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Epigeal arthropod communities in intensively farmed landscapes: Effects of land use mosaics, neighbourhood heterogeneity, and field position

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ABSTRACT

Trophic guilds of epigeal arthropods regulating insect pest populations may be affected by factors acting across spatial scales. Although the influence of landscape factors associated with farming effects on arthropod assemblages has received increasing attention in the last decades, most research was carried out in fine-grain landscapes by comparing conventional and organic cropping systems. Here, we aimed at identifying the role of fencerows and crop heterogeneity in defining arthropod diversity in intensively farmed, coarse-grain landscapes. Hence, we developed a multi-scale heterogeneity approach based on fitting linear-mixed models to elucidate the effects of three spatial scales (local, neighbouring crop types, and landscape) on arthropod diversity. Mixed models were fitted to arthropod data obtained by pitfall trap samplings in 22 field pairs. Field position was a major determinant of arthropod species diversity at local scale, due to the contrasting disturbance regimes of fencerows and adjoining field edges. Fence density at landscape scale contributed to retain diverse arthropod assemblages in farmland mosaics by supplying habitats and refuges. In addition, extended fence network may function as corridors for dispersal, increasing connectivity between dissimilar habitats. Fence habitats, as well as their density in the landscapes, enhance both richness and abundance of beneficial arthropods. Our findings indicate that the overall arthropod diversity was benefited by landscape complexity, being the presence and density of fencerows key landscape attributes. Contrasting disturbance regimes at different field positions emerged as a major driver modulating arthropod species diversity in intensively managed farmland mosaics. Non-cropped habitats associated with fencerows and field margins play key ecological functions that are of vital importance for providing ecosystem services in agro-ecosystems. Complex landscapes may help to conserve overall plant diversity in agro-ecosystems, as well as the spillover of arthropod species from fencerows towards crop fields. Even in heavily intensified landscapes, where crop diversity is the main source of heterogeneity, promoting measures intended for both restoring and managing fencerow and non-cropped habitats through landscape planning will contribute to maintain arthropod richness (almost 70% of total richness) across the entire landscape.

1. Introduction

The natural complexity of pristine ecosystems has been considerably simplified by the progressive intensification of agriculture (Benton et al., 2003). Crop productivity improvement, mostly due to the adoption of high yielding crops and the increased use of off-farm inputs, has been paralleled by the disruption of biogeochemical fluxes and biotic interactions (Matson et al., 1997). Farmland biodiversity decline has altered the provisioning of ecological services in agro-ecosystems, which mediate energy and material fluxes or alter abiotic conditions (Chapin et al., 2000). Environmental conditions prevailing in non-cropped habitats, such as field margins and fencerows, are usually more stable than those in the neighbouring crop (Burel et al., 1998; Poggio et al., 2013). Moreover, plant communities in non-cropped habitats are usually more diverse and complex than weed communities within fields (Poggio et al., 2013). Thus, conditions in non-cropped habitats may provide a wider variety of resources for arthropods than the adjoining crop fields.

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Fencerow vegetation supplies refuges and overwintering shelter for arthropods, as well as food resources, such as alternative preys, pollen, and nectar sources (Landis et al., 2000). Retaining viable arthropod populations in farmed landscapes is critical for sustaining the provision of ecosystem services, such as pest regulation and pollination (Öckinger and Smith, 2007; Flynn et al., 2009). Farmland mosaics comprising different land uses usually support higher overall arthropods diversity, which result from complex combinations of resources and abiotic conditions that satisfy the requirements of different guilds (Moonen and Bàrberi, 2008). In addition, the association between specific ecosystem services and land use diversity at landscape scale may present an asymptotic relationship. Hence, this pattern suggests that a relatively small number of different land uses in a landscape will satisfy the minimum functional requirements associated with the provisioning of particular ecosystem services (Swift et al., 2004).

Land use heterogeneity produces bottom-up effects throughout the trophic web via heterogeneity in resource distribution, structure and plant composition (Tscharntke et al., 2005a,b), as well as the availability of refuges, which affects the behaviour and movement of arthropods. In addition, landscape structure may influence species diversity at local scale through dispersal between neighbouring patches having contrasting environmental conditions. Such a patch dynamics has been characterised for arthropods ("spillover" effects; Rand et al., 2006) and plants ("mass" effects; Shmida and Wilson, 1985). Hence, resources in a patch may subsidise shared consumers that could have greater impacts on resources within an adjoining habitat. This dispersal-driven dynamics may therefore produce effects differing from those expected from considering only the *in situ* dynamics (Pulliam and Danielson, 1991; With and Crist, 1995).

Recent agricultural expansion in Argentina has been led by soybean cultivation, whose rapid adoption was accompanied with the parallel increase in input use and no-tillage (Poggio et al., 2010). These technological advances homogenised land use patterns by promoting row crops, sowing fewer crop types, and removing fencerows to enlarge field areas (Ghersa and León, 1999). In the current scenario, remnant non-cropped habitats represent reservoir areas for species of low frequency or that are not able to complete their development (or life) cycles within crop fields (Le Cœur et al., 2002; Poggio et al., 2010). Retaining non-cropped habitats in intensively farmed mosaics, such as fence and field margin networks, may help to maintain landscape heterogeneity and, therefore, to sustain diverse arthropod assemblages (Marshall and Moonen, 2002).

