



Soil arthropod composition differs between old-fields dominated by exotic plant species and remnant native grasslands

Gimena Vilardo^{a,b}, Pedro M. Tognetti^{b,c}, Adelia González-Arzac^c, Laura Yahdjian^{a,b,*}

^a Universidad de Buenos Aires, Facultad de Agronomía, Departamento de Recursos Naturales y Ambiente, Catedra de Ecología, Buenos Aires, Argentina

^b CONICET – Universidad de Buenos Aires, Instituto de Investigaciones Fisiológicas y Ecológicas vinculadas a la Agricultura (IFEVA), Buenos Aires, Argentina

^c Universidad de Buenos Aires, Facultad de Agronomía, Departamento de Métodos Cuantitativos y Sistemas de Información, Buenos Aires, Argentina

ARTICLE INFO

Keywords:

Pampa grasslands
Biological invasions
Soil invertebrate composition
Isopods
Hymenoptera
Soil respiration

ABSTRACT

Secondary succession after agriculture abandonment (old-fields) is mostly dominated by exotic grass species. Non-native plant invasions may alter soil fauna, potentially inducing plant-soil feedbacks. Despite their importance in nutrient cycling and plant-soil interactions, meso and macrofauna received less attention than bacteria or fungi. Here we compared the composition of the soil arthropod community in native remnants and plant exotic-dominated old-fields grasslands in the Inland Pampa, Argentina. We sampled independent remnants and old-field grassland plots within a 100 km² agricultural landscape to test the hypothesis that the abundance of soil arthropod organisms is related to the quality of the plant biomass, whereas the diversity of the soil biota is related to plant species richness, resulting in a different soil biota composition because of differing plant communities. When compared to non-invaded remnant grasslands, soil activity and soil food-web characteristics of the old-fields sites included: 1. Higher total arthropod abundance, particularly of Isopoda, Pseudoscorpionida and Blattaria; 2. Lower abundance of Hymenoptera and Entomobryomorpha (Collembola); 3. Lower diversity, and evenness, but similar richness of soil organisms orders; 4. Higher soil respiration rates and soil temperature; and 5. Higher total soil N and K⁺ content, but lower soil P content. These results illustrate that soil arthropod composition can vary widely within grasslands patches depending on plant species composition. Also, the more diverse plant community of remnant grasslands supports a more diverse soil biota, although soil activity is slower. Our results support the strong linkage between plant community and soil arthropod composition and suggest that changes in soil biota composition might promote plant-soil feedback interactions inducing the persistence of these alternative grassland states in new agricultural human-modified landscapes.

1. Introduction

Exotic plant invasions can disrupt key ecosystem processes (Mack et al. 2000), such as nutrient cycling (Evans et al. 2001; Ashton et al. 2005), water balance, and plant-soil interactions (Klironomos, 2002), with consequences in other trophic levels such as herbivores and soil community decomposers (Belnap et al. 2005; Vilà et al. 2011; Schirmel et al. 2015). Much of the work related to biological invasions has focused on aboveground flora and fauna, but soil communities also respond to changes in plant community composition (Wolfe and Klironomos, 2005) and can mediate exotic plant invasions through plant-soil feedbacks (Kardol et al. 2013; Yelenik & D'Antonio, 2013). Understanding the changes in soil biota with exotic plant invasions may help to assess the impacts on the functioning of these invaded ecosystems.

Arthropod community composition may depend on plant species

composition through changes on resources (amount and quality) and soil environment (Wolfe and Klironomos, 2005; Wigginton et al. 2014). Arthropod abundance has been hypothesized to be correlated with plant diversity, but the results of previous studies have been equivocal. In contrast, plant productivity, vegetation structure, abiotic conditions, and the physical disturbance of habitats, are factors that interact with plant diversity, and that have been shown to influence arthropod abundance. For example, a diverse litter quality leads to resource heterogeneity, affecting arthropods diversity and abundance which depend on plant community composition (Wardle, 2002; Bardgett et al. 2005). There is evidence that changes in soil arthropod communities are more related to the identity of the invading species than with changes in primary production (Van Hengstum et al., 2014; Litt et al. 2014). Previous studies showed both decreases (Schirmel et al. 2015) and increases in arthropod abundance (Gratton and Denno, 2005; Kappes et al. 2007; Meisner et al. 2014) associated with plants invasions. These

* Corresponding author. Av. San Martín 4453, Ciudad de Buenos Aires, C1417DSE, Argentina.

E-mail addresses: vilaro@agro.uba.ar (G. Vilardo), tognetti@agro.uba.ar (P.M. Tognetti), agoarzac@agro.uba.ar (A. González-Arzac), yahdjian@agro.uba.ar (L. Yahdjian).

contrasting results may depend on the traits of invasive species compared with natives regarding for example the litter quality. For instance, litter decomposition may be affected by changes in the C:N ratio (D'Antonio and Hobbie, 2005; Spirito et al. 2014) or through litter compounds such as lignin and polyphenols, decreasing or increasing litter palatability and litter decay rate (Gabriel et al. 2013).

The changes in arthropod communities with exotic plant invasions and the consequences on soil processes have been scarcely explored (De Deyn et al. 2003). The different soil fauna components affect soil processes at different temporal and spatial scales (Swift et al. 1979; Peters, 1983). Soil macrofauna (i.e. organisms with body size > 2 mm) are mainly composed by arthropods that have a key role in soil structure and functioning. This diverse group of organisms participates in the carbon cycling by fragmenting litter and mixing organic matter with soil (Lavelle et al. 2006; Culliney, 2013) and regulates the activity of bacteria and fungi populations (i.e. microfauna, with body size < 0.2 mm; Schulmann & Tiunov 1999). Particularly, in agricultural systems, decomposition is mostly regulated by the combined activity of the macro and mesofauna (body size between 0.2 and 2 mm; Castro-Huerta et al. 2015). Therefore, some arthropod species that belong to the detrital food-web have an important role in increasing nutrient availability for plants (Moore et al. 2003).

The Inland Pampa is one of the most productive and fragmented units of the Rio de la Plata grasslands (León et al. 1984; Baldi and Paruelo, 2008). In this region, remnants of native grasses have been largely reduced in the landscape (Baldi and Paruelo, 2008; Lara and Gandini, 2014). Secondary succession after agriculture abandonment in the Pampas (old-fields) is mostly dominated by exotic grass species (Omacini et al. 2005; Tognetti et al. 2010). Previous studies showed that exotic-dominated patches have higher soil respiration and litter decomposition rates than their native counterparts (Spirito et al. 2014). In addition, exotic species invading Inland Pampas have higher litter quality than local native species (Yahdjian et al. 2017). The differences in soil processes between remnants and old-fields might result from greater arthropod abundance associated with a lower C:N ratio of exotic species comparing with natives (Yahdjian and Piñeiro, 2014). While some studies have documented soil food-web changes after grass invasions into natural communities disturbed by livestock or fire (Trent et al. 1994; Monroe et al. 2017), there is much less information in the absence of such disturbances.

