Effect of land use intensification on specialization in plant–floral visitor interaction networks in the Pampas of Argentina

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ABSTRACT

Land use intensification reduces natural areas and alters landscape heterogeneity diminishing species richness and changing ecosystem functionality. The analysis of interaction networks is a useful tool for estimating the degree of change experienced by ecosystems. Here, plant–floral visitor networks from fragments of grassland restored by agricultural activities discontinued over a long time were compared with networks from agriculturalized fragments nearby. The hypothesis evaluated was that land use intensification changes the structure of the original networks by modifying species richness and the network degree of specialization. The study was carried out at three sites located over a 700 km transect across the provinces of Buenos Aires and La Pampa, Argentina. At each site, four fragments were selected (two restored and two agricultural). Five monthly samplings were taken between November and March along three consecutive years. Entomophilous plants and their floral visitors were identified and all plant–floral visitor interactions were recorded. With these data, richness of plants and visitors were calculated, interaction networks were constructed and the degree of specialization was calculated for each network. Land use intensification caused changes in the community composition and degree of specialization. When cropping was the predominant farming enterprise, richness of floral visitors and plants decreased as compared to restored fragments. When cattle production was the predominant land use, richness of floral visitors remained stable. However, at one of the sites plants richness was 48% higher in the grazed fragments than in those restored. In the agricultural fragments, the abundance of units of floral attraction due to exotic plants increased, but the visitation rates were the same as in the restored fragments. The networks in the agricultural fragments were more generalist than in restored fragments, in agreement with previous studies on the effect of land use intensification on natural systems.

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1. Introduction

Land use intensification is one of the disturbances that causes the greatest changes in ecosystems (Ellis et al., 2010), affecting biodiversity at a global scale (Tscharntke et al., 2005). This intensification reduces natural areas and alters landscape heterogeneity, thus diminishing species richness and changing ecosystem functionality (Tscharntke et al., 2005; Steffan-Dewenter and Westphal, 2008). Locally, land use intensification increases the use of fertilizers and pesticides, which leads to death of pollinators and/or reduction of floral resources and nesting sites (Tscharntke et al., 2005). Moreover, at landscape scale, land use intensification generates more homogeneous landscapes (Tscharntke et al., 2005). Ecosystem services are a set of activities and functions that are useful to human beings (Dobson et al., 2006; Mace et al., 2012) and many of these services, such as climate regulation, air purification and pollination of crops, are essential for humans' survival (Kremen, 2005). The estimation of ecosystem services, pollination among others, is an issue of fundamental importance in studies related to ecosystem maintenance (Constanza et al., 1997; Allsopp et al., 2008; Dobson et al., 2006; Garibaldi et al., 2011).

Most studies on the relationship between diversity and ecosystem function have focused on the role of species richness, but ecosystem function also depends on identities, densities and biomass of the populations that constitute a community, and on interactions between populations (Kremen, 2005). When studying species richness or particular interactions, it is assumed that these interactions are homogeneously distributed among the species that make up the ecosystem. However, actual interactions occur heterogeneously and form complex networks linking organisms in the ecosystem (Vázquez et al., 2009). Interaction networks are

graphic representations of biological systems that make it possible to interpret the structure of communities (Bascompte, 2009), and their study is of increasing interest in current literature (Ings et al., 2009). Such studies are aimed at understanding the structure of plant–pollinator networks (Bascompte and Jordano, 2007; Burgos et al., 2007; Alarcón et al., 2008; Vázquez et al., 2009; Eklöf et al., 2013), the effect exerted by habitat degradation (Vázquez and Simberloff, 2003; Valladares et al., 2006; Cagnolo et al., 2009; Tylianakis et al., 2010; Devoto et al., 2012; Ferreira et al., 2013) and/or the impact of introduced species (Memmott and Waser, 2002; Aizen et al., 2008; Padrón et al., 2009). Studies on habitat degradation estimate the loss of species richness (Mace et al., 2012), and in some cases, describe changes in the functionality of the system due to human impact (Blüthgen, 2010; and citations therein). Knowledge about the way in which these changes might affect the feeding behaviour of species in a community is scarce (Aizen et al., 2008).

Interaction networks permit to evaluate biological aspects, such as the state of conservation of an ecosystem (Memmott, 1999; Vázquez and Simberloff, 2002, 2003; Memmott et al., 2004; Bascompte and Jordano, 2007). Additionally, functional changes in ecosystems can be estimated and thus, processes of habitat degradation can be better understood (Macfadyen et al., 2009). Interaction networks may be qualitative when formed from data on the presence–absence of interactions, or quantitative when the presence of an interaction is recorded with the frequency of visits, quantity of pollen grains transported by a floral visitor, etc. Analysis of networks makes it possible to calculate indexes obtained at different sites and/or in different years that can be compared among networks (Bascompte and Jordano, 2007). Although indexes calculated from qualitative networks may be influenced by the size of the network (Blüthgen, 2010), those obtained from quantitative data allow to evaluate networks properties regardless of their size (Blüthgen et al., 2006; Tylianakis et al., 2007).

Direct effect of agriculture on habitat degradation has been evaluated (Cagnolo et al., 2009; Tylianakis et al., 2007), as well as cattle production as a cause of changes in ecosystem biodiversity and interaction networks (Vázquez and Simberloff, 2003). An increase in the use of agricultural technology and agrochemicals leads to a decrease in ecosystem biodiversity (Steffan-Dewenter and Westphal, 2008; see Medan et al., 2011 for the Pampean region). Cattle ranching may also produce different effects, sometimes causing an increase in the ecosystem biodiversity (Chaneton et al., 2002).

