

RESEARCH ARTICLE

Structural complexity of arthropod guilds is affected by the agricultural landscape heterogeneity generated by fencerows

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Boundary; carabid beetles; dispersal; field margin; natural enemies; Rolling Pampas; trophic interactions.

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Abstract

Intensive farming imposes harsh conditions impeding the persistence of most arthropod species within crop fields. Hence, arthropods surviving the unfavourable conditions prevailing within crop fields may disperse towards nearby uncropped margins, such as fencerows. Here, we evaluate the influence of landscape heterogeneity on the abundance of different guilds, particularly herbivores and their natural enemies. Said heterogeneity mostly derives from fencerow network density. Hence, we developed an approach based on fitting linear-mixed models to elucidate the effects of landscape heterogeneity and field position (fencerows and crop interiors) on arthropod diversity. Mixed models were fitted to arthropod data obtained by pitfall trap samplings in 36 crop fields. Arthropod communities were structurally and functionally more complex along fencerows than within nearby crop interiors. Arthropods abundance was modulated by landscape heterogeneity, increasing the abundance of natural enemies as the landscape heterogeneity increased. On the contrary, herbivores abundance decreased as landscape heterogeneity increased. Consequently, the ratio between herbivores and natural enemies also decreased as landscapes became more heterogeneous. Natural enemies with larger body sizes, mostly carabid beetles, were more sensitive to landscape homogenisation. Our study reveals that, despite the coarse-grained landscapes in the Rolling Pampa, fencerow density appears as a key factor for structuring complex arthropod guilds in intensively farmed agricultural mosaics. In landscapes with higher density of fencerows, arthropods tend to concentrate along them, thus increasing the community structural complexity as well as the predation pressure over herbivores. This structural complexity of upper trophic levels enhances the 'top-down' regulation of herbivore populations, consequently decreasing the probability of pest outbreaks within crop fields.

Introduction

Agricultural intensification, which has significantly increased yields due to greater use of off-farm inputs, has also homogenised farmlands in time and space (Denys & Tschardtke, 2002; Tschardtke *et al.*, 2005). Land-use composition and configuration consequently became simpler in homogeneous farmlands (Fahrig *et al.*, 2011). Moreover, fencerows and roadsides in farmlands offer wider ranges of microenvironmental conditions for arthropod populations than in nearby crop fields (Marshall & Mooney, 2002), such as sites for overwintering, feeding or

ovipositing (Landis *et al.*, 2000; Olson & Wäckers, 2007; Torretta & Poggio, 2013). However, fencerow removal to enlarge annually cropped areas consequently reduced arthropod species richness (Burel *et al.*, 1998; Östman *et al.*, 2001).

Many arthropod species move between uncropped habitats and neighbouring cropped fields (spillover effects, Rand *et al.*, 2006), which constitutes a vital ecological process for ensuring biological control and resilience in agro-ecosystems (Tschardtke *et al.*, 2005). Thus, uncropped habitats may function as arthropod

sources for reassembling communities within fields after farming acute effects. In intensively managed farmlands, boundaries dividing fields and nearby uncropped margins, such as fencerows, offer varied resources and stability compared to conditions prevailing within fields (Landis *et al.*, 2000; Poggio *et al.*, 2010, 2013). These favourable conditions sustain plant diversity in uncropped habitats, which contribute to concentrating arthropod species. Landscape heterogeneity modulates the predation pressure on herbivores in fencerows, thus controlling smaller populations and decreasing the outbreak probability (Bommarco, 1998; Bianchi *et al.*, 2006). Predation should be more severe in heterogeneous landscapes due to the more complex trophic structure of arthropod communities (top-down effects; Bommarco, 1998). For example, generalist natural enemies can suppress pest outbreaks, or at least reduce their incidence, but effectiveness decreases as landscape homogeneity increases (Östman *et al.*, 2001; Tschardtke *et al.*, 2005). In more homogeneous farmlands, where trophic structure has been simplified, effects of upper levels are less strong, mainly due to lower diversity and abundance of natural enemies (Östman *et al.*, 2001; Purtauf *et al.*, 2005).

Arthropods respond to landscape heterogeneity at different spatial scales, which depends on species-specific dispersal abilities and foraging ranges (Bommarco, 1998; Baranovská & Knapp, 2014). Many species attributes may determine scale-dependent responses to landscape heterogeneity, such as trophic level, body size and specialisation to particular resources or habitats (Burel *et al.*, 2004; Purtauf *et al.*, 2005; Tschardtke *et al.*, 2005). Species at upper trophic levels, such as predators and parasitoids, are expected to be more vulnerable to local extinction by stochastic events than their hosts or preys. Those guilds, usually having smaller populations and being more dependent on lower trophic levels (Fenoglio *et al.*, 2010), are assumed to be more vulnerable than their prey to reductions in both habitat connectivity and landscape heterogeneity (Steckel *et al.*, 2014). Besides, large arthropods have greater energy requirements and higher mobility (some exceptions are Linyphiidae spiders and several small carabids), which allow exploring wider feeding ranges and therefore accessing resources distributed throughout larger areas. Conversely, smaller arthropods satisfying their requirements in restricted areas are hence more sensitive to local factors (Bommarco, 1998). Regarding carabids, it is expected that arthropods having, on average, large body sizes are numerous in more stable landscapes, while arthropods with greater dispersal abilities are mainly abundant in those highly disturbed (Burel *et al.*, 2004).