The objective of this study was to describe the taxonomic composition of the soil arthropod community in invaded old-fields and remnants of native vegetation in the Inland Pampa, Argentina. The main hypothesis is that the abundance of soil arthropod organisms is related to the quality of the plant biomass, whereas the diversity of the soil biota is related to plant species richness, resulting in a different soil arthropod composition because of differing plant communities. We expected greater abundance of macro and mesofauna in old-field patches than in native remnant grasslands because old-fields sustain a plant community that produce litter of higher quality (i.e. lower C:N ratio) than native grasslands (Spirito et al., 2014; Yahdjian et al., 2017). However, remnant grasslands may sustain a higher diversity of soil arthropods than old-fields because remnants sustain a more diverse plant community (Yahdjian and Piñeiro, 2014). To test these hypotheses, we sampled the soil arthropod community in independent old-fields and remnant-grasslands patches in an agricultural landscape in spring and summer. Additionally, we analyzed the relationship between soil arthropod composition and environmental variables, including plant composition and soil variables.

2. Methods

2.1. Study site

The study was conducted in Estancia San Claudio, in the Inland Pampa grassland (35° 53' S; 61° 12' W), Buenos Aires, Argentina. The

climate is sub-humid, with a mean annual rainfall of ~1030 mm, evenly distributed throughout the year. Mean monthly temperatures range from 24 °C in January to 7 °C in July. The landscape comprises a mosaic of cultivated land, sown pastures, and old-field grasslands (Tognetti et al. 2010). Original vegetation was described as tall tussock grasslands (Soriano et al. 1991). Nowadays unmanaged vegetation can be found in two alternative states dominated by native or exotic plant species (Tognetti et al. 2010; Tognetti and Chaneton, 2015). On one hand, native remnant grasslands are dominated by the native C4 tussock grass *Paspalum quadrifarium*, representing near 90% of above-ground biomass (Chaneton et al. 2004), and a bunch of subordinate native species (i.e. *Bothriochloa laguroides*, *Briza subaristata*, *Melica brasiliana*, and *Schizachirium spicatum*; Chaneton et al. 2001). These grasslands are located in paddock corners, railway and dust roads borders, representing an important conservation value (Baldi and Paruelo, 2008). On the other hand, post-agricultural old-fields are dominated by exotic C3 and C4 grasses such as *Schedonorus arundinaceum* (ex *Festuca arundinacea*), *Cynodon dactylon*, and *Sorghum halepense*; Tognetti et al. 2010), which strongly suppress native species recovery even after accounting for seeds limitation (Tognetti and Chaneton, 2012).

2.2. Experimental design and data collection

We haphazardly selected seven independent remnants and seven old-field grasslands within a region of near 100 km². Each grassland patch was at least 0.7 ha and was separated by more than 100 m from each other. In each site, we established a 64 m² plot under similar soil (i.e. topography) and plant structure conditions (i.e. height, cover, disturbance).

In October 2010 and February 2011 (spring and summer, respectively) we sampled ground-dwelling arthropods using pitfall traps, a valuable sampling method for estimating the abundance of active ground-dwelling surface arthropods by counting the number of individuals in each category after extraction. Traps were 6.5 cm diameter, 12 cm deep buried into the soil, and filled with a solution of propylene glycol 50% (Gist and Crossley, 1973). We installed four traps per plot, uniformly distributed, and left them in the field during one week in each sampling date. To prevent pitfalls overflow during rainfall events, a 20 × 20 cm plastic cover was conveniently installed 10 cm above each trap. All collected specimens were identified with a Nikon SMZ800 magnifying glass to the order taxonomic level, and some of them to family level or functional-groups.

Soil, plants, litter biomass, and environmental variables were recorded at each sampling date, when pitfalls were placed in the field. In each plot, we listed all vascular plant species and estimated plant cover to the nearest 5% using a modified Daubenmire method (Tognetti et al. 2010) in two 1 m² randomly distributed quadrats in each plot. Total live, dead and litter biomass was estimated by consecutive harvests and weighting after drying at 65 °C 72 h. Soil temperature was measured with thermometer sensors buried at 10 cm next to pitfalls. Gravimetric soil water content was calculated as percentage of dry soil by weighing soil samples from top 15 cm before and after 48 h at 105 °C. Bare soil respiration was estimated in 4 positions (subsamples) within each plot using a portable EGM-4 CO₂ Analyzer, a non-dispersive infrared gas analyzer connected to a soil respiration chamber SRC-1 (PP Systems, Hitchin, United Kingdom). Measurements were taken by first sampling for ambient CO₂ concentrations and then holding the chamber on a bare soil spot to 1 cm depth for 1 min. The four measures were then averaged to obtain a single value per plot in each date. Soil variables were estimated from a composite soil sample of five sub-samples (6.5 cm diameter) haphazardly selected within each plot. The samples were extracted using a 2 N KCl solution within one day of collection; extracts were assessed colorimetrically using an elemental Analyzer (Alpkem® autoanalyzer O-I Corporation, College Station, TX, USA). We analyzed soil pH, soil electric conductance (CE), total soil carbon (Ct,

Walkley and Black, 1934), total nitrogen (Nt, Kjeldahl, 1883), extractable phosphorous (Pt, Bray-Kurtz 1, 1945), cation exchange capacity (C.E.C), calcium (Ca^{2+}), magnesium (Mg^{2+}), sodium (Na^+) and potassium (K^+) and soil texture as % of sand, silt and clay (INGEIS Instituto de Geocronología y Geología Isotópica, CONICET-UBA).

2.3. Data analysis

Total abundance of ground-dwelling arthropods was analyzed separately in each sampling date, but the abundance of both periods for each arthropod taxa was summed to give the total number of caught individuals. To avoid groups that are not adequately represented by the pitfall trap method, Diptera specimens were excluded from analyses assuming that they are not real residents. This modification of the data set helps to overcome inconsistencies in the trapping method (Finch, 2005).

Arthropod diversity was estimated with Shannon's Index $H' = -\sum p_i \ln(p_i)$, where p_i is the importance value of each entity as a proportion of total entities (Shannon and Weaver, 1949). Evenness was calculated with Pielou's Index $J' = H'/\ln(S)$, where S is the number of total entities (Magurran, 1988). Given that species richness depends on the number of specimens collected, individual-based rarefaction curves with unconditional confidence limits were used as an additional measure of alpha diversity (Gotelli and Colwell, 2001) using Estimats software (Colwell, 2013). Ground-dwelling arthropod abundance, diversity indexes, and environmental and soil variables, were compared throughout a one-way ANOVA. If ANOVA's assumptions were not met after transformation, a non-parametric Kruskal-Wallis test was performed (Zar, 2010). These analyses were performed using Infostat (Di Rienzo et al. 2014).

Overall differences in composition assembly between remnants and old-fields were analyzed through a distance-based permutation ANOVA (PERMANOVA, *adonis* function in 'vegan' Package, Oksanen et al., 2018). This method uses Euclidean distances to estimate pseudo F statistics for p -values and pseudo R^2 (Anderson, 2001). To consider differences independently of season, we used $\log_{10}(x+1)$ transformed count data, where x is the summed individuals in spring and summer. To represent community ordination in multivariate space, we performed a non-metrical multidimensional scaling. We used the Bray-Curtis dissimilarity index as distance measure, and a two-dimensional configuration was retained as an adequate portrayal of the distance structure in the data (Monte Carlo w/1000 randomisations; (McCune and Mefford, 1999). We overlapped environmental and soil variables in the ordination space (*envifit* function in 'vegan' package, Oksanen et al., 2018) to explore the arthropod-environment relationship, given that data did not met canonical correspondence assumptions (McCune and Mefford, 1999). The analyses were performed with R Statistical software (Team R. Core, 2012).

