1980; Dunne, 2005). These graphs allow the identification of predation guilds and give a qualitative idea of the competition for resources. Some properties of these graphs can be related to biological characteristics of the community (Sugihara, 1982; Cohen, 1977; Putman, 1996).

In order to compare the diversities, the Shannon-Wiener index was calculated for each season in each of the treatments.

### 2.3. Statistical processing of data

The differences among treatments for density of trophic species, *S*, *L*, *C* and Shannon-Wiener index were evaluated with non-parametric test because data were not normal, and the total number of samples per site and time were low. At Site 1 we had three treatments, thus we compared them using a Kruskal-Wallis test for three independent samples; at Site 2

we had only two treatments (grassland and 10 years old *Eucalyptus*), thus we made comparisons using the U of Mann-Whitney test for two independent samples. When these tests yielded significant main results, in order to detect between treatments differences we applied a Tuckey test. Analyses were performed using the software *Infostat/P v1.1 (2002)* and considering in all cases a significance level of  $p < 0.01$ .

## 3. Results

### 3.1. Soil food webs

The physical-chemical parameters show a high homogeneity, due to that the different land uses studied were developed on very similar soils (Table 1). Eight trophic species were defined for the studied treatments (Table 2). As those trophic species were all found in both Site 1 and Site 2, only one food web diagram was depicted (Figure 2) to represent the five treatments. It can be observed that more trophic species belonged to the secondary decomposers (nodes 2 to 6) than to the primary decomposers (node 1).

Regarding the structure of the food webs, no significant differences among the treatments were found in the number *L*, *S*, and *C* in either Site 1 or Site 2. However, the dispersion of the data was higher in the 10-year-old plantations (1b; 2b) than in the grasslands (1a; 2a) and the 20-year-old plantation (1c) (Figure 3). In relation to diversity, the Shannon index was lower in the 10-year-old plantations (1b; 2b) than in the grasslands of reference (1a; 2a) in both sites ( $p < 0.10$ ) but no differences were observed between the oldest plantation (1c) and the grassland (1a) (Figure 3).

**Table 3.** Density ( $individual \cdot m^{-2}$ ) of soil organisms and trophic species as in Table 2, in the grasslands and the *Eucalyptus* plantations in the studied sites. Values shown are means ( $n = 12$ )  $\pm$  standard error.

