



The arable plant diversity of intensively managed farmland: Effects of field position and crop type at local and landscape scales

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ABSTRACT

Agro-ecosystem biodiversity is threatened by increasing spatial homogenisation of intensively managed farmland. Yet current understanding of patterns of arable plant diversity at various scales remains limited. We evaluated the extent to which species richness of arable plants in the Rolling Pampas of Argentina is determined by field position (fencerow, edge and centre) and crop type, at both field (local) and landscape scales. Plant richness was assessed in maize, soybean and wheat–soybean fields across four landscape types differing in spatial complexity, as defined by percentage area devoted to cropland. Species richness was hierarchically nested within landscape types, field positions and crop types. Landscape richness (γ -diversity, the cumulative number of species in a set of fields) was additively partitioned into two components, one for local richness (α -diversity, the mean number of species per field) and one denoting differences in species composition among fields (β -diversity, where $\beta = \gamma - \alpha$). Field position was the main determinant of landscape-scale plant richness. Overall, γ -diversity declined from fencerows, through field edges to field centres, but was unaffected by crop type. Spatial variation in species composition (β -diversity), rather than species packing within fields (α -diversity), accounted for most of the variation in arable γ -diversity. Higher β -diversity in field edges than in field centres suggested that propagule dispersal from fencerow vegetation may create a ‘mass effect’ onto certain crop types. Shifts in γ -diversity of major perennial life-forms (chamaephytes and phanerophytes) between field positions and crop types reflected the contrasting disturbance regimes affecting plant communities of fencerows and cultivated fields. Our results indicate that preserving coherent and extensive fencerow networks is essential to conserve farmland biodiversity. Moreover, maintaining landscape heterogeneity to support elevated β -diversities of arable plants requires cropping systems that promote crop diversity in both space and time.

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1. Introduction

The ecological functions that biodiversity provides to agriculture are threatened by ongoing homogenisation of intensively managed cropping systems. Historically, agricultural expansion created new environmental mosaics by fragmenting and converting original forests and grasslands into arable land. More recently, however, farmland homogenisation has been encouraged, as present cropping systems comprise just a few highly productive crops with narrow genetic backgrounds, which are grown under standardised management strategies (Evans, 1998).

Moreover, successful spread of invasive ‘weedy’ species has promoted the biological homogenisation of farmland floras at regional scales (McKinney and Lockwood, 1999). In this context, preserving and re-creating the habitat heterogeneity of farmland landscapes simplified by agricultural intensification appears to be a crucial step towards maintaining biodiversity and associated ecosystem services (Burel et al., 1998; Benton et al., 2003; Tschardt et al., 2005).

Spatial habitat heterogeneity is widely recognised as a key determinant of plant species diversity (Shmida and Wilson, 1985; Crawley and Haral, 2001). Several recent studies show that farmland heterogeneity modulates weed species richness at both local and landscape scales (Wagner et al., 2000; Gabriel et al., 2005, 2006; Roschewitz et al., 2005; Poggio et al., 2010). For instance, local plant richness (α -diversity) in wheat fields of northern Europe was mainly associated with landscape structure (i.e. perimeter–area ratio of cropland), and to a lesser extent with agronomic management (Gabriel et al., 2005). Moreover, spatial variation of plant

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species composition among crop fields (β -diversity) explained most variation in total arable plant richness at landscape scales (γ -diversity) in different agro-ecosystems (Gabriel et al., 2006; Poggio et al., 2010). On the other hand, both α - and β -diversities were found to be higher in crop edges than in field centres, a pattern attributed to the higher environmental heterogeneity of field edges (Wagner et al., 2000; Gabriel et al., 2006). Lastly, in the Pampas of Argentina, γ - and β -diversities of both fencerows and crop fields were positively related to landscape complexity, supporting the role of spatial heterogeneity in maintaining farmland plant biodiversity (Poggio et al., 2010).

In agro-ecosystems, environmental heterogeneity is partly created by the contrasting disturbance regimes affecting different zones of arable fields. Field centres are disturbed recurrently by cropping activities. Conversely, disturbance is much less frequent and intense in field margins associated with fence lines or hedgerows, which therefore represent more stable habitats for plant populations. Field edges, which may be seen as 'ecotones' or 'buffer zones' between field margins and centres, are assumed to receive the same management as the field centre, although they are also physically and biotically influenced by neighbouring, uncultivated linear habitats (Kovar, 1992; Le Cœur et al., 2002; Marshall and Moonen, 2002; Gabriel et al., 2006). Consequently, field position is expected to influence not only arable plant richness, but also the prevalence of various life-forms adapted to different disturbance levels. Further, at local scales, arable richness can be strongly affected by crop type and agronomic management. Crop species represent distinct biotic 'filters' to weed community structuring (Holt, 1995; Poggio, 2005; Poggio and Ghera, 2011). Tillage mode, fertilisation and herbicide application are widely recognised as major drivers of differences in plant composition and diversity among fields (Pyšek and Lepš, 1991; Zanin et al., 1997; Bärberi et al., 1997; de la Fuente et al., 1999; Hyvönen and Salonen, 2002; Poggio et al., 2004; Andreasen and Skovgaard, 2009). Importantly, crop type and field position may interact in determining arable plant diversity at both local and landscape scales. Yet, whether shifts in plant diversity between field positions depend on crop type remains poorly known.