3. Results

A total of 19,312 individuals were collected in both sampling dates in both grassland types (4384 in spring and 14,928 in summer). Total active ground-dwelling number of arthropods in spring was significantly higher in old-fields than in native-remnant grasslands (498.4 ± 400 vs. 142.4 ± 65 individuals per plot respectively; Kruskal-Wallis, $H = 3.43$; $P = 0.062$) and the same trend occurred in summer, but differences were not statistically significant (1185 ± 1068 vs. 963 ± 888 individuals respectively; $F_{1,12} = 0.4$; $P = 0.85$). The main macrofauna taxa found were the orders Hymenoptera, Isopoda, Diptera, Hemiptera, Orthoptera, Coleoptera, Thysanoptera, Heteroptera, Blattaria, Psocoptera, Araneae, Pseudoscorpionida, Scorpionida, Opilionida; the classes Diplopoda, Gasteropoda, and the subclass Oligochaeta (Fig. 1 a, b). Class Collembola and subclass Acari represent the epigeic mesofauna taxa found (Fig. 1 c, d). Pseudoscorpionida and Blattaria were present exclusively in old-fields.

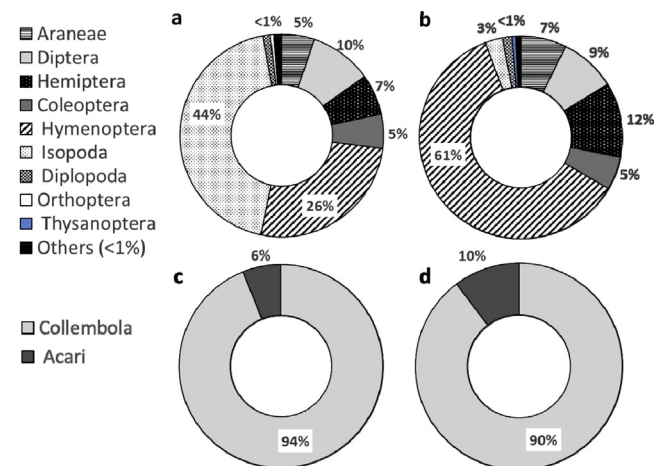


Fig. 1. Relative abundance of surface ground dwelling macrofauna (upper panels) and epigeic mesofauna (lower panels) taxa in old-fields (left: panels a, c) and native-remnant grasslands (right: panels b, d) of the Inland Pampas. The relative abundance was estimated from the addition of soil organisms collected in the two sampling dates, October and February, in both grasslands types.

Accounting both sampling dates, Isopoda was most abundant in old-fields (Kruskal-Wallis, $H = 9.02$ $P = 0.0012$; Fig. 2), whereas Hymenoptera, mostly Formicidae (ants) abundance was higher in native remnants ($F_{1,12} = 7.20$; $P = 0.019$; Fig. 2). The abundance of Araneae, Coleoptera, Hemiptera and Diplopoda did not show significant differences between both grassland types (Fig. 2). Epigeic mesofauna were overall represented by Collembola (springtails; 92%) and Acari (mites; 8%) and their abundance was not significantly different between grassland types (Acari $F_{1,12} = 0.06$; $P = 0.8$; Collembola $F_{1,12} = 0.98$; $P = 0.34$). Due to their dominance, Collembola was further identified into orders, the most abundant being Poduromorpha, followed by Entomobryomorpha and Symphyleona (Fig. 3). Only Entomobryomorpha was significantly less abundant in old-fields than natural remnant grasslands ($F_{1,12} = 4.81$; $P = 0.0048$).

Overall soil arthropod taxonomic composition differed between native-remnant grasslands and old-fields (PERMANOVA, $F_{1,12} = 3.85$; $P < 0.002$). Grassland type explained near 25% of variation in arthropod composition. Even when both grasslands shared most taxa, the ordination analysis discriminated two groups (Fig. 4). Orthoptera ($P = 0.01$), Isopoda ($P < 0.001$) and Pseudoscorpionida ($P = 0.06$) were the most influencing orders discriminating the two groups in the non-metrical analysis (Fig. 4). Soil respiration, plant biomass and some soil variables were related to the composition of the remnants and old-field grasslands in arthropod ordination space (Fig. 4).

Diversity and evenness indexes of the soil arthropod community were higher in native remnants than in old-fields (Shannon's $H = 1.04 \pm 0.09$ vs. 0.39 ± 0.07 , respectively; $P < 0.05$, evenness: $J' = 0.44 \pm 0.03$ and 0.15 ± 0.03 respectively ($P < 0.001$)). Grassland types did not differ in alpha richness when calculations were standardized to 7640 individuals with rarefaction curves (Figure S1).

Plant species richness and composition strongly differed between remnants and old-fields. A distance based multivariate analysis of variance (PERMANOVA) indicated that grassland type explained 81% of the variance in plant composition ($F_{1,12} = 51.52$, $P < 0.001$, Table S1). Environmental and soil variables differed between remnants and old-fields grasslands (Tables 1 and 2). In spring, native remnants had significantly higher plant biomass (including, green, standing dead, and litter) and soil moisture. In contrast, old-fields showed higher soil respiration rates and temperature than native remnants (Table 1). In summer, differences in temperature, soil respiration, and total and green biomass remained significant but litter and dead biomass did not differ between grasslands (Table 1).