The degree of specialization of the system is a measurement derived from the analysis of interaction networks that could provide information about the conservation status of a community (H$_2'$, Blüthgen et al., 2006). This index permits to estimate the degree of specialization from data on the frequency of visits to flowers (Schleuning et al., 2012). Floral visitors in a community may visit many flowers, but if the visits do not take place homogeneously (e.g. if most visits are made to a reduced group of flower species), those visitors will show specialist behaviour. This heterogeneous distribution of visits will create specialization in the system, with some plants having many visits and others only a few (Blüthgen et al., 2006; Blüthgen, 2010; Blüthgen and Klein, 2011). The H$_2'$ index was recently used in a grassland system to measure changes in the degree of specialization of a community of plants and their floral visitors under different intensities of land use (Weiner et al., 2011). However, it is still unknown to what extent anthropic disturbances modify the degree of specialization in ecosystems.

Grassland cover is one of the most extensive vegetation types on the planet, with an estimated coverage of nearly a quarter of the earth's surface (39 million km^2) (Bilenca and Miñarro, 2004). Grasslands are dominated by anemophilous plant species of the Poaceae family, but they also include entomophilous species. These systems offer numerous goods (e.g. meat, milk, leather, and cereals) and services (e.g. maintenance of atmospheric gases through CO_2 sequestration). The Pampas region has different climates and land use regimes, as well as diverse degrees of landscape heterogeneity (Burkart et al., 2005). In the Pampas region, original areas of grassland are almost nonexistent (Bilenca and Miñarro, 2004). The transformation of Pampas grassland caused by land use intensification received considerable attention in recent years (Medan et al., 2011). However, there is insufficient knowledge about how specialization in plant–floral visitors interaction (estimated as the way in which interactions are distributed in a community) can change at community level and how land use intensification modulates the process. Finally, we deemed it necessary to evaluate how grassland ecosystems were changing due to land use intensification.

In our study, the hypothesis that land use intensification would change the structure of the original plant–floral visitor networks was evaluated. Plant–floral-visitor networks of grassland fragments in the Pampas of Argentina were studied, placing emphasis on the attributes of the plant–floral visitor networks related to the magnitude and stability of pollination. These grassland fragments showed different levels of landscape heterogeneity. Those that had never been disturbed, or that have recovered after a long time without any agricultural activities, (hereafter called restored fragments), were compared with networks of nearby fragments currently used for some kind of agricultural activity (cropping and/or cattle production, hereafter called agricultural fragments). We expect to find that: (a) cropping reduces species richness creating homogeneous habitats, with an inherent decrease in the size of the network; (b) cattle production creates patches in the grassland matrix where entomophilous plants are abundant, creating microhabitats with greater resources for floral visitors, which at the same time would increase the size of the network; and (c) both cropping and cattle production modify ecosystem functionality, causing a decline in the rate of visitations and in the degree of specialization of the interaction networks. Moreover, it is possible that all previous effects be modulated by landscape heterogeneity. In order to account for this potential factor, landscape heterogeneity was measured and included in the analysis.

2. Material and methods

2.1. Study sites

The study was carried out at three sites along a 700-km-long transect located at 36°S in the provinces of Buenos Aires and La Pampa, Argentina (Fig. 1). The site to the extreme east was in Estancia Las Chilcas (Pila, Prov. Buenos Aires; hereafter referred to as 'LC'). This site is located in a subregion of the Pampas known as the Flooding Pampas. It has a humid temperate climate, with mean annual temperatures of 14.8 °C. The annual precipitation ranges between 850 and 900 mm (Perelman et al., 2001). The landscape is characterized by its extremely flat topography and the vegetation is a complex mosaic of herbaceous plant communities devoid of trees (Chaneton et al., 2002). The intermediate site was in Estancia San Claudio (Carlos Casares, Prov. Buenos Aires; hereafter 'SC'). This site is located in the Pampas subregion known as Inland Pampas. The climate is subhumid, averaging 1022 mm of annual rainfall during the last 25 years and with mean annual temperature of 15.8 °C. The landscape is a mosaic of wooded areas, cultivated land, planted pastures and seminatural grassland used for grazing (Tognetti et al., 2010). Lastly, the site to the extreme west end of the transect was located in Estancia Anquilóo (Toay, Prov. de La Pampa; hereafter 'AN'). This site is located in a transition zone between the Pampean grassland and the Espinal region, characterized by woodland dominated by "Caldén" (Prosopis caldenia) with a perennial
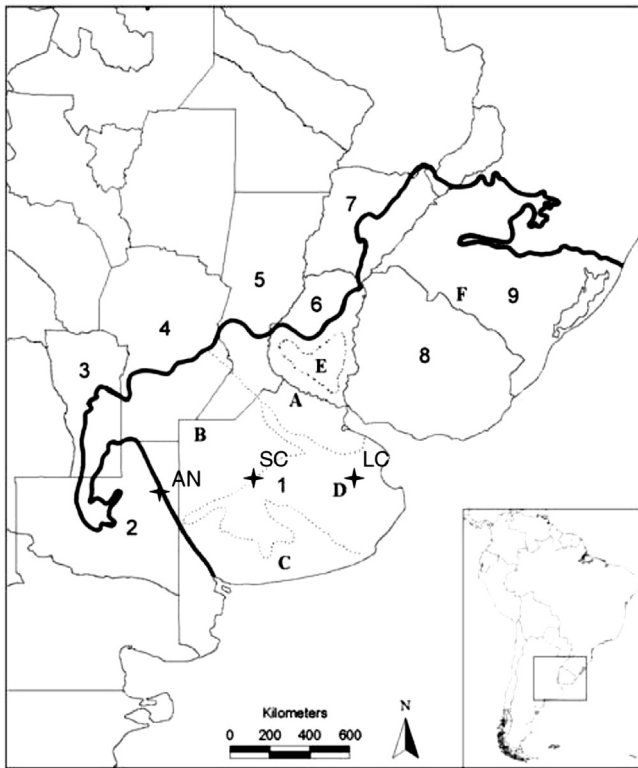
Fig. 1. Location of the sampling sites (LC: Las Chilcas, SC: San Claudio, and AN: Anquilóo) within the grasslands of Río de la Plata (the area surrounded by a thick line). The subdivisions of the grassland are shown with dotted lines and labelled with capital letters; the political limits are shown with continuous lines and labelled with numbers. A—Rolling Pampas; B—Inland Pampa; C—Southern Pampas; D—Flooding Pampas; E—Mesopotamic Pampas; F—Northern Campos. 1–7 Argentine provinces: (1) Buenos Aires, (2) La Pampa, (3) San Luis, (4) Córdoba, (5) Santa Fe, (6) Entre Ríos, (7) Corrientes, (8) Uruguay and (9) Brazil (state of Rio Grande do Sul) (modified from Medan et al., 2011).