The main objective of our research was to assess the value of fencerows for sustaining arthropod diversity in intensively farmed mosaics. In addition, our study is also aimed at identifying the factors associated with the spatial heterogeneity at different scales that influences the structure of epigeal arthropod assemblages. Many arthropod species that live in field margin vegetation perform ecological functions such as pollination and biological control (Elliott et al., 1998; Torretta and Poggio, 2013). Thus, some arthropods may *spillover* into neighbouring crop fields. Within this framework, we evaluate: (1) the effects of spatial heterogeneity at multiple scales (*i.e.* field position, neighbouring fields, and land use mosaic) on the species richness and abundance of arthropods, (2) the importance of fencerows to retain arthropods diversity, and (3) the effects of spatial heterogeneity on arthropod guilds, as well as the "redundancy" (diversity) within each guild. We expect that fencerows not only will play a key role for both sustaining arthropod diversity in farmland mosaics, but will also strongly interact with heterogeneity at wide spatial scales and hence contribute to retain arthropod populations that provide ecosystem services to agriculture.

2. Materials and methods

2.1. Study site

The study was carried out in a farm located in the Rolling Pampa, a sub-region of the Rio de la Plata grassland (Soriano, 1991). Pristine vegetation corresponded to mesic tussock grasslands dominated by a species-rich combination of C3 and C4 grasses (Parodi, 1930; Soriano, 1991). Topography is gently undulated and crossed by shallow streams. Climate is temperate sub-humid, with warm summers and no marked dry season. Mean annual rainfall is ca. 1000 mm and mean annual temperature is 17 °C (Hall et al., 1992).

The region has been extensively transformed to cattle husbandry and row-crop agriculture since the mid 19th century (Viglizzo et al., 2011). Currently, herbicide-tolerant soybean is the prevalent summer crop (*ca.* 65% of cropland), which is mostly sown at optimum dates in early November, whereas maize is usually sown in early October. Soybean is also sown as a double crop in mid December, immediately after the harvest of wheat, which is the prevalent cool-season crop in this region. Thus, the common crop sequence in the study area is maize, soybean, and wheat/soybean double crops. Virtually all field crops are currently sown using no-till practices, whereas ploughing has become very infrequent and almost exclusively used to grow maize (Poggio et al., 2010, 2013).

2.2. Sampling of arthropods and plants

Surveys were performed during spring and summer of two consecutive growing seasons (2009–2010 and 2010–2011) in crop fields belonging to the farm "Las Polvaredas" (34° 07′S, 60° 34′W). The farm comprises 4400 ha, where most of the arable land is planted with annual crops (84% of the total area), whereas pasture are concentrated along the margins of a stream that crosses the farm (11% of the total area). Small woodlots, houses and corrals are scattered over the landscape. Fencerows occupy an area slightly larger than 1% of the total farm area. Wire-fencerows divide fields (or paddocks) with different land uses or crop types. The farm has 64 fields (mean area 62 ± 2.8 ha) most of them bounded by wire fencerows (90%).

Arthropods and plants were surveyed in 22 pairs of adjoining fields (44 sampling plots) that were separated by a fencerow. Minimum and mean distances between field pairs were 458 m and 4428 m (SEM = 253 m), respectively. Each pair of fields was occupied by one of all possible combinations of the three crop types prevailing in the study region: maize, soybean, and wheat/soybean. Thus, field pairs occupied by either the same crop or different crops, respectively, which thus defined the two sets of homogenous and heterogeneous neighbourhoods (11 pairs each). In each field pair, sampling points were placed in seven positions. The first sampling position corresponded to the fencerow dividing both fields. The other sampling positions within adjoining fields were placed at increasing distances from the fencerow (edge: 4 m, headland: 20 m, and field interior: 100 m). The decision of sampling these three positions within fields was based on the observation in previous studies that plant species richness decreases from the fencerow towards the field centre in response to the different environmental conditions prevailing in fences, edges, and the interior of fields (Poggio et al., 2013).

Arthropods were captured by using pitfall traps (8 cm diameter, 12 cm depth), which were buried with the rim at ground level. This method is the most commonly used for studying invertebrate assemblages, even though capture rates may be affected by invertebrate activity (Fournier and Loreau, 2002). Traps were then filled with 200 mL of a solution of propylene glycol and water (1:3), and detergent was added to reduce surface tension. Two traps per sampling position were placed at each field pair. Traps were

active during seven consecutive days during each sampling round (November 2009, January 2010, March 2010, January 2011, and February 2011). Arthropods were taxonomically identified at the order level in all cases and at the lowest taxonomic level when possible (*i.e.* family, genus, or species). Individuals that could not be identified were assigned to morphospecies groups.

Species richness of arthropods was expressed as the mean number of taxa at each sampling position. Arthropod abundance was also counted. Afterwards, arthropod taxa were classified into trophic guilds according to general traits reflecting functional attributes primarily associated with resource acquisition, determining habits and food preferences using anatomic characteristics and bibliography (Imms et al., 1994). Phytophagous insects were sub-divided into leaf chewers, sap feeders and pollen or seed feeders. The remaining groups were predators, parasitic wasps, detritivores/fungivores, and mites. The transformed Shannon diversity index ($e^{H'}$, being H' the Shannon diversity index) was computed from the proportion of predator morphospecies within the predator guild, reflecting redundancy of predators.