In relation to soil nutrients, old-fields contained higher total N and

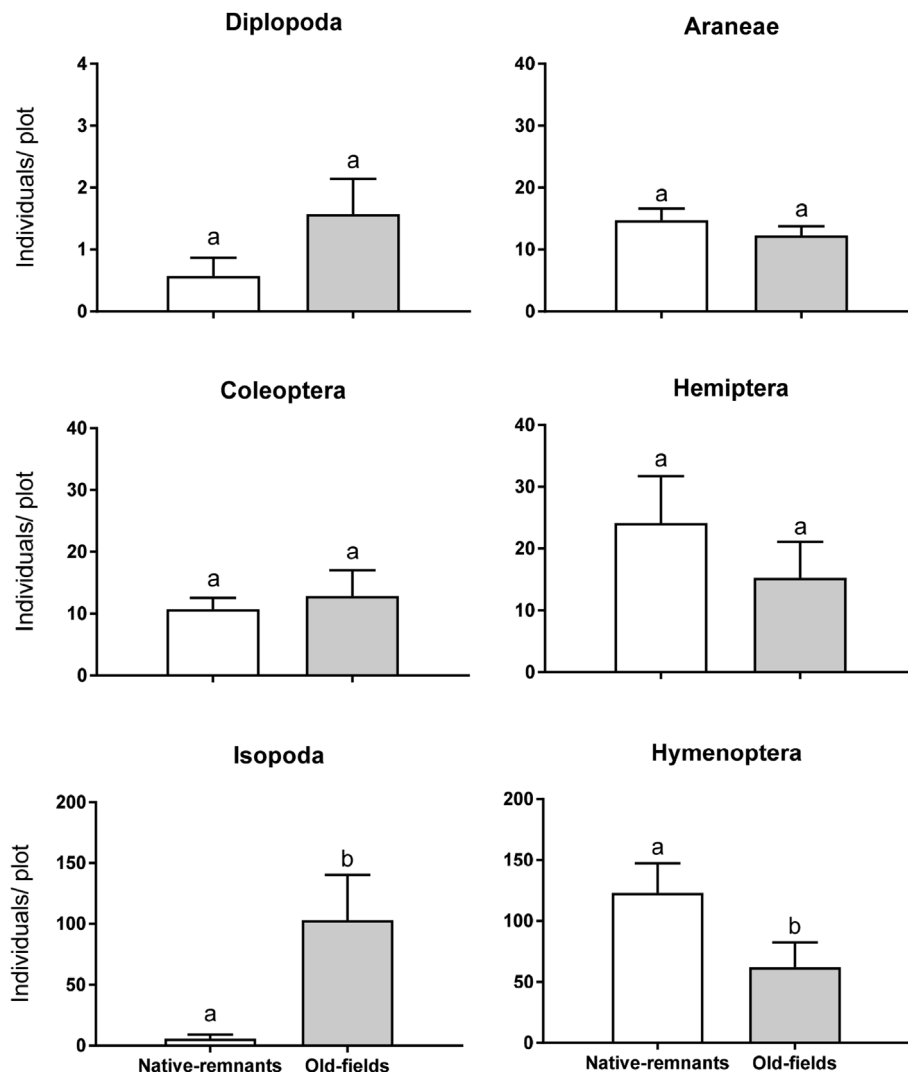


Fig. 2. Macrofauna abundance of the most representative taxa in native-remnant grasslands (open bars) and old-field (shaded bars). Bars show non-transformed means (summed of the two sampling dates) \pm 1 standard error for $n = 7$. Different letters represent significant differences between grassland types at $P < 0.05$.

K^+ , whereas native remnants showed higher soil P content (Table 2). Environmental and soil variables were related to the composition of the remnants and old-field grasslands in arthropod ordination space (Fig. 4).

4. Discussion

Soil biota taxonomic composition was very different in the two dominant grasslands of the agricultural Pampas landscape, the native-remnants and old-fields, especially at the arthropod order level. As we expected, total abundance of active surface ground dwelling organisms was higher in old-fields than in native remnants, whereas the diversity and evenness of the soil arthropod taxonomic composition were higher in native-remnants than in old-fields. When compared to non-invaded remnant grasslands, soil activity and soil food-web characteristics of the old-fields invaded sites included: 1. Greater total abundance, particularly of Isopoda; 2. Lower abundance of Hymenoptera and Entomobryomorpha (Collembola); 3. Lower diversity and evenness, but similar richness of soil organisms taxa; 4. Higher soil respiration rates and soil temperature; and 5. Higher total soil N and K^+ content, but lower soil P content. Interestingly, the arthropod taxa that changed more were those linked to specific functions, so beyond differences in plant species composition, plant invasions show impacts on other trophic levels such as detritivores and other soil organisms that may

produce differences in ecosystem functioning.

The differences in macrofauna between remnants and old-fields were driven mostly by differences in the abundance of Isopoda and Hymenoptera, the two dominant orders. Isopods are terrestrial crustaceans (“rolly pollies”) which have a key role in nutrient cycling as detritivores (Paoletti and Hassall, 1999). Isopoda were more abundant in old-fields, where plant community was dominated by exotic species with higher litter quality (Spirito et al. 2014). Similar differences were found in shrublands of New South Wales where Isopoda were more abundant in plots invaded by the high-quality litter weed *Chrysanthemoides monilifera* sp. (Lindsay and French, 2006). These organisms were also described as important fauna for early successional fast-growing plant abundance (Paoletti et al. 2007). These evidences illustrate that isopods consume preferably on high quality litter and suggest that the impact of invasive species on isopods is rather mediated by the quality (Kautz et al. 2000) and the palatability of the litter than by its origin (Quadros et al. 2014).

Invertebrate detritivores generally exhibit significant preferences for labile litter. There is evidence that they may increase the exotic plant species litter decay and therefore make the nutrients available to higher trophic levels (Meisner et al. 2014). Our results support previous studies where exotic species with higher nutrient concentration and higher growth rates than natives, were associated with high detritivore abundances (Belnap et al. 2005; Meisner et al. 2014). The most

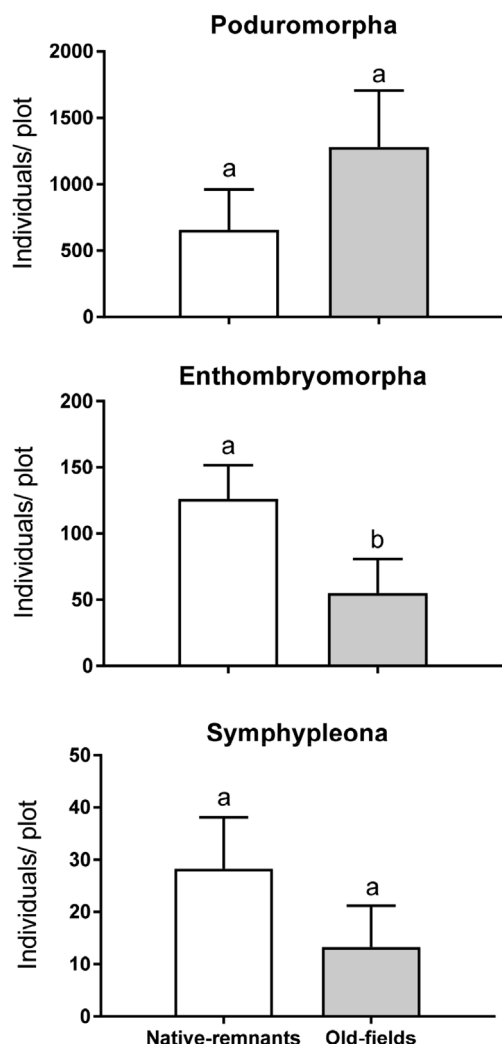


Fig. 3. Abundance of Epigeic Collembola orders in native-remnants (open bars) and old-fields (shaded bars). Bars show non-transformed means (summed of the two sampling dates) \pm 1 standard error for $n = 7$. Different letters represent significant differences between grassland types at $P < 0.05$.

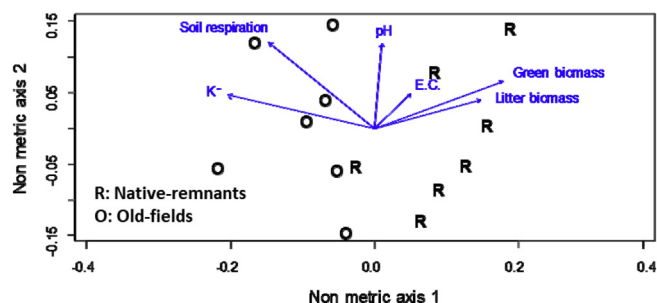


Fig. 4. Nonmetric multidimensional scaling of arthropod taxonomic composition in native-remnants (R) and old-fields (O) in the Inland Pampa. Each point represents the relative position of one grassland site based on abundance of arthropod taxa (log (spring + summer abundance)). Arrows represent the variation (sense and magnitude) of the most important environmental variables along sites on the two axes of the ordination: E.C. electrical conductivity (dS m^{-1}); Soil respiration ($\text{g CO}_2 \text{ m}^{-1} \text{ h}^{-1}$); Litter (g/m^2); Green biomass (g/m^2); K^+ (Cmolc/soil Pg) and pH.

abundant isopod specie (*Armadillum vulgare*) found in our study became an important pest in some crops under no-tillage, a common practice in our agricultural study system (Fabri et al. 2011). Therefore, old-fields

gain its legacy from agricultural history and may offer an adequate habitat for isopods from surrounding cultivation paddocks activities.