grass understory (González-Roglich et al., 2012). The climate is dry-temperate, with a mean annual temperature of 15.5 °C, the annual precipitation ranging between 500 and 600 mm (Cano, 1998). The three sites represent three phytogeographic districts of the Pampas region (Burkart et al., 2005) (Fig. 1).

The predominant land use varied among sites as a function of precipitation and soil types. In LC, extensive cattle production on seminatural pastures is predominant and no insecticides or farm machinery were used during this study. The main entomophilous crop found in our plots was bird's-foot trefoil (*Lotus tenuis*). In SC, cropping is predominant in a mixed farming system and there is frequent use of herbicides and pesticides in the agricultural fragments. The main crops found in our plots were soybean (*Glycine max*), corn (*Zea mays*), and, less frequently, alfalfa (*Medicago sativa*) and sunflower (*Helianthus annuus*). Lastly, production in AN is mixed farming with a predominance of extensive cattle production and controlled grazing. Here, the agricultural fragments were sown with alfalfa (*M. sativa*) and weeping lovegrass (*Eragrostis curvula*) as forage. The use of insecticides and farm machinery was infrequent in AN during the three sampling years (each activity was carried out only once along the whole study). In LC the stocking rate was 75% of the carrying capacity, whereas in AN, it was nearly 100%.

In LC and SC, restored fragments were enclosures with permanent fences which had not been cultivated or grazed for the last 20 years (SC) or for approximately the last 3 years (LC). In AN, restored fragments were sites where cattle had been absent in the last 30 years from September until April, the time of year when sampling was carried out. In these fragments, farm managers had intentionally conserved the woody elements of the vegetation, including

many entomophilous species (*P. caldenia*, *Condalia microphylla* and *Geoffroea decorticans*, among others), although trampling by cattle may have affected the entomophilous herbaceous plants. It is important to emphasize that woodland clearance has traditionally been the greatest modification undertaken by human beings in this region, thus, making access for cattle easier and obtaining larger grazing areas (González-Roglich et al., 2012).

At each study site, four fragments of one hectare were selected, two restored and two agricultural (except for LC where there was only one restored fragment, see "Sampling limitations" below). At each study site the restored and agricultural fragments were at least 500 m apart in order to guarantee their independence. Unlike the cattle production sites (LC and AN), the field margins in SC (4% of total area) are included in the cropping areas as they are part of the agroecosystem and are generally considered to be important biodiversity reservoirs (Olson and Wäckers, 2007; Torretta and Poggio, 2013).

The use of two replicates of each treatment at each site (i.e. two pairs of restored and agricultural fragments), and the repeated sampling of these same fragments along several seasons (temporal replicates), was firstly aimed at increasing the power of the analysis. Second, it allowed the detection of interannual fluctuations of the populations of floral visitors (Arroyo et al., 1985; Herrera, 1988) to verify possible changes in the topology of the interaction networks (Alarcón et al., 2008; Petanidou et al., 2008).

2.2. Floral visitor and vegetation surveys

At AN and SC sites, a monthly sampling of each fragment was performed during November, December, January, February and March, in three consecutive periods (2008–2009, 2009–2010 and 2010–2011) (total = 15 samplings per fragment). At LC site, samplings were carried out in 2009–2010 and 2010–2011, because at this site the restored area became first available in 2009 (total = 10 samplings per fragment). During each sampling, all entomophilous plants in flower were identified and the floral visitors found feeding on flowers were caught. The plants were collected and dried for identification in the laboratory, and they were also classified according to their geographical origin (natives and exotics). Floral visitors were caught with a net, placed in a killing jar, mounted with entomological pins and identified in the laboratory to the lowest taxonomic level possible. Individuals were grouped into morphospecies when they could not be identified to species level. All insects found feeding on a unit of floral attraction (hereafter UFA), i.e. individual flowers (in most cases) or inflorescences (for species of Asteraceae, Dipsacaceae, Apiaceae, Fabaceae, Rubiaceae, Brassicaceae and Lamiaceae) were considered as floral visitors. Sampling effort was held constant across fragments, sites and years (2 h/fragment/sampling; 300 h of capture in total).