|   | Site 1           |  |  | Site 2           |  |
|---|------------------|--|--|------------------|--|
|   | Grassland        | 10-year-old <i>Eucalyptus</i> plantation | 20-year-old <i>Eucalyptus</i> plantation | Grassland        | 10-year-old <i>Eucalyptus</i> plantation |
| 1 - Macrofauna decomposers:   | 56 $\pm$ 22b     | 276 $\pm$ 116b                           | 1490 $\pm$ 297a                          | 230 $\pm$ 87a    | 255 $\pm$ 78a                            |
| Symphyla (Scolopendrellidae)  | 11 $\pm$ 6       | 133 $\pm$ 97                             | 833 $\pm$ 311                            | 20 $\pm$ 17      | 1 $\pm$ 1                                |
| Isopoda   | 32 $\pm$ 16      | 131 $\pm$ 42                             | 656 $\pm$ 162                            | 205 $\pm$ 87     | 125 $\pm$ 38                             |
| Diplopoda   | 1 $\pm$ 1        | 11 $\pm$ 5                               | 1 $\pm$ 1                                | 0 $\pm$ 0        | 124 $\pm$ 72                             |
| Diptera (Sciaridae)   | 12 $\pm$ 11      | 1 $\pm$ 1                                | 0 $\pm$ 0                                | 5 $\pm$ 3        | 5 $\pm$ 3                                |
| 2 - Coleoptera detritivores and fungivores:   | 25 $\pm$ 6a      | 4 $\pm$ 3b                               | 19 $\pm$ 4ab                             | 20 $\pm$ 6a      | 3 $\pm$ 2b                               |
| Scarabeidae, Cryptophagidae, Anthicidae, Phalacridae  |                  |  |  |                  |  |
| 3 - Diptera and coleoptera fungivores:  | 30 $\pm$ 10a     | 5 $\pm$ 2b                               | 16 $\pm$ 6b                              | 121 $\pm$ 25a    | 14 $\pm$ 7b                              |
| Coleoptera (Scaphidiidae, Endomychidae, Corylophidae, Ptiliidae)  | 19 $\pm$ 6       | 4 $\pm$ 2                                | 16 $\pm$ 6                               | 117 $\pm$ 24     | 13 $\pm$ 7                               |
| Diptera (Cecidomyiidae)   | 11 $\pm$ 6       | 1 $\pm$ 1                                | 0 $\pm$ 0                                | 4 $\pm$ 2        | 1 $\pm$ 1                                |
| 4 - Mesofauna decomposers:  | 5522 $\pm$ 1813b | 11187 $\pm$ 4246a                        | 12707 $\pm$ 6589a                        | 8058 $\pm$ 2763a | 15096 $\pm$ 5424a                        |
| Collembola  | 363 $\pm$ 78     | 495 $\pm$ 127                            | 1135 $\pm$ 439                           | 704 $\pm$ 69     | 253 $\pm$ 45                             |
| Acari (Oribatida)   | 5159 $\pm$ 1834  | 10692 $\pm$ 4233                         | 11572 $\pm$ 6428                         | 7354 $\pm$ 2764  | 14843 $\pm$ 5430                         |
| 5 - Oligochaeta:  | 341 $\pm$ 68a    | 49 $\pm$ 14c                             | 105 $\pm$ 18b                            | 474 $\pm$ 67a    | 10 $\pm$ 5b                              |
| <i>A. caliginosa</i> , <i>A. rosea</i> , <i>A. trapezoides</i> , <i>M. dubius</i> , <i>M. phosphoreus</i> , <i>O. tyrtaeum</i> , <i>B. parvus</i> , <i>Eukerria</i> sp. |                  |  |  |                  |  |
| 6 - Diptera microphage:   | 7 $\pm$ 4a       | 0 $\pm$ 0a                               | 11 $\pm$ 7a                              | 0 $\pm$ 0b       | 40 $\pm$ 16a                             |
| Chironomidae  |                  |  |  |                  |  |
| 7 - Mesofauna predators:  | 483 $\pm$ 188a   | 843 $\pm$ 347a                           | 1197 $\pm$ 524a                          | 612 $\pm$ 183a   | 1735 $\pm$ 995a                          |
| Acari (Mesostigmata, Prostigmata)   |                  |  |  |                  |  |
| 8 - Macrofauna predators:   | 152 $\pm$ 27ab   | 77 $\pm$ 14b                             | 207 $\pm$ 49a                            | 424 $\pm$ 52a    | 159 $\pm$ 25b                            |
| Arachnida (Araneae)   | 48 $\pm$ 14      | 44 $\pm$ 11                              | 95 $\pm$ 41                              | 97 $\pm$ 28      | 55 $\pm$ 10                              |
| Pseudoscorpionida   | 0 $\pm$ 0        | 0 $\pm$ 0                                | 21 $\pm$ 6                               | 0 $\pm$ 0        | 7 $\pm$ 3                                |
| Chilopoda   | 19 $\pm$ 7       | 16 $\pm$ 6                               | 59 $\pm$ 28                              | 44 $\pm$ 13      | 68 $\pm$ 23                              |
| Coleoptera (Carabidae, Staphylinidae, Cucujidae, Pselaphidae, Histeridae)   | 84 $\pm$ 19      | 16 $\pm$ 7                               | 32 $\pm$ 10                              | 283 $\pm$ 53     | 13 $\pm$ 4                               |
| Diptera (Empididae, Asilidae)   | 1 $\pm$ 1        | 1 $\pm$ 1                                | 0 $\pm$ 0                                | 0 $\pm$ 0        | 16 $\pm$ 16                              |

Different letters (a, b, c) indicate significant differences between treatments for each site ( $p < 0.01$ ).