In this study, we examine the extent to which the species richness of arable plants in agro-ecosystems of the Rolling Pampa, Argentina, is modulated by field position (fencerow, edge and centre) and crop type at field (local) and landscape scales. Given the environmental contrast between cropped fields and adjacent, non-cropped margins, we hypothesised that field position exerts a greater influence than the crop type on both α - and γ -diversity of arable plants. We predicted species richness to be higher at fencerows than at the interior of crop fields at both local (α) and landscape (γ) scales. In addition, we expected that plant perennial life-forms would be more responsive than short-lived plants to environmental differences among field positions. Plant species richness was assessed in maize, soybean, and wheat–soybean fields in four landscape types differing in spatial heterogeneity and percentage cropland area. Plant richness was then additively partitioned into α , β and γ components for fencerows, field edges, and field centres.

2. Methods

2.1. Study area

The study was carried out in the central Rolling Pampa region, which extends from 32° to 34°S and 60° to 61°W within the Buenos Aires province of eastern Argentina (Soriano, 1991). The study area comprised about 7000 km² of farmland in Pergamino, Ramallo, Rojas and Salto. 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). Soils are mainly Mollisols with a deep top horizon rich in organic matter. Topography is gently undulated and crossed by shallow streams (Soriano, 1991). The region has been extensively transformed to row-crop agriculture and cattle husbandry since the late 19th century (Viglizzo et al., 2001, 2004). The original vegetation corresponded to mesic tussock grasslands dominated by a species-rich mix of C₃ and C₄ grasses (Parodi, 1930, 1947; Lewis et al., 1985; Ghera and León, 1999; Burkart et al., 2011). Landscape alteration by human disturbances determined the introduction of many exotic plant species, which nowadays represent major components of the arable flora (Rapoport, 1996; Ghera and León, 1999; Poggio et al., 2004, 2010).

Within the study region, landscape heterogeneity varies gradually along a geomorphological gradient, involving changes in topographic relief, dominant soil type, and land-use patterns (Poggio et al., 2010). On the southwest of the region, highly productive Typic Argiudoll soils dominate on levelled topographic reliefs. Landscapes in this area comprise extensive, almost continuous croplands, with large fields averaging ca. 60 ha in size and small perimeter/area ratios. Towards the northeast, topography becomes gently undulated. Vertic Argiudoll soils with a higher clay content become increasingly common, and landscapes comprise a larger proportion of riparian and lowland habitats. In this part of the region, cropland areas are less extensive, fields are smaller, and networks of wire-fencerow become denser. Grazing paddocks and woodlots are also more common in these more heterogeneous landscapes (Poggio et al., 2010). Nevertheless, climatic conditions and agricultural practices are very similar throughout this region-wide gradient in landscape heterogeneity.

2.2. Crop management

Maize, the dominant summer crop for more than a century, has been rapidly displaced by soybean after the inception of herbicide-tolerant GM cultivars in 1996. Nowadays, soybean is the prevalent warm-season crop, being mostly sown at optimum dates in early November (ca. 75% of cropland; DPEBA, 2011). Soybean is also sown as a relay crop in mid December, immediately after the harvest of winter crops, mostly wheat, which has been the prevalent cool-season crop in this region since late 19th century. Relay soybean crops typically have lower yields due to the late sowing dates. Thus, the common crop sequence in the study area is maize, soybean and wheat–soybean relay crop. Where maize has been totally replaced by soybean, the crop sequence has been simplified to soybean–wheat/soybean, even though it is not unusual to find a few fields sown with soybean for several consecutive years.

Virtually all field crops are nowadays sown using no-till practices; ploughing has become very infrequent and almost exclusively used to grow maize (Satorre, 2001; Manuel-Navarrete et al., 2009). Soybean and maize crops differ markedly in their agronomic management. Maize are generally fertilised with nitrogen and phosphorus as urea and diammonium phosphate. Fertilisation of soybean crops, usually less widespread than in maize, is mainly based on phosphorous as monocalcium superphosphate, whereas relay soybean crops are rarely fertilised. Inoculation of soybean seeds, by using specific symbiotic rhizobia that fix atmospheric nitrogen, is a widespread practice in the study area. Sulphur fertilisation has increased in both crops during the last years. Herbicide application in soybean fields relies exclusively on glyphosate applications, while post-emergence applications of residual herbicides (e.g. atrazine and metolachlor) are commonly used in maize.

2.3. Vegetation sampling

Fields were surveyed during the summer of two consecutive years (January–February of 2003–2004 and 2004–2005). Main crops during this season are maize and soybean, the latter being sown at optimum date (early November) or as a relay crop after the harvest of wheat (mid December), hereafter referred as wheat–soybean crops. In each field, the number of vascular plant species was recorded for fencerows, edges and centres of fields (see Poggio et al., 2010, for details). The length of fencerow to be surveyed was determined using a species accumulation curve based on samples of increasing length according to a power of 2 series between 1 and 128 m. Fencerow surveys were thus performed along 1-m wide by 100-m long belt transects; this sample length included over 90% of species in the accumulation curve. Sampling transects were randomly located at the centre of one of the four field sides, avoiding field entrance and corners, ditches, areas shaded by trees, and any fencerow discontinuities. Fencerow vegetation was mainly herbaceous and woody plants such as small shrubs were only occasionally present. Field edges and centres can be regarded as different habitats because of their differing environmental conditions, especially with regard to soil compaction from vehicle transit along field edges and distance to the fence line. Field edges were surveyed along parallel strips located at 4 m from the fencerow, whereas field centres were surveyed beyond a 10 m distance from the fencerow. Plant surveys at field centres were restricted to areas having homogeneous crop cover; low-lying topographic positions were excluded. Sample stands fulfilled the following requirements (Mueller-Dombois and Ellenberg, 1974): (1) area was large enough to include most species belonging to the weed community (at least 25–100 m² for arable weed communities); (2) macroscopic habitat properties were uniform within the stand area; (3) plant cover was homogeneous. Field surveys were performed for at least 30 min to record a complete list of species within each cropped field.

