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

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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 km^2 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, Pseudoescorpionida and Blattaria; 2. Lower abundance of Hymenoptera and Enthomobryomorpha (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

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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 aboveground 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 km^2. 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 m^2 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 m^2 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 CO_2 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 CO_2 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,