Fifty-metre-long transects were placed randomly in each fragment to estimate the abundance of flowers and floral visitors during the 2009–2010 and 2010–2011 periods (for a similar approach see Memmott, 1999). Each transect was sampled twice: the first time to count the UFAs found in a 2 m wide strip (1 m on either side of the transect), and the second time to catch all the floral visitors seen in the same strip, by walking at a pace of 10 m/min. This procedure was performed randomly in one transect before midday (from 10:00 to 12:00) and another in the afternoon (14:00 to 17:00). Quantitative interaction networks were generated from this data, representing the identity and frequency (frequency of interaction) of all links between the floral visitors and the plants visited. All interactions observed in the same fragment during the same sampling period were put together in one network. In total, 22 interaction networks were constructed: 11 from the fragments

sampled during 2009–2010 and another 11 from the 2010–2011 period.

2.3. Characterization of landscape

To measure landscape heterogeneity, we analyzed circular areas of landscape, each centred on one of the fragments sampled. We delineated circles, 300 m in diameter, on images obtained from Google Earth software (version 5.2, server: kh.google.com) (Google Earth, in press), within which we defined landscape units as polygonal patches. Each patch was assigned to one of the following 10 landscape types: edges of fences and roads, pastures, roads, crops, buildings, low-lying flooded areas, ponds or lagoons, restored areas, isolated trees and woodlands. The images obtained were analyzed using ArcGIS9.3 (ESRI, 2011). We calculated landscape heterogeneity for each image as the Shannon diversity index for landscape (SDI), which reports on the number and size of patches on an image. A SDI value was obtained for each fragment. These 11 SDI values were categorized (in ascending order: lower, middle, high and highest) using the frequency distribution that best fitted a normal distribution. In this way, we obtained a numeric variable and categorical variable (hereinafter used in the ANOVAs) of landscape heterogeneity (SDI). For each fragment, the SDI value remained constant across sampling years because landscape did not change during the study. Values of landscape heterogeneity were included in all analyses as a fixed factor to estimate this factor's influence on the other variables associated with pollination service. Moreover, the possible existence of spatial autocorrelation was evaluated by computing the Moran's I index using ArcGIS9.3 (ESRI, 2011). In general, comparing study fragments, patterns of spatial autocorrelation were not found (Supplementary material Table 1).

Previous studies that included estimations of landscape heterogeneity tended to use larger circles. However, those studies usually concentrated on measuring the responses of selected bumblebee species with large foraging areas (Elliott, 2009; Devoto et al., 2013). In our study sites, bumblebees were very scarce, and we did not focus on particular pollinator species but worked with the whole community of floral visitors, which usually consisted of relatively small-bodied insects. Flies, thought to have relatively small foraging areas (Rader et al., 2011), either dominated the visitor assemblages or contributed a substantial part thereof.

2.4. Statistical analyses

Because our study sites differed in composition of the insect fauna and flora, we used a nested sampling design, and we employed an index of interactions networks (H_2') that is not affected by the network composition.

In order to test predictions (a) and (b) (see Section 1) an ANOVA test was performed (ln-transformed data, when the data were not normally distributed) of the number of plant species and floral visitors recorded during the three sampling periods (2008–2009, 2009–2010 and 2010–2011), using "restored" and "agricultural" as treatments (random factor). Annual values corresponding to a given fragment were pooled, and mean values were reported by site and treatment. In the model, we considered the "site" (LC, SC and AN), the "period" of sampling and "landscape heterogeneity" (lower, mid, high and higher) as fixed factors. We conducted an a-posteriori Fisher LSD test to determine differences between treatment means. To represent the hierarchical structure of the data, the analysis considered the treatments nested within sites (site > treatment). Only plant species and floral visitors that showed at least one interaction in one fragment in one sampling period were taken into account. Moreover, ANOVAs tests were performed with the abundance data of UFAs of the entomophilous

exotic and native plant species using 'restored' and 'agricultural' as paired treatments from each site (ln-transformed data were compared in separate tests). The model used was similar to the previous one, with three fixed factors (site, period and landscape heterogeneity) and a random factor (treatment) nested within site (site > treatment). Also, we conducted an a posteriori Fisher LSD test to determine differences between treatment means.

The quantitative interaction networks were analyzed with the R statistical program (R Development Core Team, 2007). The degree of specialization (H_2', Blüthgen et al., 2006) was estimated for the 22 interaction networks. Also, the community visitation rate (hereafter CVR) was determined for the 11 fragments (Supplementary material Table 2) in both sampling periods, being

$$CVR = \sum \frac{VR_p}{N_p}$$

where VR_p is the rate of visits to an entomophilous plant p, and N_p is the number of species of entomophilous plants recorded in flower in that fragment and sampling period. The VR_p for a species of plant i was calculated as $VR_{pi} =$ total number of visits received by that species in that fragment and sampling period, divided by the total number of UFAs of that species counted in that fragment and sampling period. The CVR value was not divided by the sampling time in each individual case, since transects sampled in all fragments were equal in number ($n = 10$) and all transects had the same duration (5 min). The CVR values were always positive, and CVR values may be greater than one only if all recorded UFAs receive more than one visit per minute.