The abundance of specimens from the Hymenoptera order (mostly ants) was higher in native remnants than in old-fields. Although there is evidence that ants may increase in disturbed habitats (Folgarait, 1998), a recent metanalysis on the effect of invasive plants on the arthropod community found that 47% of the studies showed decreased ant abundance and diversity after plant invasion (Litt et al. 2014). For instance, previous studies in a scrubland of southern California showed that most common ants declined after an annual grass invasion (Wolkovich et al. 2009), and in an agricultural landscape in Southern Poland, ant abundance was lower in grasslands invaded by goldenrods (*Solidago* sp.) than in those dominated by native species (Lenda et al. 2013). Ants might indirectly affect fast-growing plant species in less fertile environments by feeding on fungi and consequently leading to lower decomposition rates (Brewer and Arguello, 1980). This constitutes an advantage for less palatable species with poor litter quality. On the other hand, there is evidence that ants may play an important role in the pollination of native plants (Schneemilch et al. 2011) and seed dispersal (Folgarait, 1998).

The greatest epigeic mesofauna component was Collembola, but there were no differences in its abundance between old-fields and native remnants. Only Entomobryomorpha specimens were more abundant in native remnants than old-fields. Collembola and Acari usually account for up to 95% of total soil microarthropods (Seastedt, 1984), and previous studies in the inland Pampa grasslands, showed that Collembola was the most abundant group along with mites (37% and 35% respectively; Ferraro and Ghera, 2007). These organisms have a strong effect in recalcitrant litter decomposition (Gabriel et al. 2013; Gergocs and Hufnagel, 2016). For instance, in agricultural fields with continued crop cultivation collembolans have a key role in litter decomposition (Castro-Huerta et al. 2015). This suggest that these organisms may have an important role driving a faster litter decay in the habitat from which its originated than away from it (“home-field advantage”, John et al. 2011). In our study site, the internal differences within Collembola seems to be linked to the different decomposition rates of native and non-native litter decay in old-fields and remnants found in previous studies (Spirito et al. 2014).

Although the total richness was similar, arthropod composition was more diverse in native-remnant grasslands than in old-fields, because of a higher evenness in the main arthropod taxa, which support our hypothesis. Both remnants and old-fields were immersed in the same agricultural matrix (Spirito et al. 2014; Tognetti and Chaneton, 2015). In agricultural systems, land-use intensity reduces the number of functional groups and the complexity of soil food-webs (Tsiafoulis et al. 2015). Accordingly, our results suggest that remnant grasslands might act as refuges for a more diverse assembly of arthropods, conserving diversity by reducing the likelihood of competitive exclusion (Bardgett et al. 1998).

Arthropods might discriminate small discontinuities in the landscape (Giraldo Mendoza, 2014). Temperature and moisture are very important variables influencing the microarthropod community in the litter layer (0–10 cm) (Klironomos and Kendrick, 1995) including ants (Retana and Cerda, 2000). For example, ants nesting habits from the *Acromyrmex*, were positively correlated with the soil temperature regime (Bollazzi et al. 2008). We found differences in soil temperature, soil moisture, and soil respiration between native remnants and old-field grasslands that might in turn be perceived by soil arthropods. Interestingly, there is evidence that isopods can increase soil respiration through microbial activity (Kautz and Topp, 2000; Tripathi and Sharma, 2006). These environmental differences accompanying soil arthropod composition in native remnants and old-fields may offer a better habitat in each case and promote the “home-field advantage”.

Native-remnants and old-fields differed in plant community composition (Table S1; see also Tognetti et al., 2010, Yahdjian and Piñeiro, 2014, Tognetti and Chaneton, 2015) and in surface ground dwelling

Table 1

Environmental and soil variables of native remnants and old-fields in both sampling dates. P-values are the result of ANOVA (temperature, dead biomass and soil respiration) or Non-parametrical analysis Kruskal-Wallis (Humidity, Litter, Green and Total Biomass) (mean \pm 1 standard error, n = 7). P values in bold show statistically significant differences between grassland types at $P < 0.05$.

	Spring			Summer		
	Native- remnants	Old-fields	P value	Native-remnants	Old-fields	P value
Soil Temperature (C°)	11.7 \pm 0.2	12.4 \pm 0.2	P = 0.015	20.2 \pm 0.2	21.7 \pm 0.4	P = 0.0072
Soil Humidity (%)	26.8 \pm 1.8	20.8 \pm 4.0	P = 0.02	23 \pm 2.3	20.4 \pm 1.3	P = 0.92
Litter (g/m2)	1057.3 \pm 250.5	303.1 \pm 75.9	P = 0.01	874.1 \pm 204.3	573.8 \pm 88.4	P = 0.2
Green biomass (g/m2)	502.2 \pm 55.3	160.4 \pm 15.3	P = 0.0006	448.3 \pm 54.6	223.6 \pm 14.9	P = 0.0006
Dead biomass (g/m2)	1029.5 \pm 159.9	497.6 \pm 88.1	P = 0.01	1145 \pm 216.9	613.2 \pm 74.4	P = 0.08
Total biomass (g/m2)	2405.8 \pm 365.2	961.1 \pm 86.5	P = 0.001	2650.6 \pm 455.4	1410.7 \pm 104.2	P = 0.01
Soil respiration (g CO ₂ m ⁻¹ h ⁻¹)	0.3 \pm 0.0	0.7 \pm 0.1	P = 0.0001	0.83 \pm 0.08	1.1 \pm 0.4	P = 0.04

Table 2

Soil variables (mean \pm 1 standard error, n = 7) of native-remnants and old-fields at the beginning of the experiment. P-values from analysis of variance. P values in bold show statistically significant differences between grassland types at $P < 0.05$.

	Native-remnants	Old-fields	P value
Nt (g/soil kg)	1.4 \pm 0.09	1.75 \pm 0.13	P = 0.05
Ct (g/soil kg)	17.6 \pm 1.26	20.31 \pm 1.16	P = 0.13
Ca ²⁺ (Cmol _c /soil Pg)	7.2 \pm 0.67	7.96 \pm 0.20	P = 0.51
Mg ²⁺ (Cmol _c /soil Pg)	2.5 \pm 0.14	2.57 \pm 0.21	P = 0.86
Na ⁺ (Cmol _c /soilPg)	0.6 \pm 0.25	0.45 \pm 0.33	P = 0.68
K ⁺ (Cmol _c /soilPg)	1.4 \pm 0.07	1.96 \pm 0.14	P = 0.003
P (Cmol _c /soilPg)	12.9 \pm 1.68	7.74 \pm 2.03	P = 0.04
C:N	12.4 \pm 0.43	8.66 \pm 2.03	P = 0.20
pH	6.0 \pm 0.11	6.00 \pm 0.16	P = 0.99
% Sand	44.68 \pm 7.01	46.8 \pm 4.00	P = 0.47
% Silt	37.76 \pm 5.50	37.36 \pm 4.34	P = 0.92
% Clay	17.62 \pm 1.55	15.88 \pm 0.92	P = 0.42

soil arthropod taxonomic composition (Figs. 1–4). Both components may interact to modulate soil activity (Wolfe and Klironomos, 2005). Plant biomass influences arthropod activity through its quantity and quality (Chen and Wise, 1999; Perner et al. 2005). In our case, remnant grasslands had greater plant biomass while old-fields were associated with greater plant quality (Spirito et al. 2014). Detritivores (e.g isopods; Dindal, 1990) were more abundant in old-fields, suggesting that litter quality, rather than its quantity, might modulate the abundance of this arthropod group (Lindsay and French, 2006). Exotic plant species exhibit higher litter quality (Spirito et al. 2014; Yahdjian et al. 2017) which may impact soil biota (Van der Putten et al. 2013) and change soil nutrient content (e.g., N, P, and K), affecting soil invertebrate communities (Davis et al. 2006). In our study, we found higher soil P content in sites characterized by higher Enthomobryomorpha abundance, in accordance with previous studies (Wu et al. 2014). In contrast, detritivores such as isopods are associated with high N contents (Quadros et al. 2014).