Four landscape types were identified a posteriori through cluster analysis, based on the similarity of landscape elements surrounding surveyed fields (Table 1). Area (ha) and edge length (m) of three main land-cover types (cropland, pasture and riparian) were calculated within 2-km diameter circles centred in each field using a geographic information system (GIS; ArcView 3.2, ESRI 1999). Landscape heterogeneity was characterised for each circle by calculating the percentage areas of cropland, pasture and riparian habitat, the perimeter/area ratio for cropland (P/A_{cropland} , m ha⁻¹), and the overall habitat diversity (using Shannon's diversity index) (Gabriel et al., 2006; Roschewitz et al., 2005; Tschamtker et al., 2005). Hierarchical cluster analysis was carried out using the farthest neighbour (complete linkage) algorithm and Sørensen's (Bray–Curtis) quantitative index as a distance measure (PC-ORD 4.0; McCune and Mefford, 1999).

The study comprised surveys for 84 fields spread over three crop types nested within each of the four landscape types. Each landscape comprised similar numbers of fields of each crop type. Thus, landscape types A and C (see Table 1) comprised 7 fields of each crop, for a total of 21 fields per landscape; and landscapes B and D comprised 6 and 8 fields, for a total of 18 and 24 fields, respectively.

2.4. Additive partitioning of diversity

Landscape-scale richness (γ -diversity) was defined for each crop within a particular landscape type as the total number of plant species obtained by accumulating, without repetition, all the species recorded in each field position (fencerow, edge, centre). Local richness (α -diversity) was obtained by averaging the number of species found in samples of each field positions taken at a given crop type nested within a landscape type. Thus, α -diversity corresponded to the smallest spatial scale sampled in this study.

β -diversity represented the spatial variation among fields in the species composition recorded at a given position within each landscape type (e.g. among fencerows of maize fields within landscape A). β -diversity was calculated using the additive partitioning model of species diversity (Allan, 1975; Lande, 1996; Wagner et al., 2000), as follows:

$$\bar{\beta}_j = \frac{1}{n} \sum_{i=1}^{i=n} (\gamma_j - \alpha_{ji})$$

where $\bar{\beta}_j$ and γ_j are, respectively, the average β -diversity and γ -diversity of landscape type j , α_{ji} is the species richness of the field i from a total of n fields surveyed within landscape type j . The additive model provides a simple, intuitive measure of spatial variation in species composition, which is easy to apply and communicate in a management context (Veech et al., 2002; Gering et al., 2003; Anderson et al., 2011). Similar to α -diversity, when calculated additively, β -diversity represents the average number of species within a landscape (or a set of surveyed fields), and can be interpreted as the mean number of species that, being absent from a single, random sample, would be found in further samples taken from the same landscape pool (i.e. γ -diversity). Thus, for a set of random samples having a particular mean α -diversity, large values of additive β -diversity indicate that species composition changes among samples, whereas small β values reflect a spatially homogeneous plant composition.

2.5. Classification of plant species

Plant species were classified according to their origin into natives and exotics. Only those species originally belonging to the Pampean Phytogeographic District, which comprises the whole study region, were considered as native (Parodi, 1930). Cosmopolitan species were included with the exotics. Plant species were also classified according to Raunkiaer's life-form scheme, which is based on the position of perpetuating buds, a character assumed to reflect the predominant ecological conditions, including length of the favourable growing season and disturbance levels (Raunkiaer, 1934; Crawley, 1997). In Raunkiaer's scheme, therophytes are annual or ephemeral plants that complete their life cycle rapidly when conditions are favourable and overcome unfavourable periods as seeds. Hemicryptophytes are plants with perennating buds located at ground level and aerial shoots that die back during the unfavourable season. Geophytes are plants whose perennating buds are hidden below ground in various organs, such as rhizomes and bulbs. Chamaephytes have their perennating buds located above the ground level but below 25 cm height. Phanerophytes are usually woody perennials that have buds or growth apices on aerial shoots reaching above 25 cm height. For the purpose of this study, chamaephytes and phanerophytes were classified as hemicryptophytes when they occurred within soybean fields, as during the harvest of this crop all weedy plants are cut at ground level and may re-sprout from buds placed close to the soil surface (personal observation). However, phanerophytes and chamaephytes occurring in maize fields were not reclassified, since maize harvest is performed at ear height (ca. 1 m).

2.6. Statistical analyses

Patterns in species diversity were analysed using linear mixed effect models (Pinheiro and Bates, 2000). Firstly, the effects of the crop type (maize, soybean, and wheat–soybean) and the field position (fence, edge, and centre) on γ -diversity were tested by grouping both variables within each landscape type. Thus, at the landscape scale we tested the following linear model,

Table 1
Description of the four landscape types identified in the study region. Values are the mean percentage of the landscape area occupied by cropland, pastureland and riparian habitats, and the perimeter/area ratio for cropland (P/A_{cropland} , m ha^{-1}). Ranges below each value are the 95% confidence intervals.