To test prediction (c) an ANOVA test was performed on the values of the degree of specialization (H_2') of the interaction networks and the CVR values (ln transformed), using 'restored' and 'agricultural' as treatments from each site. The model used was similar to those above, with three fixed factors (site, period and landscape heterogeneity) and a random factor (treatment) nested within sites (site > treatment). We conducted an a posteriori Fisher LSD test to determine differences between treatment means.

2.5. Sampling limitations

The work aimed at comparing 'restored' vs. 'agricultural' fragments. Since the few restored fragments available in the Pampas region happened to be located at a great distance, differences in climate, predominant land use and landscape heterogeneity among study sites were inevitable. To mitigate these undesired effects, an appropriate statistical treatment was applied. On the other hand, the existence of differences among study sites, although initially undesired, permitted to analyze the influence of additional factors (or combinations of factors, e.g. site, sampled period and landscape heterogeneity index) on pollination networks, beyond the specific effects of the condition 'restored' vs. 'agricultural'.

Fragments were chosen in which either disturbances associated with agricultural use had been discontinued for a long time, or a low-disturbance management had been consistently applied, with the consequence that the original structure and composition of the vegetation (and presumably the insect fauna) had been restored to some extent (SC, see Tognetti et al., 2010), or had only been partially lost (AN).

The restored fragments used in this study presented different states of conservation. In LC only one restored area was studied, due to the fact that no other landscape areas were found with which to adequately compare the agricultural fragments. This restored fragment had been an enclosure for more than three years, but as the perimeter fence was broken at the beginning of the study and had to be repaired, no sampling was taken in the first year. In SC the restored fragments used had been closed to agricultural activity for more than 20 years, whereas in AN, restored fragments
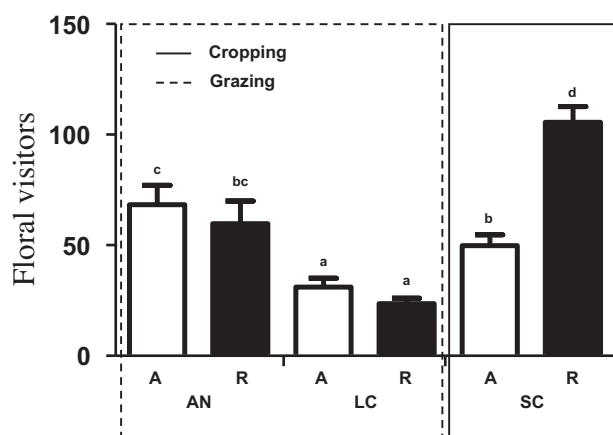
Fig. 2. Richness of floral visitors in grassland fragments under two treatments (R: restored and A: agricultural) at three sampling sites (AN, LC and SC) representative of two predominant land uses (cropping and grazing) in the Pampas region of Argentina. Data compiled from 3 sampling periods (2008–2009, 2009–2010 and 2010–2011). Mean values ± 1 standard error are shown. Different letters indicate significant differences between means ($p < 0.05$).

studied were temporary enclosures. These latter fragments were only used for cattle grazing during the autumn–winter period, so cattle were not present during the sampling period. Moreover, the difference between 'restored' and 'agricultural' fragments relates primarily to the presence, in the former, of woody plants, which are a major portion of the original plant community in the transition zone between Pampas and Espinal regions.

3. Results

In total, 584 species or morphospecies of floral visitors (115 in LC, 312 in SC and 309 in AN) and 141 plant species were recorded (42 in LC, 71 in SC and 57 in AN) (see Supplementary material, Appendices A–C). In LC, the assemblage of floral visitors was dominated by Diptera (38%) and Hymenoptera (31%), followed by Coleoptera (13%) and Lepidoptera (12%). Heteroptera, Blattaria and Orthoptera were represented by <6% of total richness. In SC and AN the assemblage of floral visitors was dominated by Hymenoptera (43% and 63% of all species, respectively), followed by Diptera (33% and 22%), Lepidoptera (10% and 7%) and Coleoptera (9% and 6%). Heteroptera, Blattaria, Neuroptera, Homoptera and Orthoptera were represented by <5% of all species. Among plants, the most visited and diverse plant family was Asteraceae (44% in LC, 27% in SC and 42% in AN). Other important and diverse families were Apiaceae (9% in LC and 11% in SC) and Fabaceae (14% in SC and 10% in AN).

When cropping was the predominant farm activity the restored fragments were twice as rich in species of floral visitors as the agricultural fragments (SC, Fig. 2); however, in predominantly cattle producing areas (LC and AN), the richness of floral visitors was not significantly different between restored and agricultural fragments (Fig. 2; Table 1). Plant species richness was not significantly different between types of fragment in AN (Table 2), it was 48% higher in the fragments with cattle than in the restored fragment in LC (Fig. 3), and it was 38% higher in the restored fragments than in the agricultural fragments in SC (Fig. 3; Table 2). The abundance of UFAs of exotic plants was significantly higher in the agricultural fragments compared to the restored fragment at all sites (Fig. 4; Table 3), but they did not differ for native plants (Supplementary material Table 3).