Taken together, our results suggest a link between plant and arthropod communities. On one hand, detritivores may enhance decomposition and nutrient cycling in old-fields, maintaining environmental conditions that promote exotic plant species persistence. On the other hand, native remnants may support soil arthropod taxonomic groups adapted to their “less disturbed” conditions. These evidences support the idea that plant species promote a decomposer community and conditions specialized to decompose the litter from their own habitat or a “home” field advantage (Wardle, 2006; Vivanco and Austin, 2008; Ayres et al. 2009). Thus, arthropods and the plant community may show positive feed-backs which can partially explain the community persistence of both, plant and soil fauna (Van Hengstum et al. 2014). Our broad scale taxonomic classification precludes a detailed description of the species involved in these mechanisms. Future studies should consider a deeper identification of the highlighted orders (e.g.

Hymenoptera and Isopoda) for being able to fully describe the most important species.

5. Conclusion

Our results showed that old field grasslands invaded by exotic plant species are associated with a particular soil arthropod taxonomic composition which differs from native remnants. This evidence supports the idea of a strong linkage between plant community composition and environmental characteristics with soil fauna structure. Exotic plant species have higher litter quality, decompose faster than native species (Spirito et al. 2014) and respond to higher resource input (Tognetti and Chaneton, 2015). These bottom-up controls may drive this food-web which in turn may increase litter decomposition, probably resulting in a positive feedback to exotic species persistence. Thus, invasive species may lead to “novel ecosystems” which are resistant to native species re-introduction. Future studies should test this hypothesis which has strong implications for the restoration of post agricultural landscapes and the ecosystem services they deliver to human wellbeing.

Authors' contributions statement

GV and LY conceived the questions, designed the study, and set up the experiment; GV and AGA analyzed the samples; GV and PMT analyzed the data; GV and LY led the writing of the manuscript. All authors contributed to successive drafts and gave final approval for publication.

Declarations of interest

None.

Acknowledgements

We thank all the people that collaborated in field sampling. Pablo Montes kindly provided the plant data for remnant grasslands. Florencia Spirito, Ximena López and Priscila Pinto provided helpful comments to improve the manuscript draft. University of Buenos Aires, Doña Francisca Perrier de Magnin, and Pavia family contributed to field experimentation at Estancia San Claudio. This work was funded by Agencia Nacional de Promoción Científica y Tecnológica (PICT 2014-3026) and CONICET (PIP 2015-0709). The authors have no conflict of interest to declare.

Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.actao.2018.06.003>.