Enhancing field margin vegetation at landscape scale to promote the diversity of natural enemies can contribute

to reduce pest incidence in nearby crops, due to the additional resources present in the surroundings (Landis *et al.*, 2000; Torretta & Poggio, 2013). Whereas field margin vegetation can attract and concentrate pests, increasing the availability of uncropped habitats in landscape, it can also regulate herbivore populations by enhancing the diversity and abundance of natural enemies in fences. Neither herbivore preference nor changes in trophic guilds structural complexity (diversity and abundance of each trophic level) have been simultaneously studied in field margins. In the coarse-grained, homogeneous farmlands characterising the Rolling Pampa of Argentina, trophic structure of arthropods was more complex along fencerows than within fields (Molina *et al.*, 2014). Moreover, richness and abundance of natural enemies were enhanced in more heterogeneous landscapes, especially due to higher fencerow density. Despite this evidence, there is scarce information about how fencerow density and landscape heterogeneity affect trophic structure and body size of arthropods to provide conditions for regulating pest outbreaks.

Here, we aim at studying the influence of landscape heterogeneity on trophic structure of arthropod assemblages in the coarse-grained, highly homogeneous farmlands prevailing in the Rolling Pampa, the corn belt of Argentina. We hypothesise that the structural complexity of arthropod trophic guilds at fences and adjoining crop fields are mostly affected by landscape heterogeneity, regardless of the toxic load (total amount of pesticides applied) at field and landscape scales. Thus, we tested the associated predictions: (a) regarding the different trophic guilds, the contrast in abundance between fences and nearby crop fields will be higher in more heterogeneous landscapes; (2) guild structural complexity will be greater at margins and the interior of crop fields in more heterogeneous landscapes, whereas the ratio between herbivores and natural enemies will be higher in more homogeneous landscapes; and (3) arthropods with larger body size will be associated with more heterogeneous landscapes having higher fencerow density. More structurally complex arthropod communities, particularly in fencerows, are expected to regulate the herbivore populations and therefore reduce the probability of generating outbreaks and dispersing towards crops (packing effect).

Materials and methods

Study site

This study was carried out during summer 2010/2011 in crop fields on the farm 'Las Polvaredas' (34°07'S, 60°34'W), located in the Rolling Pampa, a subregion of

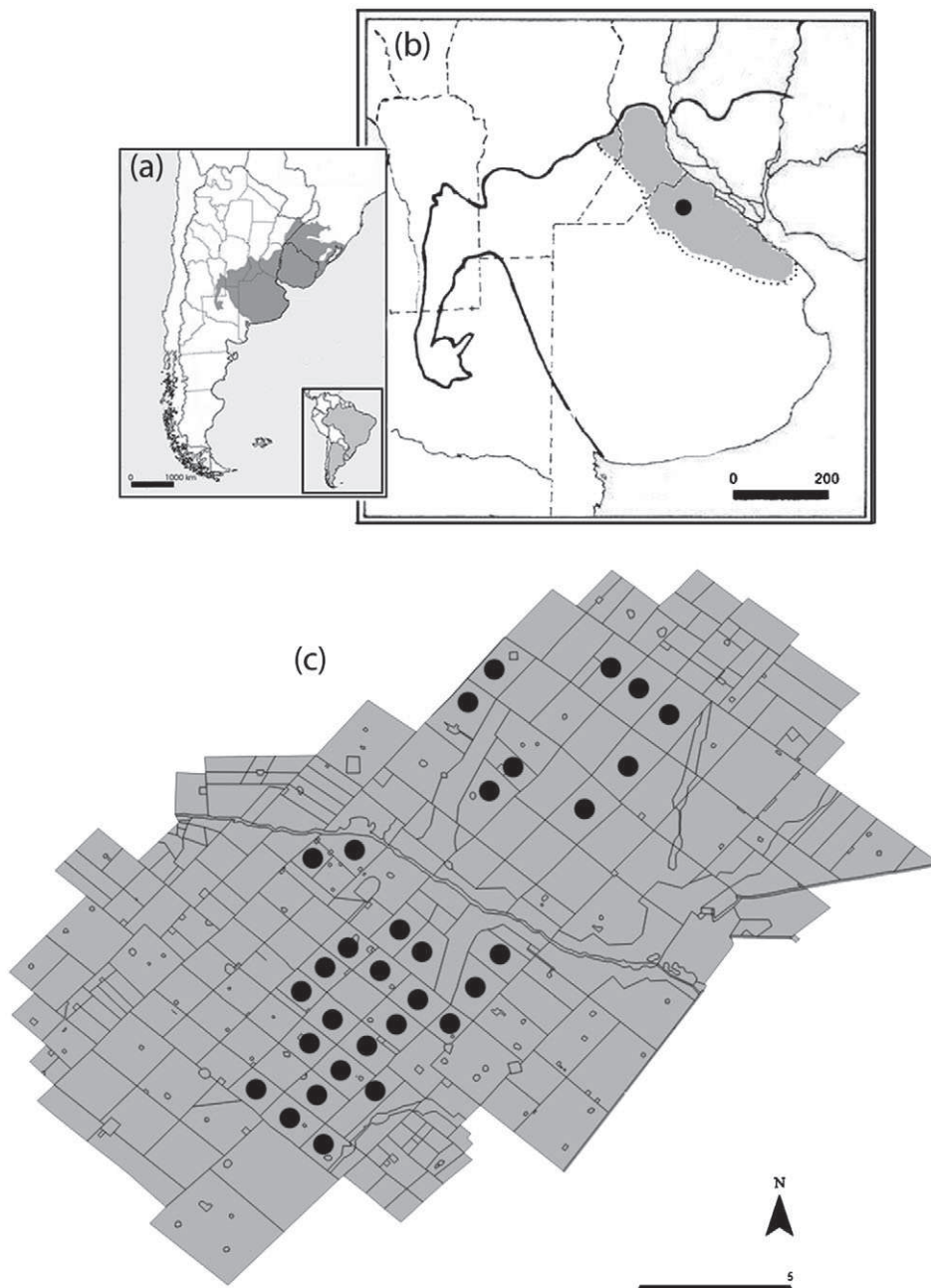


Figure 1 Location of study farm in the Rolling Pampa (b) of Argentina (a). The black dots indicate the position of all surveyed crop fields considered in this study (c). Materials and methods for further information.