The degree of specialization of the community (H_2') was significantly greater in the restored fragments than in those agricultural (Fig. 5; Table 4). The community visitation rate (CVR) did not

Table 1
Values of ANOVA of the floral visitors richness (ln-transformed) found for three sampling periods (period = 2008–2009, 2009–2010 and 2010–2011) in agricultural and restored fragments (treatment = A and R) located at three sites representative of the Pampas (site = LC, SC and AN) with different landscape heterogeneity (SDI = low, medium, high and higher).

ANOVA (floral visitors)	N = 30 (Df)	F	Values p	Error
Model	10	11.4	**0.0001**	
Site	2	2.91	0.1984	(Site > treatment)
Site > treatment	3	11	**0.0002**	
Period	2	6.68	**0.0064**	
SDI	2	1.45	0.2587	
Site × SDI	1	0.73	0.4023	

ANOVA of three fixed factors (site, landscape heterogeneity, period) and one random factor (treatment) nested within sites (site > treatment). p-Values in bold indicate the relationships with significant statistical differences.

Table 2
Values of ANOVA of the plants richness (ln-transformed) found for three sampling periods (period = 2008–2009, 2009–2010 and 2010–2011) in agricultural and restored fragments (treatment = A and R) located at three sites representative of the Pampas (site = LC, SC and AN) with different landscape heterogeneity (SDI = low, medium, high and higher).

ANOVA (plants)	N = 30 (Df)	F	Values p	Error
Model	10	2.81	**0.0022**	
Site	2	0.73	0.5527	(Site > treatment)
Site > treatment	3	2.85	**0.0217**	
Period	2	5.36	**0.0037**	
SDI	2	0.93	0.2878	
Site × SDI	1	9.55	**0.006**	

ANOVA of three fixed factors (site, landscape heterogeneity, period) and one random factor (treatment) nested within sites (site > treatment). p-Values in bold indicate the relationships with significant statistical differences.
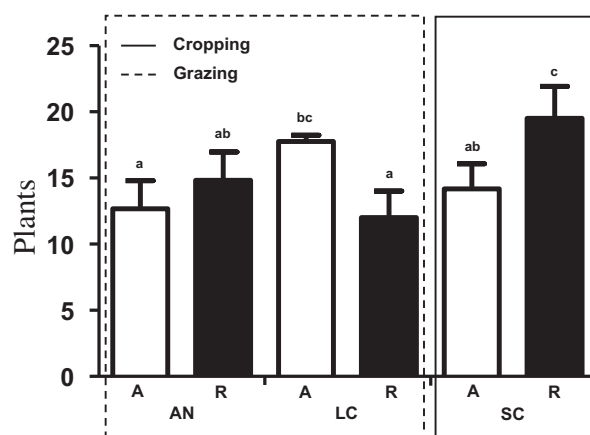

Fig. 3. Richness of plants in grassland fragments under two treatments (R: restored and A: agricultural) at three sampling sites (AN, LC and SC) representative of two predominant land uses (cropping and grazing) in the Pampas region of Argentina. Data compiled from three sampling periods (2008–2009, 2009–2010 and 2010–2011). Mean values ± 1 standard error are shown. Different letters indicate significant differences between means ($p < 0.05$).

significantly differ between treatments (Supplementary material Table 4).

Landscape heterogeneity did not affect floral visitor richness (Table 1), but it did affect plant richness (Table 2). Landscape heterogeneity did not affect the abundance of native plants (Supplementary material Table 3), but it did affect the abundance of exotic plants (Table 3). By comparing the effect of landscape heterogeneity on the functionality of the system, we did not find any significant effects on CVR (Supplementary material Table 4). However, the specialization index (H_2') of the interaction network was affected by landscape heterogeneity (Table 4).
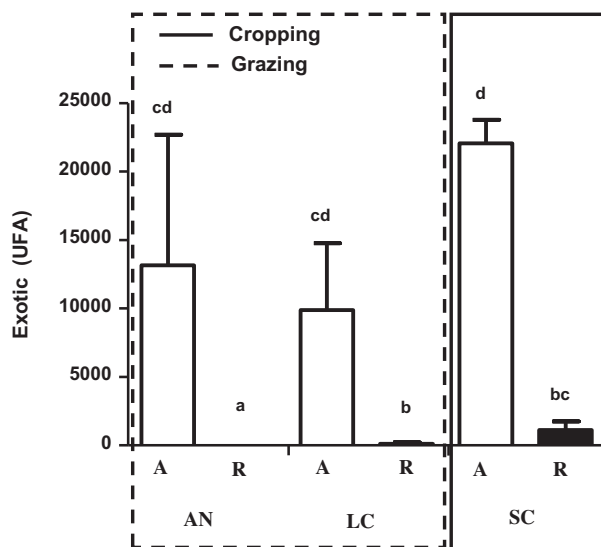
Fig. 4. Mean number + 1 standard error of units of floral attraction (UFA) of entomophilous exotic plants in restored (R) and agricultural (A) fragments, representative of two predominant land uses (cropping and grazing) in the Pampas region of Argentina. Each treatment (e.g. A in AN) unites the data from two sampling periods (2009–2010 and 2010–2011). AN–R abundance is not significant enough (<6) to be viewed in the graph. Different letters indicate significant differences between means ($p < 0.05$).