**Table 4.** Minimum and maximum values for the variables: number of connections (L), proportion of strong interactions, nodes and connectivity (C) of the predator overlap graphs for the trophic webs for Site 1 and Site 2.  $N = 12$ .

|                          | Site 1    |  |  | Site 2    |  |
|--------------------------|-----------|--|--|-----------|--|
|                          | Grassland | 10-year-old <i>Eucalyptus</i> plantation | 20-year-old <i>Eucalyptus</i> plantation | Grassland | 10-year-old <i>Eucalyptus</i> plantation |
| N° of nodes              | 7–9       | 5–8                                      | 7–8                                      | 7–9       | 4–9                                      |
| N° of connections (L)    | 12–22     | 6–15                                     | 12–17                                    | 12–21     | 2–21                                     |
| % of strong interactions | 50–75     | 67–78                                    | 47–58                                    | 52–75     | 52–100                                   |
| Connectivity (C)         | 0.57–0.61 | 0.54–0.60                                | 0.57–0.62                                | 0.57–0.58 | 0.33–0.58                                |

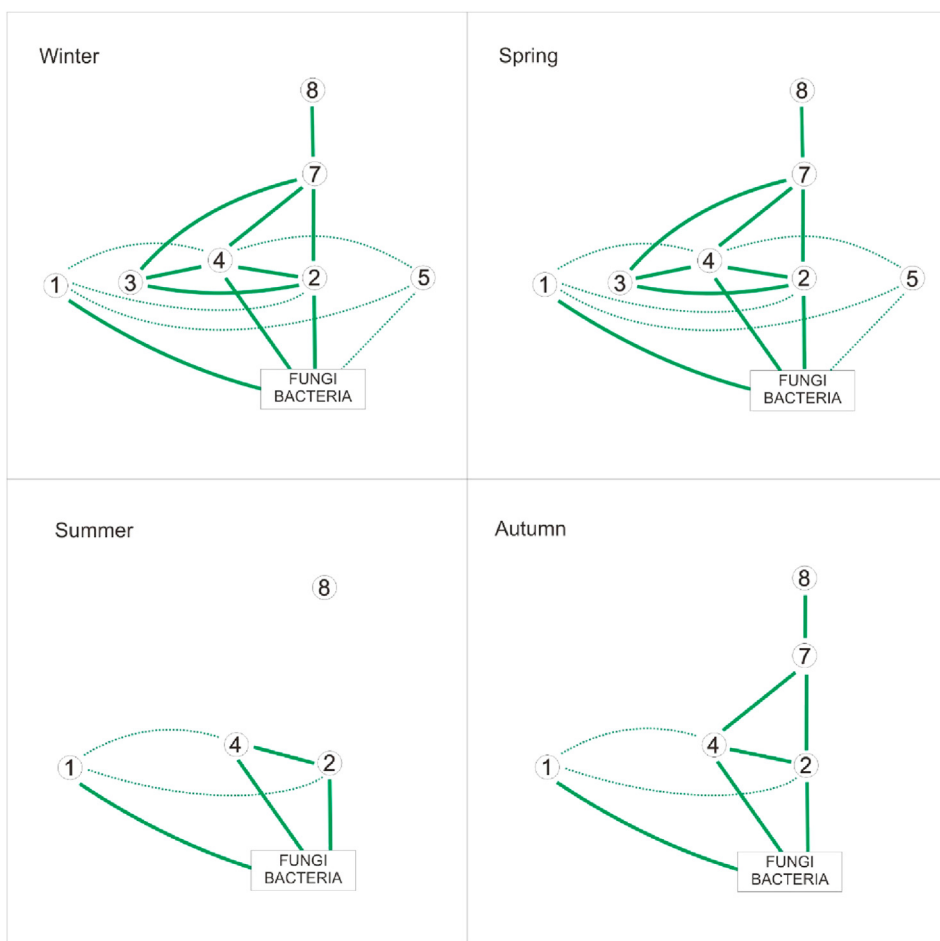
### 3.2. Trophic species densities

The standardized mean densities of trophic species corresponding to five annual food webs (1a; 1b; 1c; 2a; 2b) are shown in Figures 4 and 5 and in Table 3. The density of the macrofauna decomposers (node 1) was higher in 20-year-old plantation (1c) than in the 10-year-old plantation (1b) and the grassland (1a) in Site 1. However no differences were detected between the 10-year-old plantations (1b, 2b) and the grasslands (1a, 2a). On the other hand, detritivore and fungivore Coleoptera (node 2), fungivore Diptera and Coleoptera (node 3), and Oligochaeta (node 5) had lower densities in the 10-year-old plantations (1b, 2b) than in grasslands (1a, 2a). The density of the mesofauna decomposers (node 4) was higher in the plantations (1b, 1c) than in grassland of reference (1a) in Site 1; however no differences among the treatments were detected in Site 2. Similarly, the density of microphage Diptera (node 6) was higher in the 10-year-old plantation (2b) than in the grassland (2a) in Site 2, but no differences among the treatments were detected in Site 1. Finally, no significant differences in the density of the mesofauna predators (node 7)