Landscape type		A_{cropland}	A_{pasture}	A_{riparian}	P/A_{cropland}
A	Mixed cropland and pastureland mosaic	50.6	41.7	6.0	111.1
		26.9–58.8	30.5–61.3	0.0–22.1	62.7–154.1
B	Cropland pastures, riparian habitats and flooding grasslands	59.1	9.7	19.7	103.4
		51.2–72.4	1.9–25.9	3.8–32.7	65.8–132.8
C	Extensive cropland with alternative grazing land use	68.9	21.8	7.1	103.0
		61.0–76.3	13.8–31.5	1.4–14.7	47.3–140.1
D	Extensive and homogeneous cropland	86.0	7.1	4.3	78.6
		78.1–97.3	0.6–17.0	0.0–13.1	53.6–101.7

$\gamma = \text{crop} + \text{position} + \text{crop} \times \text{position} + \text{error}$, with the four landscape types taken as replicates. Effects on γ -diversity for native and exotic species, and for each of Raunkiaer's life forms were evaluated using the same model. Secondly, data for α - and β -diversities were analysed including the field position, crop species, and landscape type as main fixed effects. Field positions were nested within individual fields (=random effect), and the crop types were nested within each landscape type. Only first-order interactions were evaluated in the full model, which had the form, α or $\beta = \text{landscape} + \text{crop} + \text{position} (\text{fields}) + \text{landscape} \times \text{crop} + \text{landscape} \times \text{position} (\text{fields}) + \text{crop} \times \text{position} (\text{fields}) + \text{error}$. 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 part of a significant interaction (Crawley, 2007). Means were compared using 95% confidence intervals (CI 95%). All analyses were performed using R version 2.11 software (R Development Core Team, 2009). Linear mixed effect models were fitted using the function 'lme' (method REML) in the 'nlme' package. Except for γ -diversity of both total and by plant origin, α -, β -, and γ -diversities were transformed to the square root ($x+1$) before analysis. For life forms, only the γ -diversity of chamaephytes and phanerophytes was transformed to $\log(x+1)$ prior to analysis.

3. Results

A total of 143 species of arable plants were recorded in the summer crops surveyed during this study. Each landscape contained 60–78% of the total plant richness. The highest cumulative plant richness was found in fencerow strips (50–80 spp., depending on crop type and landscape) and the lowest in field centres (21–46 spp.). The arable flora of maize crop fields was slightly richer in species (107 spp.) than that of soybean (99 spp.) and wheat–soybean (96 spp.) fields. The overall arable flora of these agro-ecosystems comprised many more exotic species (86 spp.) than native species (57 spp.).

At the landscape scale, γ -diversity was significantly higher in fencerow networks than in field edges and centres (Fig. 1). Field position explained most of the variation in γ -diversity ($F_{2,18} = 39.4$, $P < 0.001$), whereas crop type did not substantially influence plant diversity at this scale ($F_{2,6} = 1.79$, $P = 0.25$; position $\times$ crop: $F_{4,18} = 0.81$, $P = 0.53$). Field position strongly affected γ -diversity of both exotic species ($F_{2,18} = 37.9$, $P < 0.001$) and native species ($F_{2,18} = 50.6$, $P < 0.001$). Total exotic richness was higher in fencerows (77 spp.) than in field edges (56 spp.) and centres (45 spp.). Total richness of native species was also higher in fencerows (50 spp.) than in both field edges (39 spp.) and centres (32 spp.). Crop type had no significant effect on either exotic ($F_{2,6} = 1.59$, $P = 0.28$; position $\times$ crop: $F_{4,18} = 2.16$, $P = 0.12$) or native ($F_{2,6} = 2.89$, $P = 0.13$; position $\times$ crop: $F_{4,18} = 0.46$, $P = 0.77$) species richness.

At the local (field) scale, patterns of α -diversity reflected the influence of field position, crop type and landscape (Table 2), but these factors did not interact with each other ($P > 0.10$). In

general, α -diversity decreased as landscape homogeneity increased from landscape A [25 ± 30 (mean $\pm$ 95% CI)] through landscape D (19 ± 26) (Fig. 2). More importantly, α -diversity significantly decreased from fencerows to field centres (Figs. 1 and 2). Thus, mean α -diversity for fencerows (15 ± 1.1), averaged across landscape types, was greater than in both edges (10 ± 1.0) and centres (8 ± 0.9) of fields. Further, α -diversity was slightly lower in wheat–soybean crops (6 ± 1.3) than in soybean (8 ± 1.6) or maize crops (9 ± 1.6), especially in the field centres (see Fig. 1).

Patterns of β -diversity in this arable flora were strongly affected by first-order interactions between all three main factors (Table 2). Overall, β -diversity was generally higher in fencerows than in field edges and centres, and was on average highest in maize fields (Fig. 1). Interestingly, differences in β -diversity among crop types were apparent in field edges and centres, but not in fencerows (see Fig. 1). Although β -diversity tended to decrease with landscape homogeneity (i.e. from landscape A through D), such landscape-level differences were markedly reduced for field centres, compared to field edges and fencerows (Table 2 and Fig. 2, upper panels). Lastly, β -diversity was on average higher in maize than in non-maize crop fields, but this pattern was only apparent in the more homogeneous landscapes (landscapes C and D, Fig. 2, lower panels).

Overall, the arable flora was largely made up of therophyte and hemicryptophyte species, although within crop fields (edge or centre) geophytes were more common than hemicryptophytes (Fig. 3). The γ -diversity of all plant life-forms was higher in fencerows than in field edges and centres (Table 3 and Fig. 3). This pattern was, however, hardly noticeable for therophytes (annuals), except in wheat–soybean crop fields (Fig. 3). On average, therophyte diversity was higher in maize than in non-maize fields. Gamma diversity of chamaephytes and phanerophytes was significantly influenced by crop type as well as by field position (Table 3). Chamaephytes and phanerophytes only occurred in maize field edges and centres, whereas both life-forms were found in fencerows associated with all crop types (Fig. 3).