Plants were also surveyed at each field pair in the same sampling positions as arthropod trapping. In fencerows, plant surveys were performed within a 1 m-wide by 100 m-long strip transects beneath the fencerow lines. This sample length was determined by using a species accumulation curve based on samples of increasing length according to the power of two series between 1 and 128 m (Poggio et al., 2010, 2013). Fencerow vegetation was mainly herbaceous and small shrubs were only rarely present. Plants at both field edges and headlands were, respectively, surveyed along parallel strips (2 m-wide by 50 m-long) located at 4 m and 20 m from the fencerow, whereas field interior were surveyed at 100 m distance from the fencerow. Plant surveys were restricted to areas having homogeneous crop cover and excluding low-lying topographic positions. Plant species richness was expressed as the mean number of plant species at each sampling position.

2.3. Landscape complexity

Landscape complexity was characterised by assessing the spatial heterogeneity of land-cover types surrounding each pair of fields. Characterisation was made by using the normalised difference vegetation index (NDVI) obtained from satellite imagery, as described in Guerschman et al. (2003). Seven land-cover classes were identified that include soybean, maize, and wheat/soybean, as cropland areas devoted to grow annual row crops, woodlots, rural buildings, grasslands, and riparian areas (ponds, stream banks, and wetlands). Classification was based on four satellite images (LANDSAT 7 ETM+, path 226 row 84) corresponding to spring, early and late summer, and early autumn. These four periods allow discrimination of different classes based of the phenological signatures derived from NDVI estimates. Scenes corresponding to December, February and March were co-registered to the October image using not less than 30 ground control points, spread throughout the scene. In all cases, the nearest neighbour method was used.

Area of each land-cover type was calculated within 500 m-diameter circles (19.6 ha) surrounding each field pair (ESRI, 2008). Then, fence density ($m\,ha^{-1}$) and the overall habitat diversity ($e^{H'}$) were calculated as straightforward measures of landscape complexity within each circle. Fencerow density was obtained by dividing the fencerow length by the area within 500-m diameter circle. The modified Shannon diversity index was computed from the proportional area occupied by the seven land-cover types in each circle. Fence density metric reflects the length of fencerow network delimiting patches occupied with annual crops while it may also reflect an increase in land use heterogeneity. Thus, low values of fence density may reflect the increase of cropped area due to fencerow removal (Poggio et al., 2010).

2.4. Statistical analysis

Changing patterns of arthropod species richness across the different field positions were compared by using a sample-based rarefaction procedure, where individuals are set as samples and curves are then calculated by using the Mao Tau estimator (Colwell et al., 2004). The significance of observed differences in arthropod species richness between field positions ($P < 0.05$) was evaluated by visually comparing rarefaction curves and their associated 95% confidence intervals. Estimated arthropod richness was calculated by using the abundance-based coverage estimator (Colwell et al., 2004).

Relative contributions to overall arthropod diversity and the abundance of the explanatory factors at the different heterogeneity spatial scales were analysed with linear mixed-effects models (Pinheiro and Bates, 2000). Mixed models, which account for non-independent errors due to the hierarchically nested nature of the sampling design, were used to test for the effects of a set of traits within the levels of field, neighbourhood, and land use mosaic. Year and sampling dates were used in the models as co-variables without significant effects in the richness and abundance of epigeal arthropods. Both field pairs and sampling plots within each pair were included as random variables in the mixed-effects models to account for the paired sampling design. Six factors were included in the model as fixed explanatory variables at each spatial scale. At field level, hereafter referred as the micro-scale, fixed-effect variables were the sampling positions within fields (fence, edge, headland, and field interior), crop type (soybean, maize, and wheat/soybean), and plant species richness. For both neighbouring fields and land use mosaics, henceforth, respectively, indicated as the meso- and macro-scales, fixed-effect variables included in the model were neighbourhood (homogeneous and heterogeneous), fence density (low and high), and habitat diversity ($e^{H'}$ of land uses in the buffer-areas of 500 m-diameter surrounding focal fields). The two levels of fence density were obtained by using the median as splitting point between both groups. A model simplification routine was applied by first removing the non-significant interaction terms (F test, $P > 0.05$). Non-significant main effects were subsequently removed only when they were not involved in a significant interaction (Crawley, 2007). Spatial autocorrelation analysis showed no significant values of Moran's I Coefficient for species richness between plots ($I = -0.0985$, $P = 0.2022$). Since linear mixed-effects models were applied to each plot individually, fence sampling points were duplicated because each field pair had a fence in common. Variability of model estimators due to the effects of duplicating fence samples were tested by using different sub-sets, with samples taken at random from the complete dataset. This test indicated that the model estimators have low variability when using different datasets. Means were compared by using 95% confidence intervals (CI 95%). All analyses were performed with R software (R Development Core Team, 2011). Linear mixed-effect models were fitted with the function 'lme' (method REML) in the 'nlme' package.