were detected in any site, while the macrofauna predators (node 8) showed different results according to site: they were more abundant in the 20-year-old plantation (1c) than in the 10-year-old plantation (1b) in Site 1, and more abundant in the grassland (2a) than in the 10-year-old plantation (2b) in Site 2.

### 3.3. Seasonal variations in trophic species densities and predator overlap graphs

The trophic species densities show seasonal variations during the year in both Sites 1 and 2, though no clear temporal pattern could be identified. The predator overlap graphs obtained from each of the 20 seasonal food webs (four seasons x five treatments) were described according to the number of nodes, L, the proportion of strong interactions and C (Table 4). The range of the number of nodes and L was higher, and the proportion of strong interactions was lower in the 10-year-old plantations (1b; 2b) than in the grasslands (1a; 2a) and the 20-year-old plantation (1c). In addition, in the 10-year-old plantations (1b; 2b), we could



**Figure 6.** Predator overlap graphs for the seasonal food webs in the 10-year-old *Eucalyptus* plantation in Site 1. The numbers represent trophic species, as in Figure 1. The species with shared preys or resources were joined with complete arrows in cases where shared resources or preys were main food sources for such species, or with dotted lines when the shared resources or preys represented complementary food sources for the species.

observe a certain degree of compartmentalization that is evidenced in the isolation of some species, such as the macrofauna predators (node 8) during the Summer in Site 1 (Figure 6), or through the existence of isolated groups of species, such as the two groups that are observed during the Autumn in Site 2 (nodes 7 and 8; node 1) (Figure 7). On the contrary, in the grasslands, there seems to be no evidence of compartmentalization.