Table 2

Statistical models testing for the effects of landscape (4 blocks), crop species (maize, soybean, wheat–soybean) and field position (fencerow, field edge and centre), on α -diversity and β -diversity components of arable plant species.

Source	α		β	
	df	F	df	F
Landscape	3,78	5.99***	3,72	18.7***
Crop	2,78	3.43*	2,72	24.2***
Position	2,166	104.6***	2,156	310.5***
Landscape $\times$ crop	–	ns	6,72	9.21***
Landscape $\times$ position	–	ns	6,156	8.27***
Crop $\times$ position	–	ns	4,156	10.6***

* $P < 0.05$.

*** $P < 0.001$.

ns, not significant.

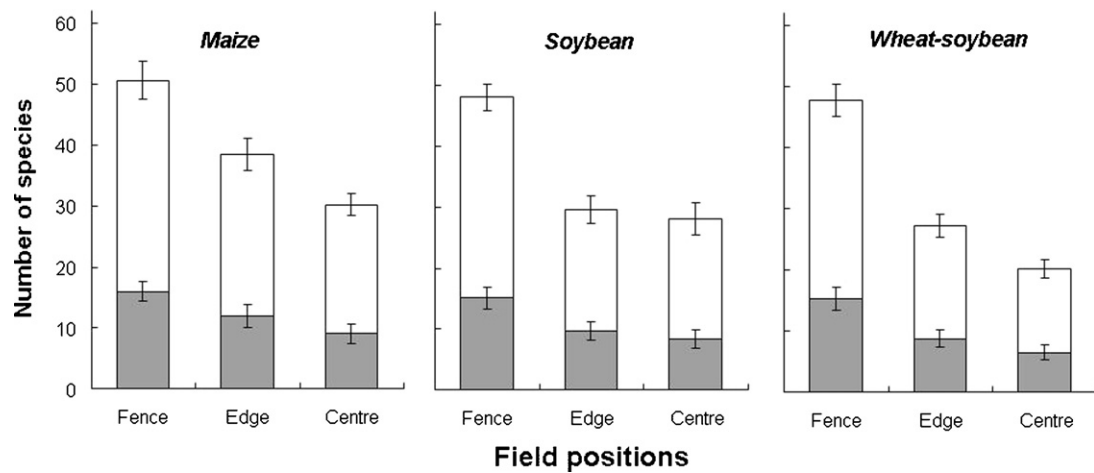


Fig. 1. Effect of field position (fencerow, field edge and field centre) and crop type (maize, soybean, wheat–soybean) on species diversity of arable plants in the Rolling Pampa, Argentina. Each bar represents landscape γ -diversity additively partitioned into mean local richness (α -diversity, grey) and spatial species turnover (β -diversity, white). Richness data were averaged over four landscape types (blocks). Error bars show 95% confidence intervals.

4. Discussion

Our results strongly supported the hypothesis that field position is a major determinant of the species diversity of arable plants in farmland mosaics. Patterns of γ -diversity were largely driven by the environmental contrast between fencerows and crop fields, and reflected the spatial turnover (β -diversity) of plant species

distributed along fencerow networks. In addition, the γ -diversity of perennial life-forms was more clearly influenced by field position and crop type than that of ephemeral species. The contrasting disturbance regimes experienced by fencerows and cultivated fields, as well as by different crop types, may help to explain observed shifts in the prevalence of major plant life-forms in farmland mosaics.