3. Results

A total of 190 morphospecies were identified from the 34,200 arthropod specimens captured. Morphospecies were classified into 12 orders (Appendix A). Most individuals belonged to Collembola (57% of all individuals captured) and Acarina (21%), followed by Hymenoptera (8%, 16 morphospecies), Araneae (4%, 10 morphospecies), and Coleoptera (3%, 60 morphospecies). Formicidae was the most representative family of Hymenoptera (95%). For Araneae,

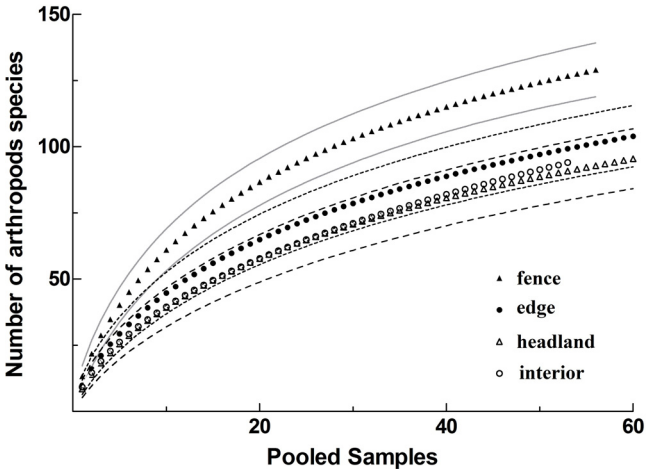

Fig. 1. Accumulation curves of arthropods species richness in different field positions (fence $0.56 \times \log(A) + 1.19$, $R^2 = 0.98$; edge $0.53 \times \log(A) + 1.05$, $R^2 = 0.99$; headland $0.54 \times \log(A) + 1.01$, $R^2 = 0.99$; and field interior $0.54 \times \log(A) + 1.03$, $R^2 = 0.99$). Solid grey line indicates 95% confidence intervals for fence, and dashed lines for positions within field.

the most representative families were Lycosidae (77%) and Linyphiidae (16%). Meloidae (24%), Staphilinidae (12%), Nitidulidae (13%), and Carabidae (8%) were the most abundant families of Coleoptera. The estimated total species richness for each field position was 77% for fences, 90% for field edges, 98% for headlands, and 74% for the field interior. These data indicate that our sampling effort was adequate for including most of the arthropod fauna occurring in the study landscape mosaic.

3.1. Species accumulation curves

Patterns of accumulated numbers of arthropod taxa differed between the four field positions. Taxa captured only once at each field position across all fields (*i.e.* unique taxa) were 44 in fencerows (35% of 127 sp.), 31 species in field edges (31% of 99 sp.), 23 species in headlands (25% of 91sp.), and 49 species in the field interior (49% of 94 sp.). The accumulation curve corresponding to fencerows differed from that of field edges, headlands, and field interior, which had similar increase rate of species numbers per unit area (Fig. 1). On the other hand, the species accumulation curve for fences had a significantly higher increment of species number per unit area than the other positions.

3.2. Arthropod species richness

Species richness of arthropod assemblages was influenced by field position, crop type, and plant species richness at the local (field) scale, whereas the effect of neighbourhood heterogeneity and fence density was significant at both meso- and macro- scales (Table 1). There were no significant interactions between the factors included in the models ($P > 0.10$). Fences sustained higher species richness of arthropods than the positions within fields in the three crop types. Indeed, arthropod richness significantly decreased from fencerows towards field interior (Fig. 2a). Furthermore, arthropod richness was slightly lower in maize crops (8 ± 0.6 sp.) than in both soybean (10 ± 0.5 sp.) and wheat/soybean crops (11 ± 0.5 sp.), particularly within fields (Fig. 2a). It is also worth noting that arthropod richness at field edges was higher in wheat/soybean (12 ± 0.8) than in both maize (8 ± 0.7 sp.) and soybean (10 ± 0.8) crops. Regarding factors operating at meso- and macro-scales, heterogeneous neighbourhood maintain higher richness of arthropods than homogeneous neighbourhood (Table 1, Fig. 2b). However, the influence of fence density on arthropod richness was stronger than neighbourhood heterogeneity (Fig. 2b). Thus, irrespective of neighbourhoods were heterogeneous or homogeneous, arthropod richness was positively associated with fence density (Fig. 2b).

3.3. Arthropod abundance

Patterns of arthropod abundance were similar to those observed for species richness. Accordingly, arthropod abundance tended to decline from fencerows towards the field interior (Fig. 3). At local (field) scale, abundance patterns reflected the influences of field position, crop type, plant richness, whereas the habitat diversity was the only significant factor at the macro-scale (Table 1). Interestingly, there was no significant effect of habitat diversity on arthropod richness. Overall, arthropod abundance in fences increased as habitat diversity ($e^{H'}$) increased ($r = 0.35$, $P = 0.0004$). Moreover, arthropod abundance was the highest at fences in all crop types (127 ± 10 individuals). As was observed for species richness, arthropod abundance was lower in maize (87 ± 10) than in both soybean (100 ± 10) and wheat/soybean (120 ± 11). In the wheat/soybean crops, arthropod abundance in fences (143 ± 11) and field edges were higher than in the other positions (Fig. 3), as it was observed for arthropods richness (Fig. 2a).

3.4. Plant species richness

Patterns of plant species richness (Appendix B) were affected by the interaction between field position and crop type (Table 1). Overall, plant species richness tended to be higher in fencerows than in the other positions within fields, but patterns differed between crop types (Fig. 4). Wheat/soybean crops had the widest difference in the plant richness surveyed at fences and the positions within fields. Plant richness within fields was higher in soybean and maize crops than in wheat/soybean (Fig. 4). The difference in the plant richness between fences and positions within fields was wider in wheat/soybean than in the others crops, where the differences were lower.