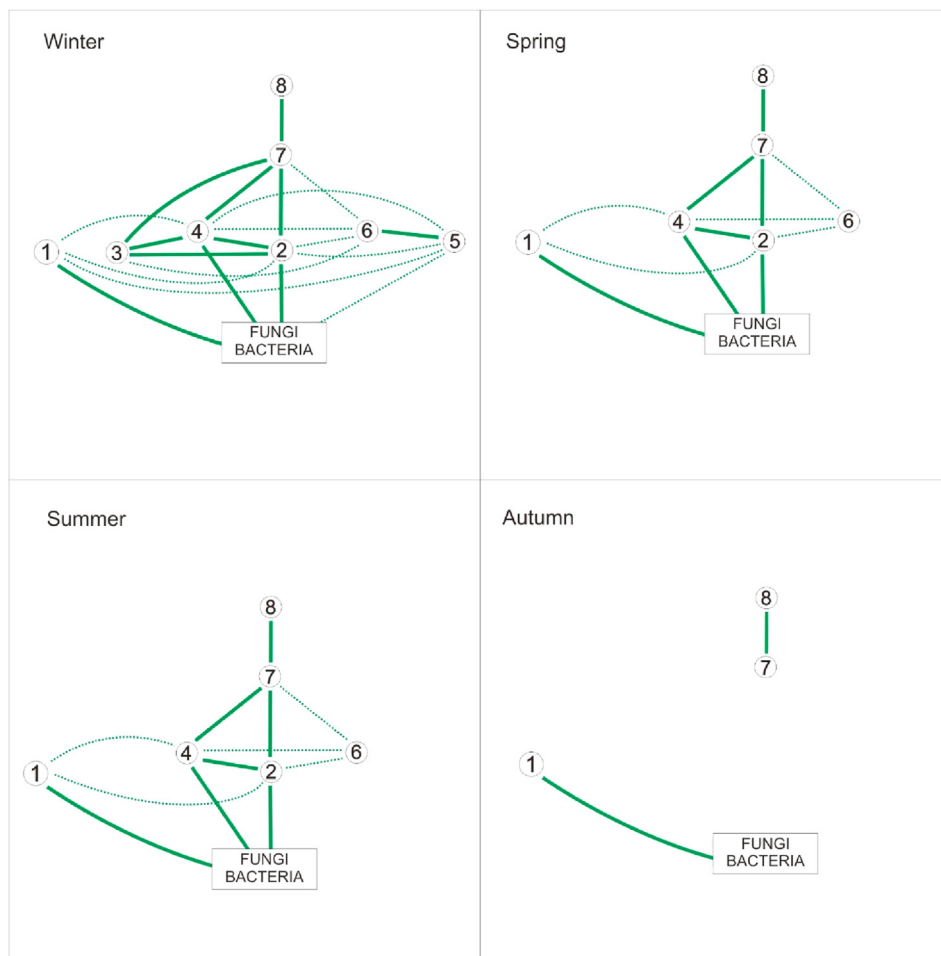
#### 4. Discussion

Press disturbances constitutes chronic stress agents that usually causes a decrease in the diversity of soil communities (Bengtsson, 2002). If we assume that forestation constitutes a press disturbance *sensu* Bengtsson, we can interpret the differences among the treatments (grassland, 10-year-old *Eucalyptus* plantation and 20-year-old *Eucalyptus* plantation) as a response of the communities to that disturbance. The decreasing diversity observed in the 10-year-old plantations in grasslands would support this hypothesis, and its recovery in the 20-year-old plantation would indicate a process of re-establishment and reorganization of the communities. These findings are consistent with other studies that have shown a declining soil fauna diversity with land use change (Mader, 2002; Culman et al., 2010). The time required for the reorganization of the soil animal community after the occurrence of a disturbance depends on the ecological memory in or near the disturbed areas and the type of disturbance (Bengtsson, 2002). In this study, we found a recovery in the diversity of meso- and macrofauna community in the 20-year-old *Eucalyptus* plantation. However, this recovery seems to be associated with a

reorganization of the community, since our results showed differences between the abundance of trophic species present in the 20-year-old *Eucalyptus* plantation and the grassland. The soil fauna community of the grasslands was dominated by earthworms and others secondary decomposers such as Coleoptera and Diptera, while the soil fauna community of the 20-year-old plantation showed an essential contribution of primary decomposers such as Shymphyta, Isopoda and Diplopoda. These differences between soil meso- and macrofauna communities could be related to the differences in litter quality and resource distribution between forest plantations and grasslands. The relation between soil fauna and resource quality and quantity has been established by several authors (Warren and Zou, 2002; Rantalainen et al., 2004; Wardle et al., 2006; Witt and Setälä, 2010; Sauvadet et al., 2016). In our study, the accumulation of tree litter on the surface of the soil in the 20-year-old plantation constitutes a new food source for the epi-edaphic primary decomposers that mainly feed on vegetal litter in different degrees of decomposition. This increase could explain the highest density of the primary decomposers observed in the 20-year-old plantation in relation to the other treatments.