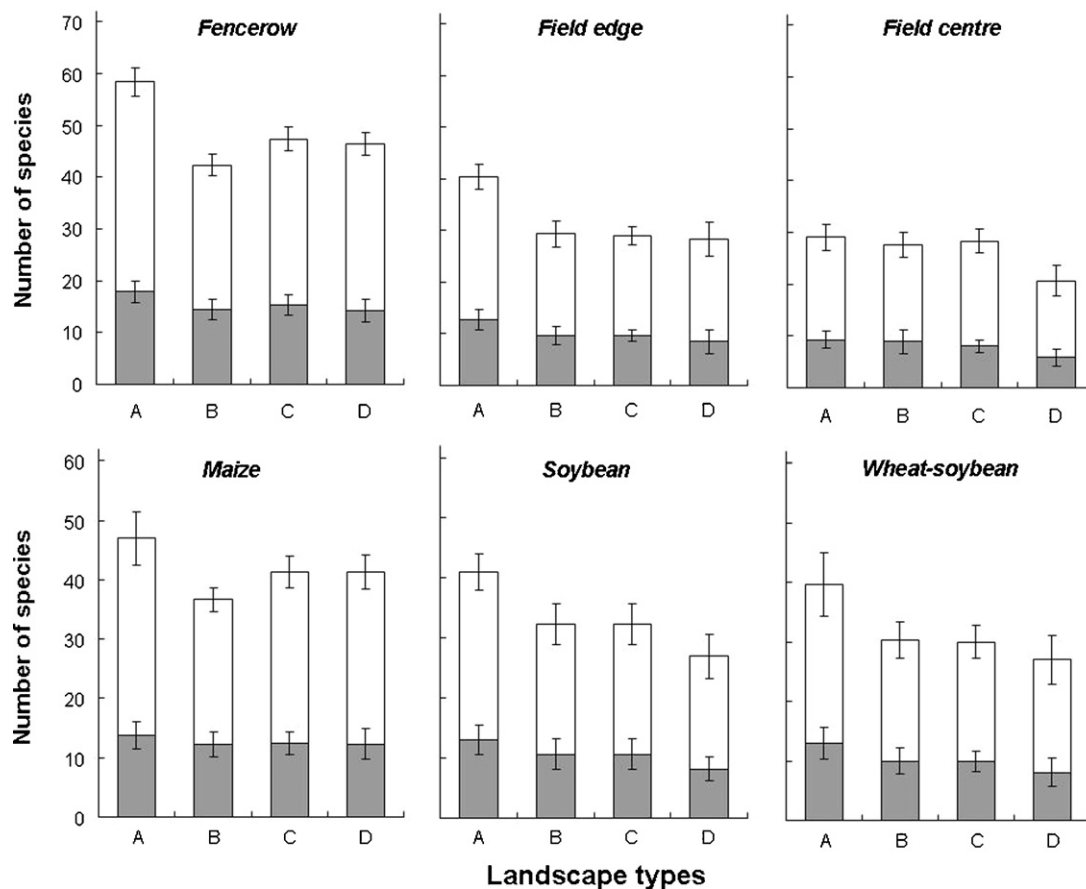


Fig. 2. Patterns in species diversity of arable plants as influenced by field position (upper panels: fencerow, field edge and field centre) and crop type (lower panels: maize, soybean, wheat–soybean) within four landscape types (A–D). Landscapes differed by the proportion of cultivated land they contained (cropland area increased from A to D, see Table 1). Bars represent landscape γ -diversity additively partitioned into mean local richness (α -diversity, grey) and spatial species turnover (β -diversity, white). Error bars show 95% confidence intervals.

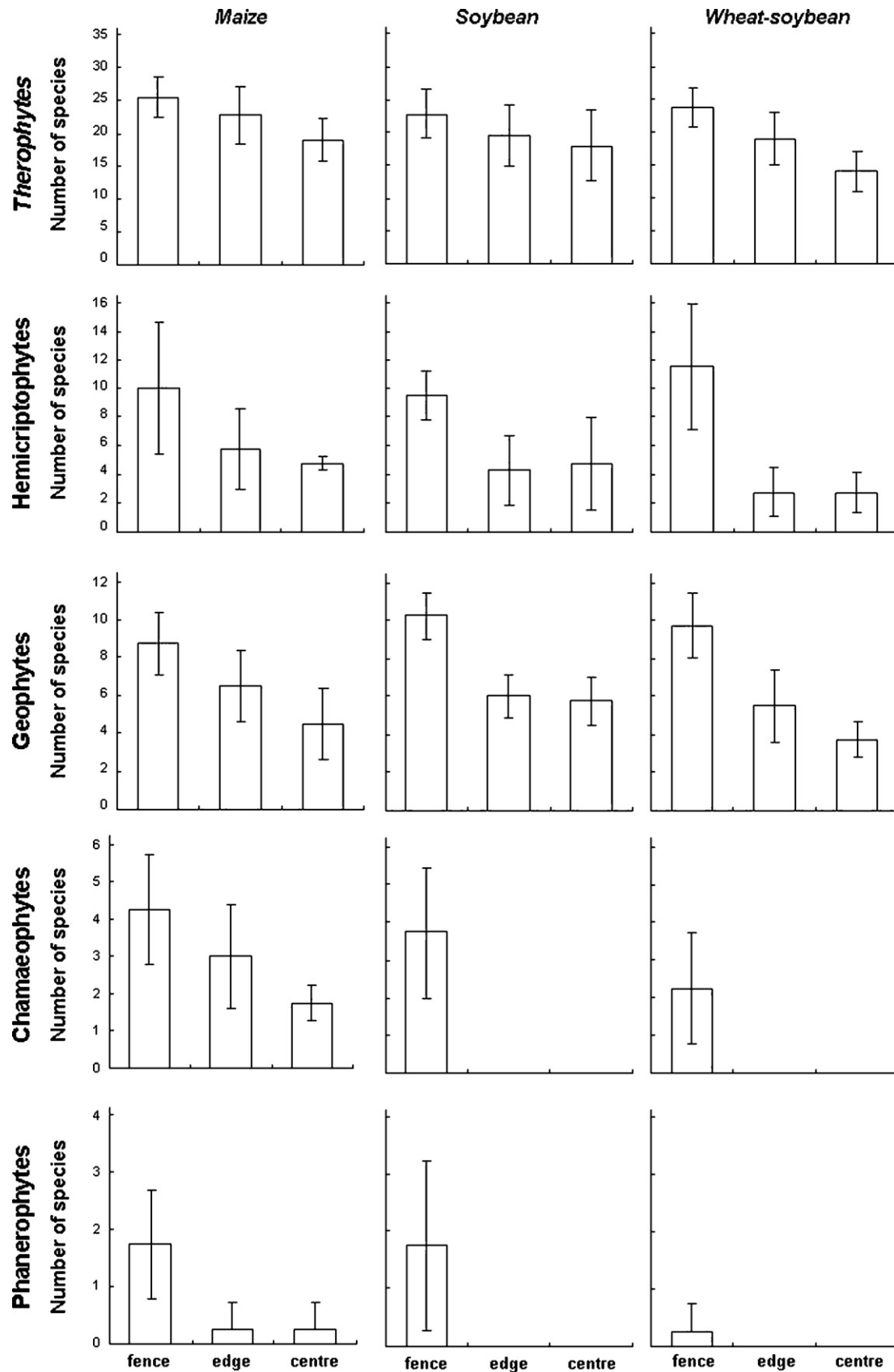


Fig. 3. Mean γ -diversity of arable plant species grouped according to Raunkiaer's life-form classification for different crop types and field positions (see Figs. 1 and 2). Data were averaged over four landscape types (blocks). Error bars show 95% confidence intervals.