the Rio de la Plata grassland (Fig. 1). Climate is temperate subhumid, with warm summers and no marked dry season. Mean annual temperature is 17°C and mean annual rainfall is c. 1000 mm (Hall *et al.*, 1992). The farm comprises 4400 ha mostly devoted to annual crops (84% of the total area), whereas pastures are concentrated at both sides of a stream crossing the farm (11%

of the total area). Small woodlots, homestead and corrals are scattered throughout the landscape. Fencerows occupy nearly 1% of the total farm area. Wire-fencerows divide fields with different land-uses or crop types. The farm consists of 64 fields (mean area 62 ± 2.8 ha). Most of them are bounded by wire-fencerows (approximately 90%).

Arthropod and plant samplings

Arthropods and plants were surveyed in 36 fields forming 18 pairs (sites) separated by a fencerow (Fig. 1). Minimum and mean distances between field pairs were 458 and 4428 m (SEM = 253 m), respectively. In each field, sampling points were placed under the wire-fence and within the adjoining fields at 100 m from the fencerow (crop interior). These two sampling positions were chosen based on previous studies that observed different environmental conditions between fences and crop field interiors (Poggio *et al.*, 2010, 2013).

Arthropods were captured with pitfall traps (8 cm diameter, 12 cm depth), which were buried keeping the rim at ground level. Traps were 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. Traps were active for seven consecutive days during each sampling round (January and February 2011). Taxonomic determination of arthropods was carried out at order level in all cases and at the lowest taxonomic level when possible (i.e. family, genus or species; Molina *et al.*, 2014). Mean number of species captured at each sampling position represented arthropod species richness. Individuals per species were also counted. Afterwards, arthropod species were classified into trophic guilds, according to general traits reflecting functional attributes, primarily associated with resource acquisition (Imms *et al.*, 1994). Phytophagous insects were subdivided into sap-feeders and chewing. Predators were all considered as natural enemies. To compare body size differences between arthropods, taxa were divided into size classes (Table 1). The herbivore/natural enemy ratio (log 10) was calculated by dividing the total number of herbivore individuals by that of natural enemies. This ratio allows knowing how many natural enemies in the community may consume herbivore individuals (as a parameter of structural complexity of guilds).

Plants were also surveyed at each field in the same two positions as arthropod trapping. In fencerows, plant surveys were performed within 1 m-wide by 100 m-long strip transects beneath fencerow lines. Sampling 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). Surveys 100 m away from the fencerow were performed by zigzag walking during at least 30 min to obtain a complete species list. Plant richness was expressed as the mean number of species at each sampling position. Sampling effort was evaluated by species accumulation curves and species richness estimators (incidence-based coverage estimator) by using EstimateS, version 9.1 (Colwell *et al.*, 2004). Plant richness at

Table 1 Ecological classification according to body size. Each taxon was divided into size classes

Taxon	Body Size (mm)	
	Small	Large
Araneae	<14	>14
Coleoptera	<11	>11
Diptera	<12	>12
Hemiptera	<6	>6
Hymenoptera	<4	>4
Myriapoda	<15	>15
Isoptera	–	18
Lepidoptera	–	20–45
Orthoptera	–	28–40
Acarina	0.2–1.4	–
Collembola	1–5.5	–
Embioptera	6	–
Thysanoptera	1–4	–
Psocoptera	6	–

landscape (γ -diversity) and field (α -diversity) scales were calculated for each field group within the landscape heterogeneity gradient (Poggio *et al.*, 2010). For each cluster, γ -diversity was estimated by the total number of plant species sampled per field group, while α -diversity was the mean species richness per field. Species turnover (β -diversity) among fields within a group was obtained as the difference between γ -diversity and α -diversity (Wagner *et al.*, 2000).

Landscape heterogeneity

Landscape spatial heterogeneity was characterised by measuring the areas of land-cover types in the mosaics surrounding each focal field. Classification was made by using the normalised difference vegetation index (NDVI) obtained from satellite imagery (Guerschman *et al.*, 2003). Four satellite images were classified (LANDSAT 7 ETM+, path 226 row 84), corresponding to spring, early and late summer and early autumn of the southern hemisphere (2010/2011). Seven land-cover classes were identified, which include croplands devoted to growing annual row crops (soybean, maize and wheat/soybean double crops), woodlots, rural buildings, grasslands and riparian areas (ponds, stream banks and wetlands). Three landscape types were identified through cluster analysis (I: homogeneous, II: intermediate, III: heterogeneous), based on the composition and similarity of landscape elements surrounding focal fields. Area of each land-cover type was calculated within 500 m-diameter circles (19.6 ha) surrounding each field (using the equidistant point between both sampling positions as the circle centre). Then, fencerow density (m ha^{-1}), a straightforward measure of landscape heterogeneity, was calculated

by dividing the fencerow length (m) by 19.6 ha. Fence density not only characterises the extent of fencerow networks delimiting fields but also it may also reflect the level of land-use heterogeneity. Landscape heterogeneity was characterised by calculating the percent of each land-use type areas within circles and the overall habitat diversity (modified Shannon's diversity index, \exp^H ; Molina *et al.*, 2014). Hierarchical clustering analysis was performed using the furthest neighbour (complete linkage) algorithm with Sørensen (Bray–Curtis) quantitative index as a distance measure.