References

Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of

- variance. *Mar. Ecol. Prog. Ser.* 26, 32–46.
- Ashton, I.W., Hyatt, L.A., Howe, K.M., Gurevitch, J., Lerdau, M.T., 2005. Invasive species accelerate decomposition and litter nitrogen loss in a mixed deciduous forest. *Ecol. Appl.* 15, 1263–1272.
- Ayres, E., Steltzer, H., Simmons, B.L., Simpson, R.T., Steinweg, J.M., Wallenstein, M.D., Mellor, N., Parton, W.J., Moore, J.C., Wall, D.H., 2009. Home-field advantage accelerates leaf litter decomposition in forests. *Soil Biol. Biochem.* 41, 606–610.
- Baldi, G., Paruelo, J.M., 2008. Land-use and land cover dynamics in South American Temperate grasslands. *Ecol. Soc.* 13 (2), 6.
- Bardgett, R.D., Wardle, D.A., Yeates, G.W., 1998. Linking Above-ground and below-ground interactions: how plant responses to foliar herbivory influence soil organisms. *Soil Biol. Biochem.* 30, 1867–1878.
- Bardgett, R.D., Bowman, W.D., Kaufmann, R., Schmidt, S.K., 2005. A temporal approach to linking aboveground and belowground ecology. *Trends Ecol. Evol.* 20, 634–641.
- Belnap, J., Phillips, S.L., Sherrod, S.K., 2005. Soil Biota Can Change after Exotic Plant Invasion: Does This Affect Ecosystem Processes?, vol. 86. pp. 3007–3017.
- Bollazzi, M., Kronenbitter, J., Roes, F., 2008. Soil temperature, digging behaviour, and the adaptive value of nest depth in South American species of Acromyrmex leaf-cutting ants. *Oecologia* 158, 165–175.
- Bray, R.H., Kurtz, L.T., 1945. Determination of total, organic, and available forms of phosphorus in soils. *Soil Sci.* 59, 39–45.
- Brewer, M.M., Arguello, N.V., 1980. Guía ilustrada de insectos comunes de la Argentina. Ministerio de Cultura y Educación. Fundación Miguel Lillo, San Miguel de Tucumán.
- Castro-Huerta, R.A., Falco, L.B., Sandler, R.V., Coviella, C.E., 2015. Differential contribution of soil biota groups to plant litter decomposition as mediated by soil use. *PeerJ* 3, e826.
- Chaneton, E.J., Omacini, M., Trebino, H.J., Leon, R.J., 2001. Disturbios, dominancia y diversidad de especies nativas y exóticas en pastizales pampeanos húmedos. *An Acad Nac Ciencias Exactas, Fis Nat* 53, 121–140.
- Chaneton, E.J., Mazia, N., Machera, M., Uchitel, Andrea, M., Ghersa, C.M., 2004. Establishment of honey locust (*Gleditsia triacanthos*) in burned pampa grasslands. *Weed Technol.* 18, 1325–1329.
- Chen, B., Wise, D.H., 1999. Bottom-up limitation of predaceous arthropods in a detritus-based terrestrial food web. *Ecology* 80, 761–772.
- Colwell, R.K., 2013. EstimateS (Version 9.1). Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, USA CT 06869–3043.
- Core, Team R., 2012. R: a Language and Environment for Statistical Computing. Foundation for Statistical Computing, Vienna, Austria.
- Culliney, T., 2013. Role of arthropods in maintaining soil fertility. *Agriculture* 3, 629–659.
- Davis, C.A., Austin, J.E., Buhl, D.A., 2006. Factors influencing soil invertebrate communities in riparian grasslands of the central Platte River floodplain. *Wetlands* 26, 438–454.
- De Deyn, G.B., Raaijmakers, C.E., Zoomer, H.R., Berg, M.P., de Ruiter, P.C., Verhoef, H.A., Bezemer, T.M., van der Putten, W.H., 2003. Soil invertebrate fauna enhances grassland succession and diversity. *Nature* 422, 711–713.
- Dindal, D.L., 1990. Soil Biology Guide. Wiley Interscience, New York, United States.
- D'Antonio, C.M., Hobbie, S.E., 2005. Plant species effects on ecosystem processes: insights from invasive species. In: *Species Invasions: Insights into Ecology, Evolution and Biogeography*, pp. 65–84.
- Evans, R.D., Rimer, R., Sperry, L.J., Belnap, J., 2001. Exotic plant invasion alters nitrogen dynamics in an arid grassland. *Ecol. Appl.* 11, 1301–1310.
- Faberi, A.J., López, A.N., Clemente, N.L., Manetti, P.L., 2011. Importance of diet in the growth, survivorship and reproduction of the no-tillage pest *Armadiillidium vulgare* (Crustacea: Isopoda). *Rev. Chil. Hist. Nat.* 84, 407–417.
- Ferraro, D.O., Ghersa, C.M., 2007. Exploring the natural and human-induced effects on the assemblage of soil microarthropod communities in Argentina. *Eur. J. Soil Biol.* 43, 109–119.
- Finch, O.D., 2005. Evaluation of mature conifer plantations as secondary habitat for epigeic forest arthropods (Coleoptera: Carabidae; Araneae). *For. Ecol. Manage.* 204, 21–34.
- Folgarait, P.J., 1998. Ant biodiversity and its relationship to ecosystem functioning: a review. *Biodivers. Conserv.* 7, 1221–1244.
- Gabriel, P., Aubert, M., Decaens, T., Trap, J., Chauvat, M., 2013. Home-Field Advantage: a matter of interaction between litter biochemistry and decomposer biota. *Soil Biol. Biochem.* 67, 245–254.
- Gergöcs, V., Hufnagel, L., 2016. The effect of microarthropods on litter decomposition depends on litter quality. *Eur. J. Soil Biol.* 75, 24–30.
- Giraldo Mendoza, A.E., 2014. Un recuento de argumentos para incluir a los artrópodos terrestres en las prácticas de evaluación ambiental. *Ecol. Austral* 24, 258–264.
- Gist, C.S., Crossley, D.A., 1973. A method for quantifying pitfall trapping. *Environ. Entomol.* 2, 951–952.
- Gotelli, N.J., Colwell, R.K., 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol. Lett.* 4, 379–391.
- Gratton, C., Denno, R.F., 2005. Restoration of arthropod assemblages in a *Spartina* salt marsh following removal of the invasive plant *Phragmites australis*. *Restor. Ecol.* 13, 358–372.
- Van Hengstum, T., Hooftman, D. a. P., Oostermeijer, J.G.B., van Tienderen, P.H., 2014. Impact of plant invasions on local arthropod communities: a meta-analysis. *J. Ecol.* 102, 4–11.
- John, M.G.S., Orwin, K.H., Dickie, I.A., 2011. No 'home' versus 'away' effects of decomposition found in a grassland-forest reciprocal litter transplant study. *Soil Biol. Biochem.* 43, 1482–1489.
- Kappes, H., Lay, R., Topp, W., 2007. Changes in different trophic levels of litter-dwelling macrofauna associated with giant knotweed invasion. *Ecosystems* 10, 734–744.
- Kardol, P., De Deyn, G.B., Laliberté, E., Mariotte, P., Hawkes, C.V., 2013. Biotic plant-soil feedbacks across temporal scales. *J. Ecol.* 101, 309–315.
- Kautz, G., Topp, W., 2000. Acquisition of microbial communities and enhanced availability of soil nutrients by the isopod *Porcellio scaber* (Latr.) (Isopoda: Oniscidea). *Biol. Fertil. Soils* 31, 102–107.
- Kautz, G., Zimmer, M., Topp, W., 2000. Responses of the parthenogenetic isopod, *Trichoniscus pusillus* (Isopoda: Oniscidea), to changes in food quality. *Pedobiologia* (Jena). 44, 75–85.
- Kjeldahl, J., 1883. Neue Methode zur Bestimmung des Stickstoffs in organischen Körpern. *Z. für Anal. Chem.* 22, 366–383.
- Klironomos, J.N., 2002. Feedback with soil biota contributes to plant rarity and invasiveness in communities. *Nature* 417, 67–70.
- Klironomos, J.N., Kendrick, B., 1995. Relationships among microarthropods, fungi, and their environment. *Plant Soil* 170, 183–197.
- Lara, B., Gandini, M., 2014. Quantifying the land cover changes and fragmentation patterns in the Argentina Pampas, in the last 37 years (1974–2011). *GeoFocus. Rev. Int. Cienc. y Tecnol. la Inf. Geográfica* 14, 163–180.
- Lavelle, P., Decaens, T., Aubert, M., Barot, S., Blouin, M., Bureau, F., Margerie, P., Mora, P., Rossi, J.P., 2006. Soil invertebrates and ecosystem services. *Eur. J. Soil Biol.* 42, 3–15.
- Lenda, M., Witek, M., Skórka, P., Morón, D., Woyciechowski, M., 2013. Invasive alien plants affect grassland ant communities, colony size and foraging behaviour. *Biol. Invasions* 15, 2403–2414.
- León, R.J.C., Rusch, G.M., Oesterheld, M., 1984. Pastizales pampeanos - impacto agropecuario. *Phytocoenologia* 12, 201–218.
- Lindsay, E.A., French, K., 2006. The impact of the weed *Chrysanthemoides monilifera* ssp. rotundata on Coastal leaf litter invertebrates. *Biol. Invasions* 8, 177–192.
- Litt, A.R., Cord, E.E., Fulbright, T.E., Schuster, G.L., 2014. Effects of invasive plants on arthropods. *Conserv. Biol.* 28, 1532–1549.
- Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M., Bazzaz, F.A., 2000. Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecol. Appl.* 10, 689–710.
- Magurran, A.E., 1988. Why diversity? In: *Ecological Diversity and its Measurement*. Springer Netherlands, Dordrecht, pp. 1–5.
- McCune, B., Mefford, M.J., 1999. PC-ORD. Multivariate Analysis of Ecological Data. Gleneden Beach, Oregon, USA.
- Meisner, A., Gera Hol, W.H., de Boer, W., Krumins, J.A., Wardle, D. a, van der Putten, W.H., 2014. Plant-soil feedbacks of exotic plant species across life forms: a meta-analysis. *Biol. Invasions* 16, 2551–2561.
- Monroe, A.P., Hill, J.G., Martin, J.A., 2017. Spread of exotic grass in grazed native grass pastures and responses of insect communities. *Restor. Ecol.* 25, 539–548.
- Moore, J.C., McCann, K., Setälä, H., De Ruiter, P.C., 2003. Top-down is bottom-up: does predation in the rhizosphere regulate aboveground dynamics? *Ecology* 84, 846–857.
- Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Simpson, G.L., Solymos, P.M., Stevens, M.H.H., Wagner, H., 2018. The vegan package, Community Ecol. Packaging vegan: Community Ecology Package. R package version 2.5-1. <https://CRAN.R-project.org/package=vegan>.
- Omacini, M., Tognetti, P., Trebino, H., 2005. Sucesión postagrícola en la Pampa Interior: invasión y dominancia de plantas exóticas durante los primeros 20 años. In: *La heterogeneidad de la vegetación de los agroecosistemas. Un homenaje a Rolando León*, pp. 215–234.
- Paoletti, M.G., Hassall, M., 1999. Woodlice (Isopoda: Oniscidea): their potential for assessing sustainability and use as bioindicators. *Agric. Ecosyst. Environ.* 74, 157–165.
- Paoletti, M.G., Osler, G.H.R., Kinnear, A., Black, D.G., Thomson, L.J., Tsitsilas, A., Sharley, D., Judd, S., Neville, P., D'Inca, A., 2007. Detritivores as indicators of landscape stress and soil degradation. *Aust. J. Exp. Agric.* 47, 412–423.
- Perner, J., Wytrykush, C., Kahmen, A., Buchmann, N., Egerer, I., Creutzburg, S., Odat, N., Audorf, V., Weisser, W.W., 2005. Effects of plant diversity, plant productivity and habitat parameters on arthropod abundance in montane European grasslands. *Ecography* (Cop.) 28, 429–442.
- Peters, R.H., 1983. The ecological implications of body size. *Limnol. Oceanogr.* 29, 763–784.
- Van der Putten, W.H., Bardgett, R.D., Bever, J.D., Bezemer, T.M., Casper, B.B., Fukami, T., Kardol, P., Klironomos, J.N., Kulmatiski, A., Schweitzer, J.A., Suding, K.N., Van de Voorde, T.F.J., Wardle, D.A., 2013. Plant-soil feedbacks: the past, the present and future challenges. *J. Ecol.* 101, 265–276.
- Quadros, A.F., Zimmer, M., Araujo, P.B., Kray, J.G., 2014. Litter traits and palatability to detritivores: a case study across bio-geographical boundaries. *Nauplius* 22, 103–111.
- Retana, J., Cerdà, X., 2000. Patterns of diversity and composition of Mediterranean ground ant communities tracking spatial and temporal variability in the thermal environment. *Oecologia* 123, 436–444.
- Di Rienzo, J., Casanoves, F., Balzarini, M.G., González, L., Tablada, M., Robledo, C.W., 2014. InfoStat. Grupo InfoStat, FCA. Universidad Nacional de Córdoba, Argentina.
- Schirmel, J., Bundschuh, M., Entling, M.H., Kowarik, I., Buchholz, S., 2015. Impacts of invasive plants on resident animals across ecosystems, taxa, and feeding types: a global assessment. *Global Change Biol.* 22, 594–603.
- Schneemilch, M., Williams, C., Kokkinn, M., 2011. Floral visitation in the Australian native shrub genus *Acrotriche* R.Br. (Ericaceae): an abundance of ants (Formicidae). *Aust. J. Entomol.* 50, 130–138.
- Schulmann, O.P., Tiunov, A.V., 1999. Leaf litter fragmentation by the earthworm *Lumbricus terrestris*. *Pedobiologia* (Jena). 43, 453–458.
- Seastedt, T.R., 1984. The role of microarthropods in decomposition and mineralization processes. *Annu. Rev. Entomol.* 29, 25–46.
- Shannon, C.E., Weaver, W., 1949. *The Mathematical Theory of Communication*. Univ. Illinois Press, London and New York.
- Soriano, A., León, R.J.C., Sala, O.E., Lavado, R.S., Derégibus, V.A., Cauhé, M.A., Scaglia, O.A., Velázquez, C.A., Lemcoff, J.H., 1991. Rio de Plata grasslands. In:

- Coupland, R. (Ed.), *Ecosystems of the World 8A. Natural Grasslands. Introduction and Western Hemisphere*, pp. 367–407.
- Spirito, F., Yahdjian, L., Tognetti, P.M., Chaneton, E.J., 2014. Soil ecosystem function under native and exotic plant assemblages as alternative states of successional grasslands. *Acta Oecol.* 54, 4–12.
- Swift, M.J., Heal, O.W., Anderson, J.M., 1979. The influence of resource quality on decomposition processes. In: *Decomposition in Terrestrial Ecosystems*. Blackwell Scientific Publications, pp. 118–166.
- Tognetti, P.M., Chaneton, E.J., 2012. Invasive exotic grasses and seed arrival limit native species establishment in an old-field grassland succession. *Biol. Invasions* 8, 2531–2544.
- Tognetti, P.M., Chaneton, E.J., 2015. Community disassembly and invasion of remnant native grasslands under fluctuating resource supply. *J. Appl. Ecol.* 52, 119–128.
- Tognetti, P.M., Chaneton, E.J., Omacini, M., Trebino, H.J., León, R.J.C., 2010. Exotic vs. native plant dominance over 20 years of old-field succession on set-aside farmland in Argentina. *Biol. Conserv.* 143, 2494–2503.
- Trent, J.D., Young, J.A., Blank, R.R., 1994. Potential role of soil microorganisms in medusahead invasion. In: Monsen, S.B., Kitchen, S.G. (Eds.), *Proceedings, Ecology and Management of Annual Rangelands*. USDA Forest Service, pp. 140–142 General Technical Report INT- GTR-313.
- Tripathi, G., Sharma, B., 2006. Fauna-associated changes in chemical and biochemical properties of soil. *Biomed. Environ. Sci.* 19, 422–426.
- Tsiafouli, M.A., Thébault, E., Sgardelis, S.P., de Ruiter, P.C., van der Putten, W.H., Birkhofer, K., Hemerik, L., de Vries, F.T., Bardgett, R.D., Brady, M.V., Bjornlund, L., Jørgensen, H.B., Christensen, S., D'Hertefeldt, T., Hotes, S., Gera Hol, W.H., Frouz, J., Liiri, M., Mortimer, S.R., Setälä, H., et al., 2015. Intensive agriculture reduces soil biodiversity across Europe. *Global Change Biol.* 21, 973–985.
- Vilà, M., Espinar, J.L., Hejda, M., Hulme, P.E., Jarošík, V., Maron, J.L., Pergl, J., Schaffner, U., Yan, S., Pyšek, P., 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecol. Lett.* 14, 702–708.
- Vivanco, L., Austin, A.T., 2008. Tree species identity alters forest litter decomposition through long-term plant and soil interactions in Patagonia, Argentina. *J. Ecol.* 96, 727–736.
- Walkley, A., Black, A., 1934. An examination of the Degtjareff method for determining soil organic matter, and proposed modification of the chromic acid titration method. *Soil Sci.* 37, 29–38.
- Wardle, D.A., 2002. *Communities and Ecosystems: Linking the Aboveground and Belowground Components*. Princeton University Press, Princeton, New Jersey, USA.
- Wardle, D.A., 2006. The influence of biotic interactions on soil biodiversity. *Ecol. Lett.* 9, 870–886.
- Wigginton, R.D., Pearson, J., Whitcraft, C.R., 2014. Invasive plant ecosystem engineer facilitates community and trophic level alteration for brackish marsh invertebrates. *Ecosphere* 5, 1–17.
- Wolfe, B.E., Klironomos, J.N., 2005. Breaking new ground: soil communities and exotic plant invasion. *Source Biosci.* 55, 477–487.
- Wolkovich, E.L., Bolger, D.T., Holway, D.A., 2009. Complex responses to invasive grass litter by ground arthropods in a Mediterranean scrub ecosystem. *Oecologia* 161, 697–708.
- Wu, P., Liu, X., Liu, S., Wang, J., Wang, Y., 2014. Composition and spatio-temporal variation of soil microarthropods in the biodiversity hotspot of northern Hengduan mountains. *China. Eur. J. Soil Biol.* 30–38.
- Yahdjian, L., Piñeiro, G., 2014. Balance de Carbono en pastizales pampeanos. In: Medina, C.P., d. I. M, M. (Eds.), *Suelos, producción agropecuaria y cambio climático: avances en la Argentina*.
- Yahdjian, L., Tognetti, P.M., Chaneton, E.J., 2017. Plant functional composition affects soil processes in novel successional grasslands Plant functional composition affects soil processes in novel successional grasslands. *Funct. Ecol.* 31, 1813–1823.
- Yelenik, S.G., D'Antonio, C.M., 2013. Self-reinforcing impacts of plant invasions change over time. *Nature* 503, 517–520.
- Zar, J.H., 2010. *Biostatistical Analysis*. Prentice Hall, Upper Saddle River, New Jersey.