3.5. Arthropod guild diversity

Guild richness of arthropod was affected by the interactions between field position and either crop type at the local scale or fence density at the macro-scale (Table 2). In addition, there was significant effect of plant species richness on arthropod guild richness. Guild richness patterns noticeably differed between crop types (Fig. 5a). Although guild richness was the highest at the fences of all crop types, it markedly decreased towards the interior of maize fields, whereas guild richness decrease was less pronounced in soybean (4.65 ± 0.46). In wheat/soybean crop, conversely, guild richness remained high and invariable across all field positions (5.42 ± 0.18, Fig. 5a). Regarding the interaction between field position and fence density, guild richness in fences was higher than in all the positions within fields only when fencerow density was high at landscape scale (Fig. 5b). On the other hand, when fence density was low, guild richness at fences only significantly differed from that at the field interior.

Diversity of the predator guild, which comprises spiders, carabids, and rove beetles, was only significantly affected by local factors (Table 2), namely, field position, crop type, and plant richness, whereas the effects of landscape variables were not significant. Predator diversity was the highest in fences (2.9 ± 0.29; Fig. 5c), then decreased in both edges (2.8 ± 0.30) and headlands (2.6 ± 0.31), and slightly increased in the field interior (2.8 ± 0.33). Regarding the differences between crop types, predator diversity presented a similar pattern to those observed for arthropod richness and abundance (Fig. 2a and 3). Thus, predator diversity was

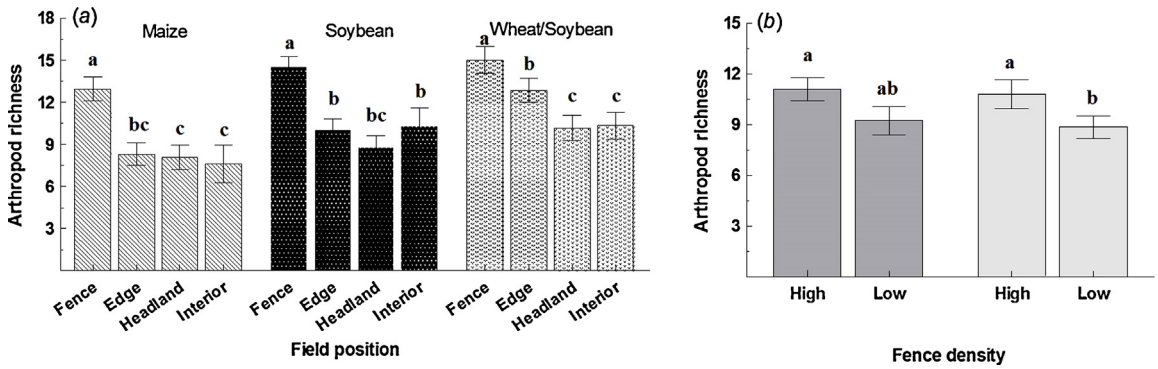

Fig. 2. (a) Mean species richness of arthropods (±SEM) in the field positions (fence, edge, headland, and field interior) for crop fields. (b) Mean arthropods (±SEM) richness in heterogeneous (grey dark bars) and homogeneous (grey light bars) neighbourhood in land use mosaic with different levels of fence density (high and low density; linear-mixed models). Statistical significance is indicated by different letters ($P < 0.05$).

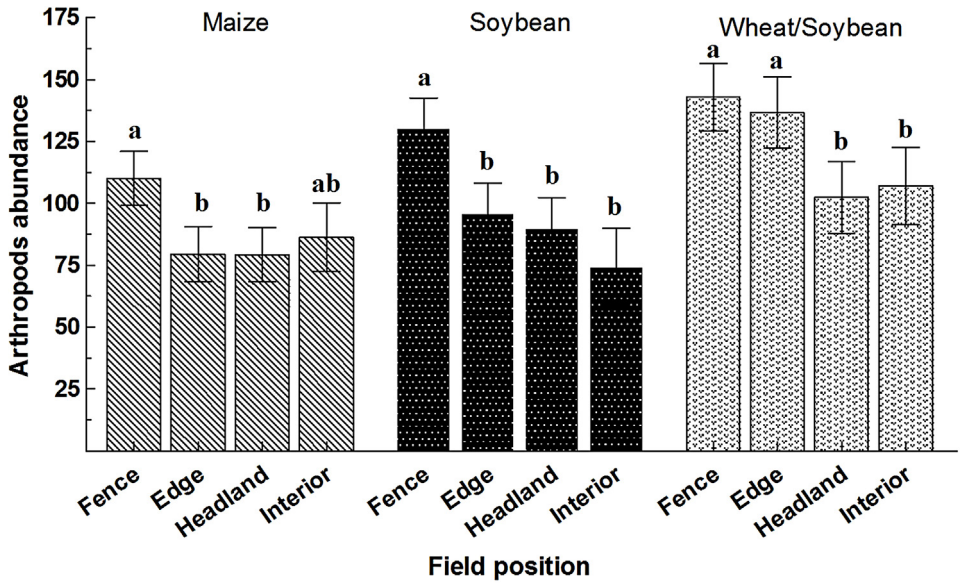

Fig. 3. Mean arthropods (±SEM) abundance in the field positions (fence, edge, headland, and field interior) for different crop types. Statistical significance is indicated by different letters ($P < 0.05$).