Table 3

Statistical models testing for the effects of crop type (maize, soybean and wheat–soybean) and field position (fencerow, edge and centre) on the γ -diversity of arable plant species grouped according to Raunkiaer's life-form categories.

	Source	df	F
Therophytes	Crop	2,6	2.45ns
	Position	2,18	15.9***
	Crop $\times$ position	2,18	0.77ns
Hemicriptophytes	Crop	2,6	0.34ns
	Position	2,18	31.0***
	Crop $\times$ position	2,18	1.48ns
Geophytes	Crop	2,6	1.52ns
	Position	2,18	50.2***
	Crop $\times$ position	2,18	135ns
Chamaephytes	Crop	2,6	32.3***
	Position	2,18	45.8***
	Crop $\times$ position	2,18	4.63**
Phanerophytes	Crop	2,6	5.89*
	Position	2,18	20.9***
	Crop $\times$ position	2,18	2.81 ^o

^o $P < 0.10$.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

ns, not significant.

4.1. β -Diversity explained most variation in γ -diversity

Changes in β -diversity contributed most of the variability in γ -diversity of arable plant species. This finding indicates that cumulative, landscape-level diversity of arable communities may be mostly determined by habitat heterogeneity among fields, both in space and time (Wagner et al., 2000; Gabriel et al., 2006; Poggio et al., 2010). The spatial heterogeneity of agricultural landscapes is often defined by topographic relief and soil properties, which provide the environmental template on which patterns of land use and habitat fragmentation have been superimposed. Habitat heterogeneity may also be determined by land use strategies, including the spatiotemporal variation in the occupancy of fields with different crop types, the specific crop sequences being implemented, and the alternation of cropping and grassing periods (Burel et al., 1998; Herzog et al., 2006). In contrast, α -diversity was a relatively minor component of landscape diversity. These results suggest that agricultural intensification would have a greater relative impact on β -diversity, because of the reduction in habitat heterogeneity. In the humid Pampas, intensification of agricultural management followed the widespread adoption of no-tillage and herbicide-tolerant GM cultivars, which imposed harsher constraints to the persistence of most weed species in crop fields (Ghersa and León, 1999; de la Fuente et al., 2006). Simultaneously, the area occupied by non-cropped habitats was severely reduced by the removal of fencerows to enlarge existing fields, as well as the intentional elimination of spontaneous vegetation along field margins through application of wide-spectrum herbicides. This process undermines the value of fencerow habitats as refugia for farmland biodiversity (Poggio et al., 2010).

4.2. Field position determined arable plant diversity at landscape scales

The γ -diversity of arable plants generally decreased from fencerows, through field edges to field centres. Fencerows, as permanent features in farmland mosaics, present environmental conditions that are relatively more stable than those within fields. While fencerows are rarely disturbed, disturbance within fields is more intense and frequent, since farming practices are aimed

to provide spatially homogeneous and suitable conditions to produce high crop yields. In addition, the environment at the crop edges may differ markedly from that at the nearby non-cropped margins, since cropping activities are usually done close to field boundaries (Marshall and Moonen, 2002). Moreover, farmers in the Pampas usually perform a more intense management of crop edges by sowing double the recommended crop density and by repeating herbicide applications, thus creating harsher environmental conditions for weeds in the field edges (personal observation). The different disturbance regimes associated with different field positions therefore emerge as a prominent force modulating the species diversity of arable plants in the intensively managed farmland mosaics of the Rolling Pampa. This finding further highlights the importance of fencerows in sustaining the overall richness of arable plants in the study landscapes (Poggio et al., 2010), and also agrees with previous studies in other agricultural regions of the world (see Fritz and Merriam, 1996; Le Cœur et al., 1997; Wagner et al., 2000; de Blois et al., 2002; Smart et al., 2002; Bokenstrand et al., 2004; Deckers et al., 2004a,b; Gabriel et al., 2006).

The extent to which β -diversity varied across field positions depended on both crop type and landscape structure. Overall, higher β -diversity in fencerows indicated that local community composition was highly variable along the fencerow network of a landscape. In contrast, lower β -diversity in field centres indicated that weed communities co-occurring with a given crop type showed little change among fields within the same landscape type. The reduced variation in species composition among field centres may result from the high environmental similarity produced by the application of standardised crop management. On the other hand, the higher β -diversity in fencerows would reflect the greater environmental heterogeneity that linear habitats may comprise in farmland mosaics. Fencerow networks extend across different soil types, thus joining and dividing contrasting land uses, such as grasslands, crop fields, riparian zones, wetlands, and urban settlements. Moreover, fencerows may experience a wide range of disturbance regimes, which can be severe, such as the intentional elimination of vegetation by burning or herbicide spray, but could also be completely absent.

Patterns of β -diversity may also be explained by the aforementioned differences in disturbance regime between fencerows and fields. Higher β -diversity in field edges suggests that this field position may behave as ecotones in farmed landscapes (Kovar, 1992; Le Cœur et al., 2002; Marshall and Moonen, 2002; Gabriel et al., 2006). Ecotones, usually defined as transitional areas between two adjacent plant communities, are dynamic boundaries whose properties may regulate the ecological fluxes between neighbouring patches (Wiens et al., 1985). Moreover, mass effects established with the nearby fencerows may be responsible for the increase of β -diversity in field edges (Fig. 1). Mass effects, the increase of species richness in local communities through seed dispersal from nearby habitats (Shmida and Wilson, 1985), have been also proposed as a plausible explanation for the increase in α -diversity of crop edges (Wagner et al., 2000; Gabriel et al., 2005, 2006; Roschewitz et al., 2005). Unlike most of previous research, the inclusion of fencerow habitats in this study provides a more comprehensive picture of the potential role of mass effects in farmland mosaics, with fencerows and crop fields working as source and sink habitats, respectively.