Table 3

Values of ANOVA of the abundance of units floral attraction (UFA) of exotic plant species (in-transformed) found for two sampling periods (period = 2009–2010 and 2010–2011) in agricultural and restored fragments (treatment = A and R) located at three sites representative of the Pampas (site = LC, SC and AN) with different landscape heterogeneity (SDI = low, medium, high and higher).

ANOVA (exotic plants)	$N = 22$ (Df)	F	Values p	Error
Model	9	14.32	**0.0001**	
Site	2	0.65	0.5825	(Site > treatment)
Site > treatment	3	26.84	**0.0001**	
Period	1	1.97	0.1863	
SDI	2	5.15	**0.00242**	
Site × SDI	1	1.18	0.2978	

ANOVA of three fixed factors (site, landscape heterogeneity, period) and one random factor (treatment) nested within sites (site > treatment). p-Values in bold indicate the relationships with significant statistical differences.
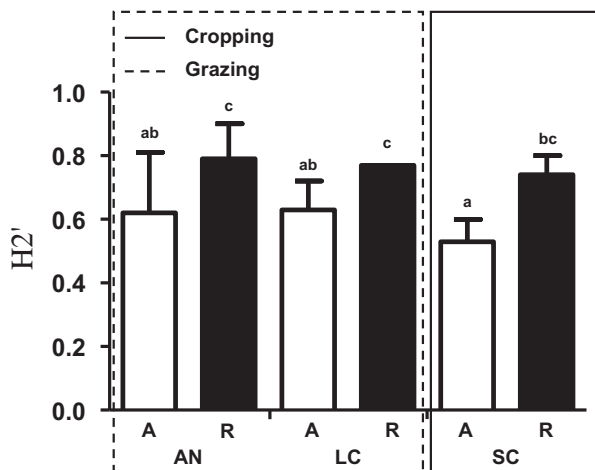

Fig. 5. Mean values + 1 standard error of the degree of specialization (H_2') of the plant–floral visitor interaction networks, of restored (R) and agricultural fragments (A), representative of two predominant land uses (cropping and grazing) in the Pampas region of Argentina. Each treatment (e.g. A in AN) unites the data of two sampling periods (2009–2010 and 2010–2011). Different letters indicate significant differences between means ($p < 0.05$).

Table 4

Values of ANOVA of the degree of specialization (ln-transformed) found for two sampling periods (period = 2009–2010 and 2010–2011) in agricultural and restored fragments (treatment = A and R) located at three sites representative of the Pampas (site = LC, SC and AN) with different landscape heterogeneity (SDI = low, medium, high and higher).

ANOVA (H_2')	$N = 20$ (Df)	F	Values p	Error
Model	9	11.96	**0.0003**	
Site	2	0.11	0.9023	(Site > treatment)
Site > treatment	3	9.12	**0.0033**	
Period	1	41.54	**0.0001**	
SDI	2	16.24	**0.0007**	
Site × SDI	1	4.32	0.0643	

ANOVA of three fixed factors (site, landscape heterogeneity, period) and one random factor (treatment) nested within sites (site > treatment). p-Values in bold indicate the relationships with significant statistical differences.

4. Discussion

Our results show that in the Pampas region of Argentina habitats where agriculture or cattle production have been suppressed (restored fragments) differ in several respects from those currently under agricultural use: abundance of exotic entomophilous plants, richness of floral visitors and plants, and degree of specialization of the community.

4.1. The species richness of floral visitors and plants is modified in agricultural sites

Although the three sites showed some differences in floral visitors' guilds, all guilds consisted mainly of Hymenoptera and Diptera. Assemblages of similar compositions were found in other sites of the Pampas region (Sabatino et al., 2010; Torretta and Poggio, 2013). The difference in the composition of floral visitors between sampling sites could be related to biogeographical conditions. Our study transect represents a humidity gradient, humidity being maximal at LC site and decreasing westwards, with AN as the driest site. LC was the richest in Diptera and AN, the richest in Hymenoptera. Hymenoptera often tend to dominate insect communities in dry climates, while flies are more common in humid climates (Devoto et al., 2005).

Agrochemicals that decrease biodiversity are commonly used in intensive agriculture (Altieri, 1999). The restored fragments act as protection where insects can find nesting sites or greater food resources (Lentini et al., 2012). Decrease in availability of natural habitats at landscape scale can isolate populations and affect the structure of biological communities (Ferreira et al., 2013). Field margins sustain populations of entomophilous plants and their floral visitors, carrying out a similar function in the agricultural fragments (Olson and Wäckers, 2007; Lentini et al., 2012; Torretta and Poggio, 2013). Here, when delimiting the crop fragments, the inclusion of field margins favoured an increase in entomophilous plant species.

In our study, the abundance of exotic flowers in agricultural fragments was always higher than in the restored ones. Exotic plants produce large quantities of food resources, they are visited by numerous floral visitors and are thus considered supergeneralists (Aizen et al., 2008). At sites with cattle production, a greater abundance of exotic entomophilous plants in the agricultural fragments may have increased species richness of floral visitors, which can explain the lack of significant differences with the restored fragments. On the contrary, at sites with cropping, high plant diversity could increase pollinators diversity (Fründ et al., 2010). However, in sites with cropping, the use of insecticides is expected to cause a decrease in the species richness of floral visitors. Although in this study land use intensification was not found to significantly increase richness of floral visitors, there are examples in which

species richness increases in disturbed areas, if the disturbance is related to an increase in landscape heterogeneity (Quintero et al., 2010). However, in our study we did not find any effect of landscape heterogeneity on richness of floral visitors.