Eco-toxicological index

Widespread use of pesticides negatively affects both abundance and diversity of nontarget organisms (Ferraro & Pimentel, 2000). To characterise these effects, the field toxic load of was calculated at local and landscape scales. Toxicity and applied doses of pesticides are considered the main factors determining the ultimate impact of pesticide applications, rather than the type of formulation, mode of action or chemical classification (Ferraro *et al.*, 2003). Toxicity of each active ingredient was classified considering the effects on insects. To assess the impact of each application, insect toxicity values were calculated by using toxic units (tu) (Ferraro *et al.*, 2003):

$$T_{\text{ins}} [\text{tu}] = D/\text{LD}_{50} \quad (1)$$

where T_{ins} is the insect toxicity of each pesticide application; D is the dose applied (g product ha^{-1}); LD_{50} is the median lethal dose for bees ($\text{g of product bee}^{-1}$); and tu the toxic units (University of Hertfordshire, 2013). The straight addition of tu of two or more toxicants would be equivalent to the actual toxicity measured for their mixture. Then, toxicity scores of all the pesticides applied in each field were integrated to calculate the overall toxicity value:

$$\text{Sum } T_{\text{ins}} [\text{tu}] = n \sum T_{\text{ins}} \quad (2)$$

where $\text{Sum } T_{\text{ins}}$ is the insect toxicity of all the pesticides applied; and n is the number of pesticide applications on each field (Ferraro *et al.*, 2003).

Toxic load was calculated at local scale by adding toxic units (T_{ins}) in the focal field (Eqn 3), while the calculation at landscape scale was obtained by averaging T_{ins} values for the surrounding fields (N) (Eqn 4).

$$\text{STI}_{\text{field}} = \text{Sum } T_{\text{ins}} \quad (3)$$

$$\text{STI}_{\text{landscape}} = \sum \text{Sum } T_{\text{ins}}/N \quad (4)$$

Dispersal probability

Dispersal probabilities of arthropods were estimated as the probability of individuals to move from fencerow towards the crop interior (parameter q , Martin *et al.*, 2001):

$$q = N_{\text{Hi}}/N_{\text{T}} \quad (5)$$

$$N_{\text{T}} = N_{\text{Hi}} + N_{\text{Hi}} \quad (6)$$

where N_{Hi} , N_{Hi} and N_{T} are the total numbers of individuals in the fencerow, the crop interior and the entire field, respectively.

Statistical analysis

Pitfall trap data were analysed with linear mixed-effects models (Pinheiro & Bates, 2000), to test landscape heterogeneity and field position effects (fixed factors) on arthropod species richness and abundance, and the ratios between trophic guilds. Sample date and site were included as random variables in the mixed models to consider the sampling design. Mixed models, accounting for nonindependent errors in the hierarchically nested nature of the sampling design, were used to test landscape heterogeneity effects. A model simplification routine was applied by first removing the nonsignificant interaction terms (F test, $P > 0.05$). Nonsignificant main effects were subsequently removed only when they were not involved in significant interactions (Crawley, 2007). Abundance data were log-transformed to meet the assumptions of variance homogeneity and normal distribution. Suitability of statistical models was checked by plotting standardised residuals against fitted values. Spatial autocorrelation analysis showed no significant values for Moran's index coefficient between adjoining fields ($I = -0.0985$, $P = 0.202$). Arthropod richness patterns at fencerows and crop interiors were compared with a sample-based rarefaction procedure, where individuals were set as samples and curves were then fitted by using the Mao-Tau estimator (Colwell *et al.*, 2004). Estimated arthropod richness was calculated with the abundance-based coverage estimator (ACE).

Mixed effects models were applied for analysing dispersion frequencies (q , binomial distribution), body size classes within guilds (Poisson error distribution, link = log) and eco-toxicology indices at local and landscape scales. Random variables in the body size and eco-toxicological models were date/site and crop type, respectively. Linear mixed-effect models were performed with R software (R Development Core Team, 2011) and fitted using the function 'lme' (method REML) in the 'nlme' package.

Table 2 Average mean and standard errors of the landscape heterogeneity, eco-toxicology index and additive components of plant diversity for each landscape heterogeneity sampled in the study area

Landscape	Fence Density	Land-use Diversity	Plant diversity		Eco-toxicology	
			α	β	STI _{field}	STI _{landscape}
I	41.7 (0.3)	2.35 (0.18)	7.7 (0.68)	30.3	0.99 (0.19)	1.11 (0.12)
II	43.7 (0.6)	1.48 (0.04)	8.9 (0.82)	43.14	0.85 (0.18)	1.02 (0.14)
III	52.3 (0.4)	2.05 (0.11)	8.1 (0.51)	32.88	0.95 (0.30)	1.17 (0.11)

Table 3 *F* values, degrees of freedom and levels of significance of linear mixed-effects models testing the effects of field position (fence and crop interior) and, landscape heterogeneity for arthropods abundance (herbivores and natural enemies), ratio herbivores/natural enemies and *q* (probability to leave fence towards crop interior)

Source	Herbivores			Natural Enemies			<i>q</i>			Ratio H/NE		
	d.f.	<i>F</i>	<i>P</i> -value	d.f.	<i>F</i>	<i>P</i> -Value	d.f.	<i>F</i>	<i>P</i> -value	d.f.	<i>F</i>	<i>P</i> -value
Position	1.34	26.83	<0.0001	1.34	7.28	0.0078	–	–	–	1.34	3.31	0.071
Landscape	2.33	3.4	0.036	2.33	7.11	0.0011	2.33	7.37	0.0087	2.33	4.25	0.016

H, herbivores; NE, natural enemies.

