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Landscape complexity differentially affects alpha, beta, and gamma diversities of plants occurring in fencerows and crop fields

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ABSTRACT

Agro-ecosystems still retain part of the original biodiversity, although agricultural intensification threatens to eliminate refuge patches from farmland mosaics. Landscape complexity resulting from networks of uncultivated corridors associated with fencerows may play a key role in sustaining biodiversity across scales, and may further influence diversity in adjacent, cultivated fields. We evaluated the relationship between farmland complexity and plant diversity of fencerows and crop fields at local and landscape scales in the Rolling Pampas of Argentina. We surveyed 222 fencerows and fields cultivated with winter or summer crops, and characterised farmland complexity by the perimeter/area ratio of cropland in 2-km diameter circles surrounding each field. Plant diversity was additively partitioned into alpha, beta, and gamma components. Fencerows had noticeably higher richness than cropped fields at local and landscape scales. Gamma and beta diversities of fencerows and fields were positively related to farmland complexity, supporting the role of spatial heterogeneity in maintaining plant diversity in agro-ecosystems. Landscape complexity did not influence alpha diversity of fencerows but significantly increased diversity within fields, a likely result of enhanced mass effects from uncultivated habitats in more varied farmland. More complex landscapes contained greater gamma diversity of exotic perennials in fencerows, and of exotic and native annuals within fields. Importantly, alpha and gamma diversities of native perennials from the pristine Pampa grassland increased with landscape complexity within cropped fields. In the face of ongoing landscape homogenisation under agricultural intensification, maintaining fencerow networks may become critical for conserving habitat heterogeneity and farmland biodiversity.

1. Introduction

Global biodiversity decline has been a major consequence of both habitat loss and land conversion from complex to simplified landscapes under increasing agricultural intensification (Foley et al., 2005; Tscharntke et al., 2005). Farmland homogenisation has resulted from forest clearance and ploughing of grasslands to grow annual crops, and more recently, from the removal of fencerows to enlarge cropping fields (Petit et al., 2003). Nevertheless, agro-ecosystems still retain a significant part of the original biodiversity to be conserved, which in turn supplies a variety of ecological services that contribute to sustain agricultural productivity (Pimentel et al., 1992; Matson et al., 1997; Norris, 2008).

Habitat heterogeneity has been traditionally recognised as a major determinant of species diversity (Whittaker, 1975; Shmida and Wilson, 1985; Ricklefs, 1987; Rosenzweig, 1995). In the same vein, landscape heterogeneity is regarded as a main factor maintaining biodiversity in cultivated systems, by creating niche opportunities for a wider variety of species (Burel et al., 1998; Benton et al., 2003; Tscharntke et al., 2005). In addition, landscape structure may influence species diversity at local scales through dispersal and 'mass' effects (Shmida and Wilson, 1985; Pulliam, 1988). Complex agricultural landscapes are thus expected to harbour plant communities with higher species richness than simplified ones (Burel et al., 1998; Benton et al., 2003; Tscharntke et al., 2005). However, this assumption has been rarely tested by addressing the scale-dependent nature of plant diversity patterns associated with both cultivated fields and uncultivated field margins. Studying how landscape-level (gamma) diversity is partitioned between within-community (alpha) and between-community (beta) components may help to identify key factors involved in determining arable plant diversity across scales (Loreau, 2000; Chase, 2003; Kneitel and Chase, 2004). The additive partitioning of diversity components (Allan, 1975; Lande, 1996; Wagner

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et al., 2000) may further allow one to relate, respectively, alpha and beta diversities to processes operating at local scales as opposed to processes generating spatial turnover of species at larger scales.