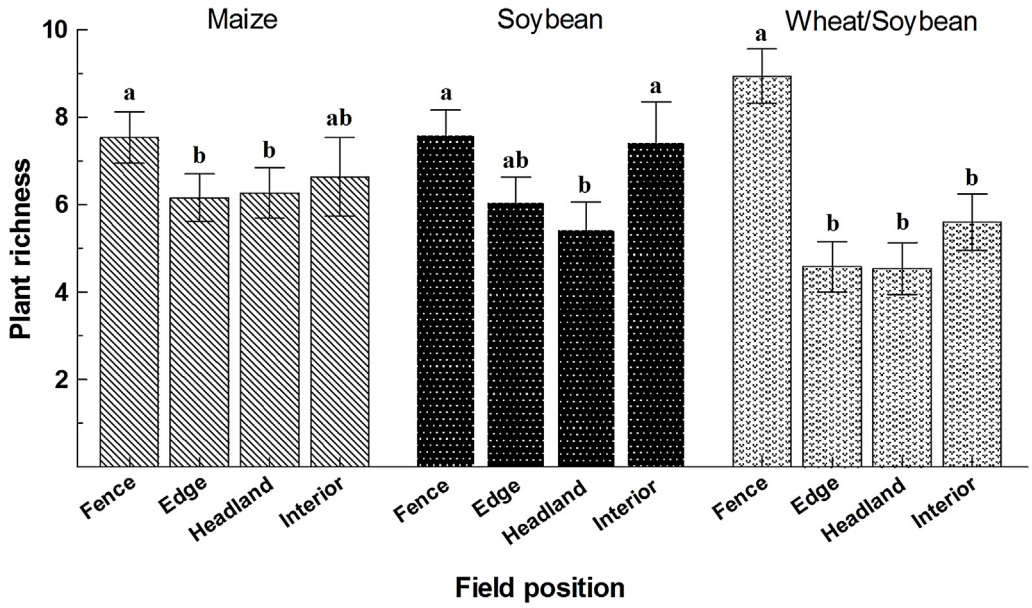

Fig. 4. Mean plant species richness (±SEM) in the field positions (fence, edge, headland, and field interior) of different crop fields. Statistical significance is indicated by different letters ($P < 0.05$).

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Table 1
F values and levels of significance of linear mixed-effects models testing the effects of micro-scale (field position, plant richness, crop type) and, meso- and macro- scale (neighbourhood, fence density, habitat diversity) for arthropods richness and abundance.

Source	Arthropod richness			Arthropod abundance			Plant richness		
	d.f.	*F*	*P* value	*d.f.*	*F*	*P* value	*d.f.*	*F*	*P* value
Macro-scale effect						<0.0001	–	ns	
Habitat diversity (e*H*′)	–	ns		1, 20	7.95				
Fence density	1, 20	17.15	0.0008	–	ns		–	ns	
Meso-scale effect									
Neighbourhood	1, 20	6.62	0.0105	–	ns		–	ns	
Micro-scale effect									
Field position	3, 18	118.30	0.0001	3, 18	11.47	<0.0001	3, 18	14.44	
Crop type	2, 19	5.03	0.0071	2, 19	57.08	<0.0001	2, 19	1.46	0.2344
Plant richness	1, 18	6.92	<0.0001	1, 18	2.06	0.0042	–	–	
Field position × crop type	–	–		–	–		6, 18	2.44	0.0256

Table 2
F values and levels of significance of linear mixed-effects models testing the effects of micro-scale (field position, crop type, plant richness) and, meso- and macro- scale (neighbourhood, fence density, habitat diversity) for arthropods guild richness and diversity within predator's guild.

Source	Arthropod guild richness			Predator diversity		
	d.f.	*F*	*P* value	*d.f.*	*F*	*P* value
Macro-scale effect						
Habitat diversity (e*H*′)	–	ns		–	ns	
Fence density	1, 20	5.45	0.0329	–	ns	
Meso-scale effect						
Neighbourhood	–	ns		–	ns	
Micro-scale effect						
Field position	3, 18	16.69	<0.0001	3, 18	11.21	<0.0001
Crop type	2, 19	1.10	0.3355	2, 19	4.03	0.0188
Plant richness	1, 18	2.24	0.0014	1, 18	3.39	<0.0001
Field position × crop type	6, 18	4.56	0.0002	–	–	
Field position × fence density	3, 18	3.55	0.0149	–	–	

the highest in wheat/soybean (3.0 ± 0.30), intermediate in soybean (2.8 ± 0.30), and the lowest in maize (2.6 ± 0.32; Fig. 5c).

4. Discussion

The importance of fence habitats for retaining diverse arthropod assemblages was revealed by the multi-scale hierarchical approach we have applied. In addition, the spatial heterogeneity of crop mosaics also contributes to sustain arthropod guilds providing ecological services in agro-ecosystems. Our study expands upon previous evidence about the relationship between arthropod diversity and landscape heterogeneity, which has been extensively studied in Western Europe and North America (Menalled et al., 1999; Marshall and Moonen, 2002; Tscharntke et al., 2005a,b). Conversely, cropland mosaics and farming practices in the Pampas starkly differ from those in agricultural regions in the Northern hemisphere. Hence, Pampean landscapes are more homogeneous, coarse-grained, and spatially extended than European ones due to, for instance, much larger fields (Poggio et al., 2010). This landscape attributes may be only comparable to situations in the Midwest of the United States (Gardiner et al., 2010). Field position was a major determinant of arthropod species diversity at the local scale due to the contrasting micro-environmental conditions prevailing at fencerows and the adjoining fields. At the landscape scale, our results indicate that fence density contributes to retain diverse arthropod assemblages in farmland mosaics by supplying habitats and refuges (Landis et al., 2000). In addition, extended fence networks may function as corridors for dispersal that may increase connectivity between areas with dissimilar environmental conditions (Marshall and Moonen, 2002). In comparison to the other factors studied here, neighbourhood heterogeneity enhances arthropod species richness to a lesser extent. Fence habitats, as well as their density in the landscapes, increase both richness and abundance of beneficial arthropods. Furthermore, variation of guild richness from fences towards the field interior was influenced by the interaction between fence density and field position (Fig. 5b).