Results

Overall, 75 arthropod morpho-species (14 orders) were identified from the 4847 specimens captured (Table S1, Supporting Information). Captures were more numerous in fencerows (3096 individuals) than in crop interiors (1751 individuals). Total morpho-species numbers in fencerows (69) and crop interiors (54) were 78% and 68% of the estimated species richness for each habitat type, respectively. These figures indicate that sampling effort was adequate for capturing most of the arthropod fauna in the study site. Most individuals belonged to Collembola (47% of all individuals captured) and Acarina (21%), followed by Hymenoptera (14%, 7 morpho-species), Araneae (8%, 4 morpho-species), Coleoptera (4%, 26 morpho-species) and Hemiptera (3%, 7 morpho-species). Formicidae was the most abundant family of Hymenoptera (97%). For Araneae, Thomosidae (49%) and Lycosidae (42%) were the most representative families. Carabidae (50%) and Staphilinidae (10%) were the most abundant families of Coleoptera. Also, Aphidoidea was the most representative family of Hemiptera (76%).

Fencerow density was the main determinant of landscape heterogeneity (Table 2), without effect of land-use diversity (\exp^H). Fencerow density increased from the most homogeneous landscape ($41.7 \pm 0.3 \text{ m ha}^{-1}$), to that with intermediate heterogeneity ($43.7 \pm 0.6 \text{ m ha}^{-1}$), and then to the most heterogeneous landscape ($52.2 \pm 0.4 \text{ m ha}^{-1}$). Besides, the eco-toxicological index did not significantly vary either between fields ($F_{2,33} = 0.03$, $P = 0.974$) or across the three landscape types ($F_{2,33} = 0.15$, $P = 0.863$, Table 2). Furthermore,

there were no significant toxic load effects on abundance patterns at local (herbivores: $F_{12,78} = 0.86$, $P = 0.589$; natural enemies: $F_{12,78} = 1.23$, $P = 0.280$) and landscape scales (herbivores: $F_{5,78} = 1.50$, $P = 0.198$; natural enemies: $F_{5,78} = 0.88$, $P = 0.501$).

Abundance of herbivores and natural enemies

Herbivores abundance was affected by both field position and landscape heterogeneity, the former being the most significant factor ($F_{1,34} = 26.83$, $P < 0.0001$, Table 3). Herbivores abundance in fencerows increased in heterogeneous landscape ($F_{2,34} = 3.40$, $P = 0.036$, Fig. 2a). Abundance pattern in crop interiors varied between landscapes. The highest and lowest herbivores abundance occurred in the landscapes with the lowest and intermediate heterogeneity, respectively (Fig. 2a).

Regarding natural enemies abundance, there were significant effects of field position ($F_{1,34} = 7.28$, $P = 0.008$, Table 3) and landscape heterogeneity ($F_{2,33} = 7.11$, $P = 0.001$). Fencerows presented the highest abundance, which increased along with landscape heterogeneity changes (landscape I: 0.68, II: 1.0, and III: 1.04, Fig. 2b). Natural enemies abundance in crop interiors was less sensitive to landscape homogenisation (landscape I: 0.62, II: 0.76, and III: 0.73, $P < 0.008$). Noteworthy, contrast between natural enemy abundance found in fencerows and crop interiors was low in the most homogeneous landscape.

Herbivore species richness was always higher in fencerows than in crop interiors in all landscape types ($F_{1,33} = 38.80$, $P < 0.0001$, Table 3). In fencerows, herbivore richness increased as landscape heterogeneity was