So far, studies of plant richness in agricultural landscapes have largely emphasised changes in weed community structure at local (field) scales. Arable weed diversity has been related to soil properties, agronomic practices, and crop species (Pyšek and Lepš, 1991; de la Fuente et al., 1999; Hyvönen and Salonen, 2002; Poggio et al., 2004). In contrast, the influence of landscape heterogeneity on species diversity of arable plant communities is still poorly understood, and available studies have been limited only to Europe (Wagner et al., 2000; Gabriel et al., 2005, 2006; Roschewitz et al., 2005; Marshall, 2009). For example, in Germany, total weed species diversity was accounted for beta diversity associated with landscape heterogeneity, an effect more conspicuous in conventional than in organically managed farms (Roschewitz et al., 2005). Additionally, local richness of weed communities in wheat fields was positively associated with landscape complexity (Gabriel et al., 2005). In southern England, conversely, weed diversity was not affected by landscape context (Marshall, 2009). Larger alpha and beta diversities in hedgerows and field margins than in the core of cropped fields has been reported for agro-ecosystems of Central Europe, suggesting that uncultivated, corridor-like habitats comprised greater environmental heterogeneity (Wagner et al., 2000; Gabriel et al., 2006).

While the above cited studies have explored a wide range of landscape complexities, they were carried out predominantly in fine-grained farmland mosaics typical of Western Europe. These landscapes are characterised by relatively small fields, dense networks of hedgerows and roads, and highly intermingled rural and urban areas. This structural complexity, however, differs starkly from the extensive and homogeneous cropland mosaics characteristic of many rural areas in the New World, which comprise large arable fields and sparse wire-fencerow networks (e.g. Baldi et al., 2006). Such structural differences raise the question of whether plant species diversity in New World farmland ecosystems, like the South American Pampas, may be influenced by landscape complexity as observed in European agro-ecosystems.

We studied how landscape heterogeneity affects plant species richness of fencerows and crop fields in agricultural mosaics of the Rolling Pampa in Argentina. As elsewhere in South America (Morton et al., 2006), during the last decade Pampean landscapes have been increasingly simplified with the adoption of no-tillage cultivation and herbicide-tolerant GM soybean. These technological changes promoted the ploughing of pastures and road verges to expand cultivated areas, and the removal of fencerows and woodlots to enlarge existing fields. In this context, landscape complexity could be maintained by retaining patches of semi-natural vegetation and networks of fencerows and field margins (Burel et al., 1998; Benton et al., 2003; Tscharntke et al., 2005). While the structure of modern farm lands has been generally simplified, disparate levels of spatial homogenisation were superimposed on the original landscape complexity (Baldi et al., 2006). Landscapes having arable soils with high crop yield potentials likely underwent greater homogenisation, whereas mixed mosaics of comprising poorly drained soils of lower productivity would have remained relatively heterogeneous. We used a regional gradient of agricultural intensification occurring in the Rolling Pampa to examine whether there is a general positive relationship between farmland complexity and plant species richness in wire-fencerows and cropped fields, at both local (alpha) and landscape (gamma) scales. We further investigated the life history attributes and origin (whether native or exotic to the Pampas region) of plant species harboured by fencerows and crop fields along the farmland complexity gradient.

2. Methods

2.1. Study area

The study was carried out in the central Rolling Pampa, which extends from 32° to 34°S and 60° to 61°W in the Buenos Aires province of Argentina (Soriano, 1991). The study area comprised about 7000 km^2 of cropland in Pergamino, Ramallo, Rojas and Salto (Fig. 1). Climate is temperate sub-humid, with warm summers and no marked dry season. Mean annual rainfall is ~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.

During the expansion of agriculture in 1880–1914, the original grassland vegetation was extensively ploughed and converted to row-crop agriculture, thus resulting in extensive farmland mosaics fragmented by intricate networks of wire-fencerows, railroads, and both main and secondary roads (León et al., 1984). Nowadays, soybean and maize prevail among warm-season crops, while wheat is the most common winter crop. Soybean is also sown as a relay crop immediately after the winter crop harvest. Native grassland remnants are virtually absent from the study region. Many native species have become rare and mostly occur only as small, scattered populations in fragments of semi-natural vegetation in grazing paddocks, wire-fencerows and roadside verges (Rapoport, 1996; Ghersa and León, 1999). Recently, however, the agricultural intensification has been pervasively accompanied by the removal of fencerows, and the opportunistic cultivation of road verges, especially in landscape mosaics with more productive soils (see below). These practices would have reduced the amount of farmland area providing refuge habitats for threatened plant species.