Arthropod richness pattern decreased from fences towards the field interior for all crop types (Fig. 2a). High species richness and abundance observed at fences may mostly result from the more stable conditions and richer resource combinations at fences than within fields (Marshall and Moonen, 2002). Thus, fence habitats offer a wide variety of micro-sites for arthropods to fulfil development and reproduction requirements, as well as to supply resources in higher levels and for longer periods than during crop growing cycles (Landis et al., 2000). Further, soil cover of the less disturbed vegetation in fencerows can reduce diurnal temperature fluctuations and diminish the mortality rates of arthropods in the topsoil (Pfiffner and Luka, 2000). Crop identity has effects in the arthropods abundance principally due to differences in ground-cover dynamics and agronomic management from the edges to the interior of fields. Low ground-cover and less intensive weed control in maize (Poggio et al., 2013) appears to leave arthropods exposed to higher pressures of predation and parasitism (Costello and Altieri, 1995). Furthermore, the larger plant size and more open canopies of maize may offer greater advantages for predators at higher trophic levels. Conversely, high arthropod abundance in wheat/soybean crops is mainly due to the denser canopy cover of wheat crops (Holt, 1995; Poggio and Ghersa, 2011), which not only reduces predation rates, but also provides a longer ground-cover period when soybean is sown as a double crop. Resources accumulated in wheat residues may last the growing period of the following soybean crop, thus offering refuges because of the abundant crop residues that cover the ground after harvest (Caviglia et al., 2004).

Fence density had the strongest influence on arthropod richness at landscape scale. Moreover, differences in species richness between homogeneous and heterogeneous neighbourhoods were larger when the landscape was more complex, arthropod diversity consequently tends to increase when fence density was higher

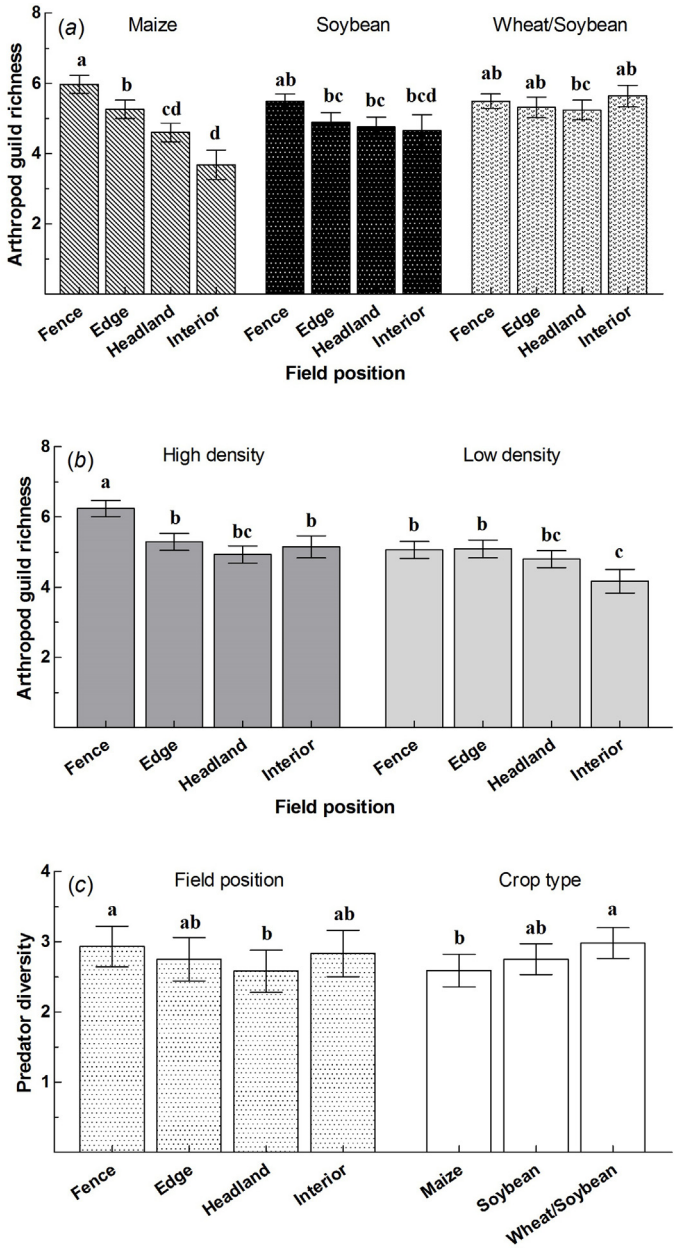

Fig. 5. (a) Mean arthropods (±SEM) guild richness in the field positions (fence, edge, headland, and field interior) of different crop fields. (b) Mean arthropods (±SEM) guild richness for field positions with high density (grey dark bars) and low fence density (grey bars). (c) Mean predator diversity index (±SEM) in the field positions (fence, edge, headland, and field interior), and in different crop fields (linear mixed models). Statistical significance is indicated by different letters ($P < 0.05$).