Under cattle production, richness of entomophilous plants was differentially affected among sites, which may reflect possible differences in grazing intensity among sites. No significant differences in richness of entomophilous plants and floral visitors were detected in the restored fragments under the higher grazing intensity (AN), but in places with lower grazing intensity (LC), the grazed fragments showed greater species richness of entomophilous plants. The infrequent use of herbicides and insecticides in cattle production sites might favour the presence of exotic entomophilous plants and floral visitors. Additionally, it is known that grazing favours the introduction of exotic plant species in grassland ecosystems leading to an increase in species richness (Chaneton et al., 2002). This might explain why under cattle production, agricultural fragments did not differ from restored fragments in richness of floral visitors.

LC site presented greater richness of entomophilous plant species in the agricultural fragments than in the restored area. Moderate grazing may produce patches that are of high quality for the establishment of entomophilous plants, due to disturbance from trampling and/or redistribution of organic matter from cattle dung, as suggested by Chaneton et al. (2002). Simultaneously, in the restored fragment (where cattle does not graze) vegetative growth of grasses dominates over entomophilous plants (Chaneton et al., 2002). On the contrary in AN, richness of entomophilous plants and floral visitors did not show any significant differences between the restored and agricultural fragments. At this site, floral visitors might nest in restored fragments and then visit agricultural fragments, where food resources are greater (mainly from exotic plants) (Klein et al., 2003; Westphal et al., 2003; Le Féon et al., 2013).

4.2. Land use intensification modifies ecosystem functionality

In this study no significant differences were detected between restored and agricultural fragments in the frequency of visits to plants. Interactions occurred with the same frequency, but in agricultural fragments most visits were made by a few species of floral visitors (low diversity of interaction). However, the degree of specialization of the community (H_2') was greater in the restored (i.e. better conserved) fragments. A possible explanation could be the greater diversity of flower visitors found in restored fragments. Fründ et al. (2010) suggested that specialization (estimated with H_2') could be related to the diversity of floral visitors, ruling out diversity of plant community as a cause. The rise in the diversity of floral visitors produces an increase in the degree of dietary specialization (Fründ et al., 2010). Another possible mechanism that explains the changes in specialization could be related to the abundance of exotic plants in agricultural fragments. Aizen et al. (2008) found that exotic species did not alter the connectivity in plant–floral visitor interaction networks, but in systems invaded by exotic plants, plant–flower visitor links are transferred from generalist native species to super-generalist exotic species. In line with Aizen et al. (2008), we found that while interactions occur with equal frequency in restored and agricultural fragments, they are differentially distributed between the plants that make up the community. In agricultural sites, floral visitors distributed their visits more homogeneously among flowering species, whereby the interaction networks in the agricultural fragments were more generalist than in the restored fragments.

Working in grasslands differing in intensity of land use, Weiner et al. (2011) failed to show significant differences in the degree of specialization in the community (H_2'). On the contrary, the restored fragments in our study showed a higher degree of specialization

than agricultural fragments, being the first record of a change in the distribution of interactions by floral visitors in a community as a consequence of land use intensification. A distribution of more heterogeneous resources would create more specialized trophic niches, leading to greater stability as the competition for resources decreases (Blüthgen, 2010; Blüthgen and Klein, 2011). Therefore, our results indicate that it is likely that restored fragments have greater stability and complementarity in resource use than agricultural fragments, which leads to an increase in specialization in the former. On the other hand, interaction networks might show a greater degree of specialization in fragments with a better conservation status due to the presence of a higher number of species that behave as specialists. The H_2' index might better relate to an index of selectivity of species (Marcelo Aizen, pers. comm.). In that case, species from the agricultural fragments would select a smaller number of species with which to interact, increasing the interspecific competition and at the same time the possibility of deposition of heterospecific pollen on the stigmas. In our study, landscape heterogeneity affected the degree of specialization and modelling results. We believe that landscape heterogeneity modulates our results, but at present no specific pattern can be discerned. In this respect our results are preliminary, and further studies are encouraged which should include a larger number of replications and a stronger gradient of landscape heterogeneity.

Exotic plants were common in agricultural fragments which, due to their great abundance, might be the main (or only) resource for floral visitors. At the same time, exotic plant species might modify the foraging behaviour of floral visitors and provoke a redistribution of the interactions, creating habitats that are more generalist, where the interactions are distributed more homogeneously among the plant species in the community (Memmott and Waser, 2002; Aizen et al., 2008). Then, abundance of units of floral attraction of exotic species might explain the variation in the specialization of the networks. This variation could also be attributed to the interaction between land use intensification and UFA abundance because the two factors are not independent in our study.

4.3. Conclusions

The results support the hypothesis that land use intensification changes the structure of the original plant–floral visitor networks, although our predictions were not equally fulfilled for plants, floral visitors and land use types (prediction a and b), or for all the indicators of the functionality (CVR and H_2') of the plant–pollinator system (prediction c). Landscape heterogeneity modulates the effects on plant richness, abundance of exotic plants and H_2' found in our study, but without a specific pattern.

Future studies should find out if the pollination service provided by floral visitors is affected by land use intensification (e.g. through the estimation of reproductive success of plant or pollen deposition on stigmas) and what degree of change in landscape heterogeneity is necessary to exert a change in the pollination service.

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.2014.02.017.

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