On the other hand, the density of macrofauna decomposers -i.e. Diptera and Coleoptera detritivores and fungivores- was smallest in the *Eucalyptus* plantations, suggesting that these trophic species were negatively affected by the change in available resources. It is known that the *Eucalyptus* litter represents a resource of lesser quality (higher C/N ratio) than grass litter (Zhang et al., 2008), and it has been suggested that changes in the C:N ratio of detritus may cause a shift between the bacterial-based and the fungal-based energy channels (Moore and Hunt,





**Figure 7.** Predator overlap graphs for the seasonal food webs in the 10-year-old *Eucalyptus* plantation in Site 2. The numbers represent trophic species, as in Figure 1. The species with shared preys or resources were joined with complete arrows in cases where shared resources or preys were main food sources for such species, or with dotted lines when the shared resources or preys represented complementary food sources for the species.

1988). It is likely that any change in the balance of the microbial populations would affect its consumers, the secondary decomposers. However, the density of mesofauna decomposers seems not to be affected in the same way by this shift in the microbial population balance, as no differences in the density of Acari and Collembola were found between the grassland and the plantation in Site 1. On the contrary, the density of this decomposer group was higher in the plantations than in the grassland in Site 2, probably because of the availability of refuges and the heterogeneity of the habitats in these environments. Oribatids response to habitat heterogeneity has been reported by other authors (Gill, 1969; Hansen, 2000), as well as the effect of the microclimatic factors and vegetation structure on Colembolla populations (Setälä et al., 1995; Wolters, 1998; Wiwatwitaya and Takeda 2004). Since the increasing resource base can be transferred to higher trophic levels (Chen and Wise, 1999; Cole et al., 2005), a similar pattern of change in density could be expected for predator guilds such as that shown by their prey. However, in our study, we could not identify any clear tendency of change in predators' guilds density as a response to the forestation with *Eucalyptus*. Therefore, our results support partially the idea that the structure of the trophic webs is regulated by the availability of base resources, the “bottoms-up” dubbed control.

In this study, we found no differences among plantations and grasslands L, S and C, indicating that the general structure of the soil food webs did not change as a result of the conversion from grassland to *Eucalyptus* plantation. However, in the seasonal analysis of the predator overlap graphs, we found evidence of compartmentalization and a smaller number of connections and a higher proportion of weak

interactions in the 10-year-old plantations than in the other treatments. In the grasslands and the 20-year-old plantation, the high interconnection observed in the predator overlap graphs could be interpreted as a significant niche overlap due to a high competition for resources. In these communities, the species are connected to each other during the four seasons of the year. These results, together with the higher dispersion of the parameters L, S, C and the lesser diversity found in the 10-year-old plantation, suggest that soil fauna communities in the youngest plantations are transitional, with greater variability and lesser stability than the communities of the grasslands and the oldest plantation.

## 5. Conclusions

In this work, we have studied the effects of land use change from grasslands to *Eucalyptus* plantations on trophic species densities, food web structure and diversity. We found that the effects of land use change on soil fauna communities are evident through changes in trophic species density between functional groups rather than changes in the parameters that characterize the structure of soil food webs. This is because the food webs studied were similar in terms of number of connections, number of species, and connectivity, but different in terms of trophic species densities and macro and mesofauna community diversity. As other authors have suggested (Caswell, 2005; Thompson et al., 2012; Maggiotto et al., 2019), food web approaches are essential for the analysis of the consequences of human activities and the sustainable management of natural resources.

## Declarations

### Author contribution statement

María Leticia Sabatté: Performed the experiments; Analyzed and interpreted the data; Wrote the paper.

Marcelo Juan Massobrio: Conceived and designed the experiments; Analyzed and interpreted the data.

Mariano Tomás Cassani: Contributed reagents, materials, analysis tools or data.

Fernando Roberto Momo: Conceived and designed the experiments; Analyzed and interpreted the data; Wrote the paper.

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### Data availability statement

Data included in article/supplementary material/referenced in article.

### Declaration of interests statement

The authors declare no conflict of interest.

### Additional information

No additional information is available for this paper.

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