Within the study region, landscape heterogeneity varies gradually along a geomorphological gradient involving change in topographic relief and dominant soil types with distance from the Paraná River (Fig. 1). On the southwest of the region, soils are dominated by highly-productive Typic Argiudolls developed on a levelled topographic relief. These landscapes comprise extensive, almost continuous croplands, with large fields averaging ~60 ha in size and small perimeter/area ratios. Toward the northeast, the topography becomes gently undulated and the dominant soils are Vertic Argiudolls with higher clay content (Fig. 1). This part of the region contains a larger proportion of riparian zones; cropland areas are less extensive, and fields are generally smaller, being delimited by dense wire-fencerow networks. Grazing paddocks and woodlots are also more common in these more heterogeneous, north-eastern landscapes. Nevertheless, both climatic conditions and agricultural practices are very similar along this region-wide gradient in land use.

2.2. Vegetation survey

A total of 222 agricultural fields were selected to encompass the landscape heterogeneity gradient described above, and were surveyed during spring and summer of two consecutive years (September–February 2003–2004 and 2004–2005). Main criteria for site selection included accessibility (e.g. owners' consent to work in their land) and the presence of continuous wire-fencerows along (at least) two sides of the field (hereafter referred as fencerows). Moreover, all study fields were distant from urban areas, local villages and other kinds of human settlements. Fields were cultivated with winter- (wheat and pea) and summer-season crops (maize and soybean). In each field, the number of vascular plant species was recorded for both fencerows and field centres. Fencerow surveys were performed along 1 m-wide by 100 m-long belt transects. This sample length was determined using a species accumulation curve based on samples of increasing length according to the