4.3. Crop type effects at local and landscape scales

Differences among crop types in their ground cover and agroeconomic management may help to explain the variability in α - and β -diversities across field positions (Fig. 1). Wheat–soybean relay crops may represent harsher environments for weeds than

soybean or maize crops. One reason for this is the dense canopy cover of cereal crops that not only suppresses the growth of understory weeds (Holt, 1995; Poggio, 2005; Poggio and Ghera, 2011), but also prevents seed germination and seedling recruitment (Batlla et al., 2000; Kruk et al., 2006). Weed suppression by wheat interference may last during the growing period of relay soybean crops, because of the abundant crop residues that remain covering the ground after harvest in no-tillage systems (Caviglia et al., 2004). In general, soybean crops are more weed suppressive than maize crops. Although soybean and maize crops may produce similar ground cover when sown at optimum densities and dates, maximum ground-cover of soybean crops is usually higher and reached earlier than that of maize crops (Flénet et al., 1996). In addition, differences in herbicide use among crop types may also affect changes in α - and β -diversity across field positions and crop types. For instance, while a single application of specific residual herbicides (e.g. atrazine and metolachlor) is usually applied to maize crops at post-emergence, up to two applications of the total herbicide glyphosate are applied to either optimum or relay soybean crops (Qaim and Traxler, 2005). Thus, the lower ground-cover and less intensive weed control in maize crops could have caused the slightly higher mean α -diversity observed in maize crops (see also Suárez et al., 2001). Crop type had little influence on γ -diversity, probably because warm-season crops share a common species pool. Yet crop type modified β -diversity across field positions. Crop type effects on β -diversity suggest that maintaining the diversity of crop sown at the landscape scale, hence avoiding extensive monocultures, can be essential to support the biodiversity of arable plants in farmland mosaics. Maize crops seemed to play a key role in sustaining richer arable plant communities in terms of both floristic and functional (life-form) composition.

4.4. Life-form composition reflects prevailing disturbance regimes

The γ -diversity of perennial life forms differed starkly across crop types and field positions. Differences in the prevalent perennial life form within fields appeared to reflect the contrast among crop types in their disturbance regimes. Since the middle 1990s, ploughing is no longer the main disturbance of arable fields in the Pampas, because of the widespread adoption of no-tillage agriculture (Satorre, 2001; Manuel-Navarrete et al., 2009). This shift in the main source of soil disturbance has promoted an increasing occurrence of perennial life-forms within fields including several exotic phanerophytes (Ghera et al., 2002), which concurs with observations in northern Italy (Zanin et al., 1997). Besides the aforementioned effects of herbicides, crop harvest is nowadays the agent of agricultural disturbance that recurrently and selectively eliminates part of total weed biomass, and hence selects for those weed life-forms that allow persistence within cropped fields.

Perennial life-forms are differently affected by the combines used to harvest maize, soybean and wheat crops. Most weeds are cut at ground level during the harvest of both soybean and wheat, whereas weeds usually are not cut during maize harvest. Soybean and wheat crops are harvested with combines having platform with cutter bars and revolving reels. Thus, soybean and wheat plants are cut at the ground level, enter the combine, and then the chaff is thrown downward remaining mangled on the ground. Conversely, the platform of maize combines has snap rolls that pull the stalks down to separate the ears, which only enter the combine throat, whereas the broken stalks remain partially upright on the ground. Thus, it is highly unlikely that tree species could occur as true phanerophytes (i.e. buds on aerial shoots at above 25 cm height) within fields regularly sown with wheat and soybean. However, tree species that grow with maize may perpetuate within crop fields probably as chamaephytes

or more seldom as nanophanerophytes, whereas tree species are more likely to persist as hemicryptophytes when crops are harvested at ground level (Fig. 3). For instance, *Gleditsia triacanthos*, an invasive exotic tree becomes dominant as phanerophyte in undisturbed habitats such as fencerows and set-aside fields (Mazía et al., 2001; Ghera et al., 2002), may re-sprout from buds on remnant rootstocks that were cut at ground level during the harvest of soybean crops, whereas a new growing period may also start from buds on short, aerial branches when the field was cultivated with maize in the previous growing season. Consequently, our results suggest that differences in disturbance regime between crop types modulate the proportion of alternative life-forms in which a given species occurs within fields or nearby fencerows.

5. Conclusions

We have shown here that arable plant diversity in farmland mosaics may be influenced by the contrasting environmental conditions prevailing in crop fields and fencerows, which in turn may interact closely with crop-specific differences in growth pattern and agronomic management. Our results provide novel information about the interactive effects of crop type and field position in determining spatial heterogeneity and diversity patterns in intensively managed farmland mosaics. In this sense, maize crop appears to be playing a key role in sustaining both the floristic and functional richness of arable plants within fields. Thus, the current trend towards displacing maize for soybean crops could promote additional biodiversity loss in the intensively managed agro-ecosystems of the Rolling Pampa. This highlights the importance of land use planning to develop schemes for conserving farmland biodiversity at landscape and regional scales. In addition, fencerow vegetation, due to its greater diversity of species and life-forms, may provide food and shelter to other taxa with key ecosystem functions in agricultural landscapes, including weed seed predators (Marino et al., 1997, 2005; Westerman et al., 2003; Menalled et al., 2007) and pollinators (Steffan-Dewenter et al., 2002; Le Féon et al., 2010). Our findings demonstrate that the existence of dense and continuous fencerow networks can play an important role in the conservation of biodiversity in intensively managed farmland mosaics.

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