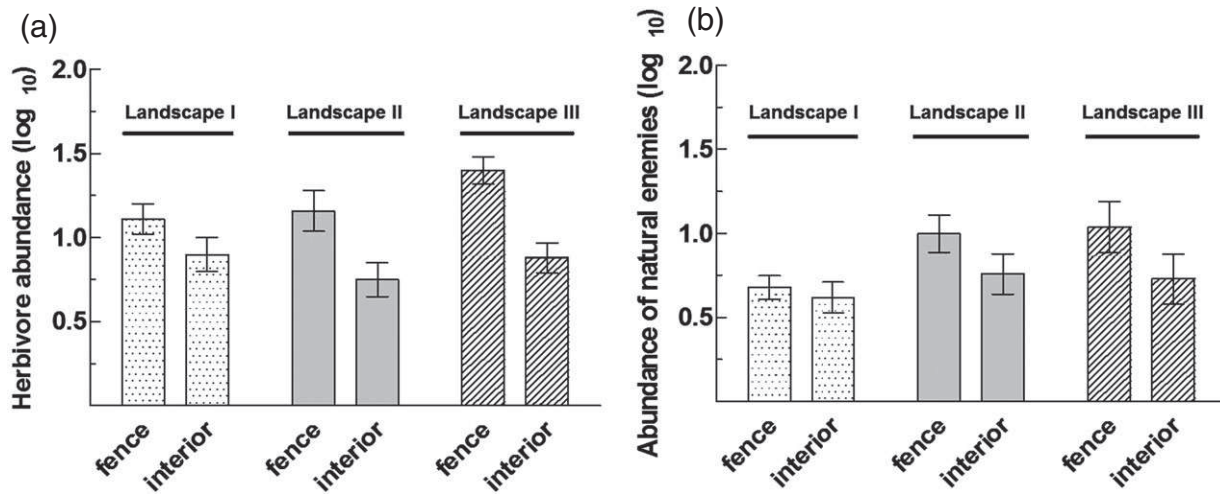


Figure 2 Mean \pm SEM abundance (\log_{10} transformed) of (a) herbivore species and (b) natural enemies species in fences and crop interior for different landscape heterogeneity. Letters represent significantly different Tukey groups ($P < 0.05$). Error bars are standard error.

greater (I: 3.8 ± 0.31 ; II: 4.6 ± 0.58 ; and III: 4.7 ± 0.46). This was due to the higher fencerow density, even though these values were not statistically significant ($F_{2,33} = 2.3$, $P = 0.103$). Moreover, mean herbivore richness in crop interiors was similar among landscape types (I: 2.6 ± 0.33 ; II: 2.4 ± 0.34 ; III: 2.5 ± 0.39).

Dispersion probability

Probability of leaving the fencerow and spreading towards the interior of nearby fields (q) was analysed to elucidate landscape heterogeneity effects on the structural complexity of trophic guilds. Dispersion probabilities (q) were similar for herbivores (0.37 ± 0.08) and natural enemies (0.38 ± 0.05) in the most homogeneous landscape. As landscape heterogeneity increased, herbivore dispersion probability significantly decreased ($F_{2,33} = 7.37$, $P = 0.009$, Table 3), whereas natural enemy dispersion did not differ among landscape types (Fig. 3).

Ratio between herbivores and natural enemies abundance

Herbivores/natural enemies ratios decreased from fencerows to crop interiors, being the effect constant in all landscape types ($F_{1,34} = 3.31$, $P = 0.071$, Table 3). As landscapes became more heterogeneous, the herbivores/natural enemies ratio decreased, even presenting negative values in some cases ($F_{2,33} = 4.25$, $P = 0.016$, Fig. 4). The ratio (\log_{10}) was close to zero in the intermediate heterogeneity landscape, which suggests that the abundance of natural enemies would have been sufficient to reduce that of herbivores.

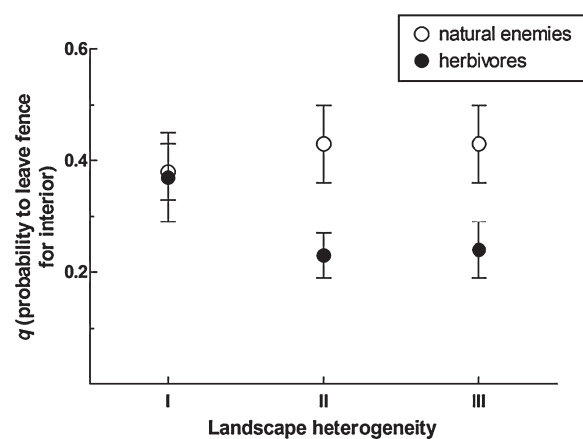


Figure 3 This graphic gives the probability of arthropod to leave fences towards the crop interior (q) for different landscapes heterogeneity. The filled dots (●) are trophic group of herbivores, and the blank dots (○) are the natural enemies group.

Landscape variability effects on body size

Body size changes among trophic guilds indicate that landscape heterogeneity has significant and contrasting effects (Table S1). Predator abundance increased in fencerows and crop interiors as landscape heterogeneity increased ($\chi^2_{2,33} = 263$, $P < 0.0001$), as well as the proportion of large size individuals ($\chi^2_{2,33} = 11.29$, $P = 0.003$, Fig. 5). In fencerows, abundance increase of natural enemies was more noticeable as the relative abundance of large-sized species increased, albeit differences were not significant ($\chi^2_{2,33} = 1.87$, $P = 0.172$). Furthermore, the high proportional increase of larger predators is noteworthy (landscape I: 16%, II: 22%, and III: 42%), which

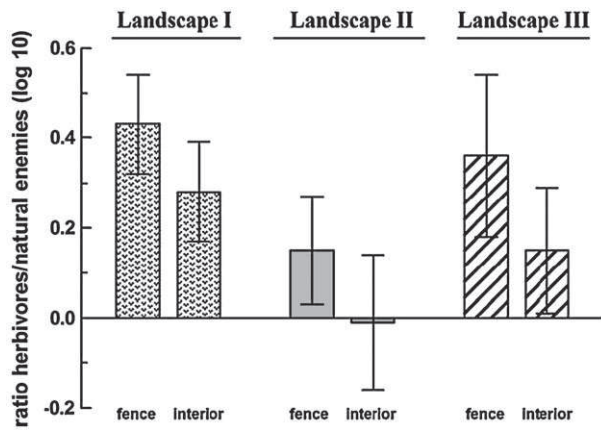


Figure 4 Ratio between herbivore and natural enemies (mean \pm SEM), in fencerows and crop interior, for landscapes with different heterogeneity.

indicates that the proportion of large body size predators increased in the crop interior (26%, 59% and 36%, data not shown). This result was also associated with landscape heterogeneity increase, being particularly evident in the intermediate landscape (Fig. 5). For natural enemies, it is also noteworthy that 98% of individuals were predators, which is a bias related to the sampling method.