in heterogeneous neighbourhoods. Fence density increase may connect habitats with heterogeneous environmental conditions (Poggio et al., 2013) and, simultaneously, increases the total area of less disturbed habitats. Additionally, neighbourhood heterogeneity enhances arthropod richness to a lesser extent than fence density, which decreased in homogeneous neighbourhoods. Thus, same crop types in a field pair share similar "sets" of species due to similar conditions. In heterogeneous neighbourhoods, assemblages in each adjoining crop comprises species sets with lower similarity, because of the addition of specialist species and other associated species, for example, secondary consumers of these species (Pfiffner and Wyss, 2004; Tscharntke et al., 2005a,b). A previous study in the Rolling Pampa indicated that richness of non-herbivore arthropods decreased as percent cover of soybean in the landscape increased (de la Fuente et al., 2010). Habitat diversity has important effects on arthropod abundance, because cropped areas are usually rich in food resources for herbivores (mainly specialist), which may in turn maintain large populations during short periods, and thus for their predators and parasitoids (Rand et al., 2006).

Heterogeneity associated with fences at both local and landscape scales was a key driver of arthropod diversity in farmland mosaics. In addition, community structure was influenced by dispersal from the surrounding non-cropped patches. Availability of a wide variety of habitats for arthropods in the landscape, which may function as source patches, allows regularly disturbed crop fields to be re-colonised by dispersing organisms (Weibull and Östman, 2003). Higher arthropod richness in linear farmland habitats, such as hedgerows, was observed at field and landscape scales in Western Europe (Burel et al., 1998; Weibull and Östman, 2003) and North America (Menalled et al., 1999). In the US Midwest, few studies showed that the distribution and abundance of non-cropped and cropped habitats greatly influence population dynamics of ground-dwelling arthropods (Gardiner et al., 2010). Also, Maisonhaute et al. (2010) observed that landscape structure was globally the main factor driving beetle abundance and diversity, whereas the contribution of both farming practices and local environmental conditions was lower. In contrast, our findings suggest that local factors defining spatial heterogeneity (position and crop type) are the main determinants of epigeal arthropod diversity and trophic structure. Studies in the US Midwest, where an extended land area is occupied by annual row crops, have been carried out in fine-grained farmland mosaics, characterised by relatively small fields (Menalled et al., 1999) and intermingled areas of remnant forests. This structural complexity, however, markedly differs from the extensive and homogeneous farmland mosaics characterising Pampean landscapes (Poggio et al., 2010).

Fences sustained high guild richness, which decreased towards the field interior. However, wheat/soybean double crops were the exception, in which guild richness remained constant at different positions within fields, suggesting a crop type effect on guild diversity. Canopy dynamics and sowing density of crops have important implications in promoting arthropod populations due to high resource availability and trophic interactions (*e.g.* predation, Bohan et al., 2007). The predator guild declined sharply with distance from fences towards the crop interior, whereas guilds of leaf chewers and sap feeders followed a similar but less steep pattern. These guilds responded similarly in their association with low levels of disturbance intensity, probably indicating trophic links. Predator redundancy declined from the fence to the field interior. These decreases in secondary consumers could have resulted from constrained niche availability in the homogeneous conditions usually prevailing within crop fields (Moonen and Bàrberi, 2008), or from impoverished plant diversity, as a cascade effect restricting energy flow towards higher trophic levels (Cagnolo et al., 2002). At landscape scale, high fence density had a positive effect on guild richness. Within fields in homogeneous landscapes, guild richness decline towards the field interior. The increased arthropod diversity at field positions nearby field edges can be explained by additive boundary effects of the fence network through *spillover* from the surrounding landscape (Öckinger and Smith, 2007). Connectivity of extensive fencerow networks contributes to maintain the species diversity through changing plant species composition and acting as dispersal corridors (Marshall and Moonen, 2002).

5. Conclusions

In our study, arthropod richness and abundance remained higher at positions closer to fences than towards the field interior, especially in wheat/soybean double crop. Therefore, we suggest

that negative effects, particularly those associated with regular farming, are being mitigated by spatial heterogeneity. Field disturbance dynamics result in the requirement for arthropods to re-establish annually from surrounding landscape via dispersal (Gabriel et al., 2010). Accordingly, after a disturbance, some species may persist in the crop fields through meta-population effects (Pulliam and Danielson, 1991). Field margins, which may be conceived as 'ecotones' or 'transitional zones' between fencerows and the adjoining crop fields, are assumed to receive the same management as the field centre, even though edges and headlands in crop field may received highly intense disturbance regimes due to the traffic of machinery and repetition of farming practices (Poggio et al., 2013). Fencerows, besides offering shelter sites, may also modulate the variations in the supply of food (Landis et al., 2000). Moreover, in landscapes with greater fence densities, arthropods may concentrate on fencerows (concentration dilution hypothesis, Tscharntke et al., 2012), thus increasing the complexity of trophic structures. These increases in complexity of food webs in fences regulate the herbivore populations, which may consequently decrease the probability of pest outbreaks due to reduced dispersal rates towards the crop fields. The fact that spatial heterogeneity factors, acting at different scales, sustains more diverse arthropod assemblage also implies that farmland mosaics could be organized to enhance spatial connectivity between crop fields and fence networks (Swift et al., 2004). Hence, increasing landscape complexity, for instance by maintaining denser fence networks and more heterogeneous land uses, may enhance both *spillover* and concentration-control in fences, and consequently maintain the *resilience* capacity and the provisioning of ecological services across the entire landscape (Moonen and Bàrberi, 2008; Tscharntke et al., 2012).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agee.2014.04.013.

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