Regarding herbivores, results highlight different patterns linked to body size and guild, despite differences not being significant. Chewing insects were negatively affected within crops in highly heterogeneous landscapes. Landscape variability effects were more severe on small-sized chewing species, with the decline higher than the expected proportion (75% and 70%, landscapes II and III, respectively). Instead, sap-feeder insects

maintained similar abundance in fencerows and crop interiors as landscape heterogeneity increased. However, relative proportion of large body size species increased in the interior of crop fields, while the large sap-feeder species occurred only in the most heterogeneous landscape. In fact, abundance of large-sized sap-feeders occurred only in the most heterogeneous landscapes (Fig. 5). Both natural enemies and chewing insects with large body size were highly sensitive to the increase of landscape variability.

Discussion

Diversity of arthropod communities has been importantly filtered out in the homogeneous, coarse-grained landscapes prevailing in the Pampas. Even in such conditions, arthropod trophic structure increased as landscape became more heterogeneous, especially due to higher fencerow density. Furthermore, the low herbivores/natural enemies ratio in more heterogeneous landscapes (Fig. 4) suggests that the higher natural enemies abundance may enhance herbivore population control. Vegetation along fencerows and roadsides play a primary role to maintain arthropod diversity, despite their simpler structure and smaller area compared to similar landscape features in the Northern Hemisphere (Baudry *et al.*, 2000; Marshall & Moonen, 2002).

Fencerows provide shelter for arthropods (Landis *et al.*, 2000; Marshall & Moonen, 2002; Poggio *et al.*, 2013; Torretta & Poggio, 2013), as well as concentration areas due to favourable and stable conditions and greater resource combinations. Natural enemies abundance increased in more heterogeneous landscapes, reaching similar values

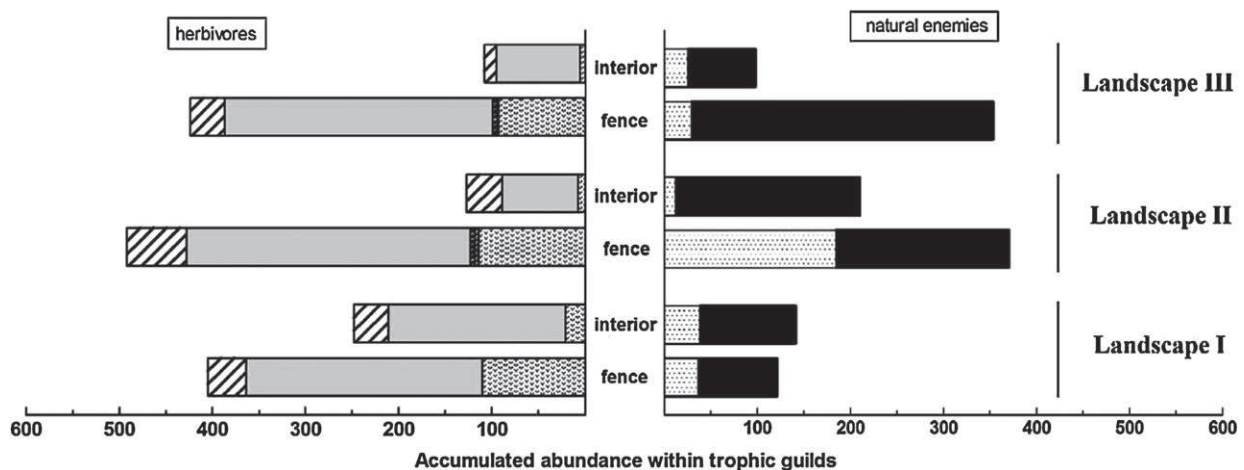


Figure 5 Mean relative body size of species within trophic guilds in different field position. Means were calculated among landscape heterogeneity. Chewing: small, large \square ; Sap-feeders: small \square , large \square ; Predators: small \square , large \square .

to those for herbivores (Fig. 4). All these effects would increase herbivores regulation due to higher landscape heterogeneity (Purtauf *et al.*, 2005; Bianchi *et al.*, 2006). Furthermore, natural enemies, mainly large size predators (>11 mm), were particularly responsive to landscape heterogeneity increase, possibly because additional resource requirements, such as food and shelter, are fulfilled (Isaacs *et al.*, 2008). Furthermore, diversity and trophic structure patterns of arthropod communities were independent of the toxic load at local (field) and landscape scales. Toxic load was similar at both scales, without detectable effects on arthropod abundance patterns.

Contrast in the arthropod abundance between fencerows and crop interiors is higher in more heterogeneous landscapes

Landscape heterogeneity influences the distribution patterns of arthropod diversity and abundance according to field position and the contrast between fencerows and crop interiors. For all landscapes, arthropod diversity and abundance were higher in fencerows, but they were differently affected by the contrast with the crop interior (Fig. 2a and Fig. 2b). Landscape heterogeneity modulates the contrast between fencerows and crop interiors by enhancing the differences between them. Homogeneous landscapes have similar abundances between positions, possibly due to critical resources for some species being scarce, which therefore limits populations size and natural enemies diversity (Thies & Tschardtke, 1999; Purtauf *et al.*, 2005; Morandin *et al.*, 2014), thereby limiting the ecosystem services that can be produced by such landscapes (Tschardtke *et al.*, 2005; Isaacs *et al.*, 2008). Species turnover significantly increased as landscape became more heterogeneous. These contrasting differences between fencerows and crop interiors were particularly noticeable in herbivores. This could be related to their low probability of leaving fencerows and spreading towards crop fields as landscape heterogeneity increases (Fig. 3).

Trophic guild structure and herbivore/natural enemy ratio are modulated by landscape heterogeneity

Arthropod trophic structure was importantly affected by landscape heterogeneity. Guild structural complexity was greater at fencerows and crop interiors as fencerow density increased. Hence, the herbivores/natural enemies ratio was lower in heterogeneous landscapes than in those homogeneous, indicating similar abundances between herbivores and natural enemies. Low ratios would infer the existence of numerous natural enemies for regulating herbivore populations (Fig. 4). Halaj & Wise (2001)

experimentally showed that predator removal led to higher plant damage levels due to higher herbivore abundance. In addition, herbivore arthropods are released from parasitism and may promote pest outbreaks, because species at upper trophic levels have large home ranges and their population dynamics is determined by landscape composition rather than by local conditions (Thies & Tschardtke, 1999; Tschardtke *et al.*, 2005). However, landscape heterogeneity can promote more complex arthropod trophic structures, thus increasing the diversity of upper trophic levels resulting from forced displacement and concentration in fencerows. High regularity of farming practices promotes dispersion and accumulation of arthropods in less affected habitats (i.e. fencerows; Tschardtke *et al.*, 2012). Fencerows, though narrow and elongated habitats, comprise more diverse and structurally complex plant communities than nearby fields (Poggio *et al.*, 2013), which provide arthropods with a wider variety of resources.

Fencerows have proved to be important habitats for plants and arthropods in the Pampas, thus increasing species richness and community structural complexity (de la Fuente *et al.*, 2010; Poggio *et al.*, 2013; Torretta & Poggio, 2013; Molina *et al.*, 2014). Undisturbed vegetated habitats, such as grasslands, fencerows and grassy strips, provide overwintering sites and alternative prey for epigeal arthropods (Landis *et al.*, 2000). Arthropod populations in fencerows can self-perpetuate, and possibly grow, but they are sensitive to landscape heterogeneity through natural enemy diversity, being modulated by predation pressure. Abundance of natural enemies and herbivores was similar in heterogeneous landscapes, hence regulating herbivores and achieving a 'packing' effect in fencerows. Previous studies showed that the herbivore/predator ratio was lower in old field margin strips than in those newly installed. This occurs because in older, undisturbed field margins, populations of upper trophic levels were assembled over longer periods (Denys & Tschardtke, 2002). Biological control effects, derived from higher abundance of natural enemies, drastically restrict pest species dispersal to crop fields (Halaj & Wise, 2001; Bianchi *et al.*, 2006).

Importance of landscape heterogeneity on arthropods is related to their body size

The organism size is the most conspicuous life history trait, and larger species usually have better dispersal abilities to bridge inhospitable areas. In our study, landscape homogenisation imposed restrictions on large body size species, mainly predators and chewing herbivores. Fast modifications in agro-ecosystems at field

and landscape scales are likely to benefit taxa using different resources, due to either high mobility or short reproductive time (Jennings & Pocock, 2009). However, fence density increase in agricultural landscapes not only increases total uncropped areas but also enhances the supply of additional resources, such as shelter and alternative prey and host (Thies & Tschardtke, 1999; Bianchi *et al.*, 2006). Furthermore, fencerow networks extend across landscapes comprising different soil types and land uses, thus joining and dividing contrasting habitat conditions (Poggio *et al.*, 2010). These linear habitat networks comprise wider ranges of environmental heterogeneity than cropped fields. Hence, fencerow networks function as corridors, offering habitat and refuge for many species, and serving as connectors (Burel *et al.*, 1998; Marshall & Moonen, 2002).

Natural enemies with large body sizes, mostly carabid beetles, are more sensitive to landscape heterogeneity decrease. This would be associated with characteristics of larger body size species, such as greater resource requirements (Jennings & Pocock, 2009), slow reproduction and extended home ranges (Honek *et al.*, 2007; Williams *et al.*, 2010). Burel *et al.* (1998) found small size species to be adapted to farming, which replaced large size species usually prevailing in stable habitats. Similar trends were observed in large size carabids in Pampean farmlands. This finding suggests that large size arthropods appear to be comparatively more tolerant to pesticide application or have greater dispersal abilities than small size arthropods (Schweiger *et al.*, 2005).

Concluding remarks

Arthropod diversity in agricultural mosaics of the Rolling Pampa concentrates on spontaneous vegetation along fencerows, without evident temporal changing patterns (Molina *et al.*, 2014). These results contradict the expected movement from highly productive areas (crop fields) towards those with low productivity (field margins; Oksanen, 1990). Our results suggest that fencerows function as a barrier effectively impeding or delaying herbivore movement into nearby crops. This capability depends on the structural complexity of guilds that result from landscape heterogeneity. Natural enemies in fencerows regulate a wide range of herbivore populations. Hence, most potential insect pests are controlled without reaching outbreak levels within crops (packing effect). Furthermore, landscape heterogeneity increase is mostly driven by fencerow density. This enhances the abundance of large size natural enemies, even within crop fields, where arthropods are usually affected by agricultural practices.

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traits predict bee species responses to environmental disturbances. *Biological Conservation*, **143**, 2280–2291.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1 Mean abundance of the 75 arthropod morpho-species sampled in the study area in fences and field interior. The abundance arthropod samples (i.e. single samples collected from each transect on a specific sampling date) were averaged for each transect over repeated samples taken at different times.