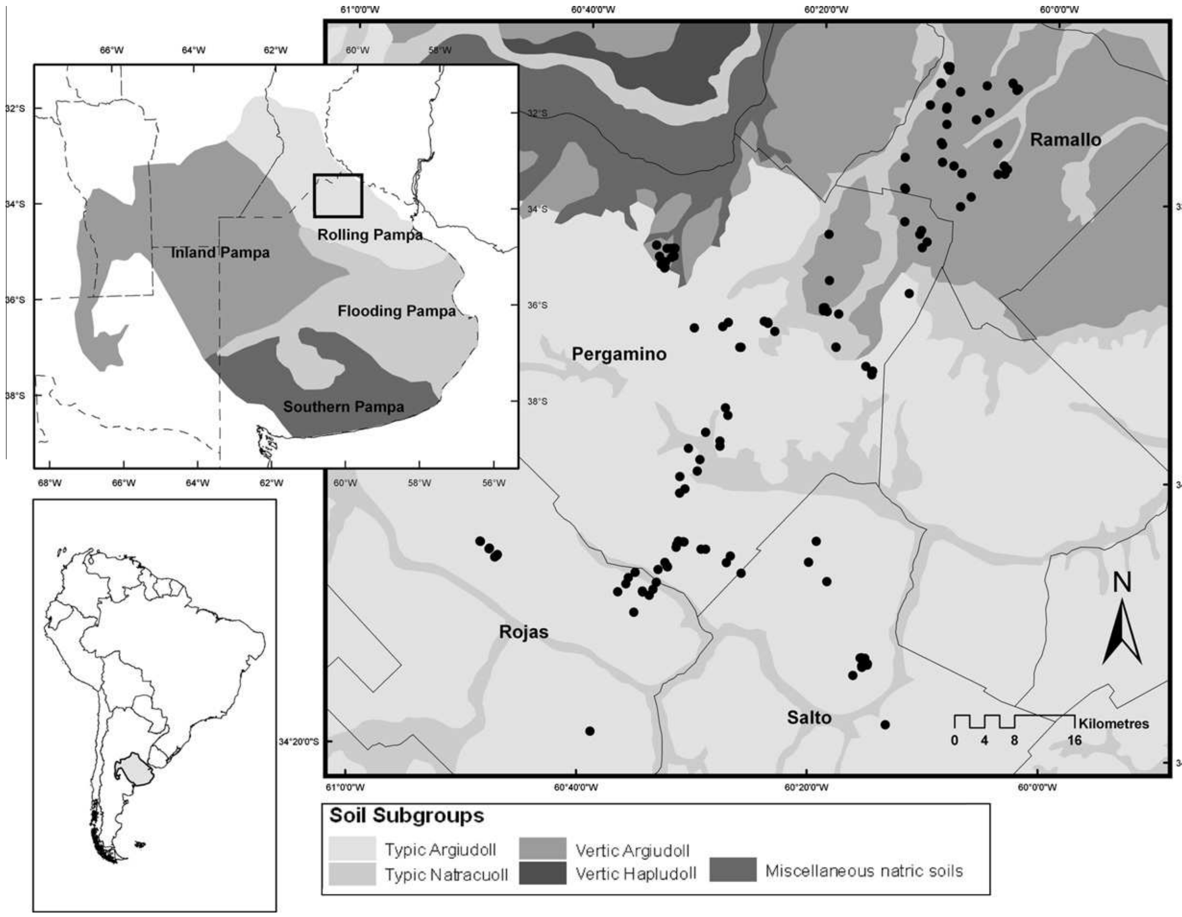

Fig. 1. Location of study sites in the Rolling Pampas of eastern Argentina. The map on the right-hand side depicts the main soil sub-groups underlying the regional land-use mosaic within the study area. The black dots indicate the position of all surveyed crop fields considered in this study. See *2.1 Study area* for further information.

power of two series between 1 and 128 m. 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 small shrubs were only rarely present. Field centres were surveyed leaving a 10 m-wide buffer zone near the fencerow to avoid possible edge effects associated with field margins. Plant surveys were restricted to areas having homogeneous crop cover and excluded low-lying topographic positions. Surveys were performed by zigzag walking during at least 30 min with the aim of obtaining a complete list of species within each cropped field. Thus the surveyed cropped areas were large enough to include most species in the weed community. The sampling effort was evaluated by species accumulation curves and species richness estimators (Incidence-based Coverage Estimator – ICE) using EstimateS, version 8.0 (Colwell, 2006).

2.3. Landscape complexity

Landscape complexity was characterised by assessing the spatial heterogeneity of the land-cover surrounding each surveyed field using the Normalised Difference Vegetation Index (NDVI) obtained from satellite imagery, as described in Guerschman et al. (2003). Three land-cover classes were identified including croplands (areas recurrently devoted to grow annual crops), pasture lands (areas largely used for cattle grazing) and riparian zones (uncultivated, sporadically grazed). Classification was based on three satellite images (LANDSAT 7 ETM+, path-row 226-84, central latitude 34° 02′S, pixels of 30 m × 30 m) corresponding to spring, early and late summer, which allow discrimination of different cover classes based on phenological signatures derived from NDVI estimates. The method requires calibration of spectral attributes using field data from several sites for which the exact geographical location (latitude, longitude) and land-cover class were already known (Guerschman et al., 2003). For each of the 222 sampling sites (see Fig. 1), a 2 km-diameter circle (314 ha) was delimited around the surveyed field, and then the area and perimeter of cropland patches occurring within that circle was calculated using a Geographical Information System (ArcView 3.2, ESRI 1999). This procedure allowed us to characterise the landscape composition around each selected field along the regional land-use gradient.

We calculated the percentage of cropland area ($A_{cropland}$, %), the perimeter/area ratio for cropland ($P/A_{cropland}$, m ha^{-1}) and the overall habitat diversity ($e^{H\prime}$, $H\prime$ being the Shannon diversity index) as straightforward measures of landscape complexity within each circle (Gabriel et al., 2005, 2006; Roschewitz et al., 2005; Tscharntke et al., 2005). The $A_{cropland}$ was chosen to characterise the extent of agricultural disturbance at the landscape scale. The $P/A_{cropland}$ of each landscape circle was calculated as:

$$P/A_{cropland} = \frac{\sum_{i=1}^{m} P_i}{\sum_{i=i}^{m} A_i} = \frac{TE_{cropland}}{A_{cropland}}$$

where P_i and A_i are the perimeter and area of patch i, respectively, m is the total number of patches, and $TE_{cropland}$ and $A_{cropland}$ are the total edge length (m) and area (ha) of cropland within a landscape circle, respectively. This metric reflects the density of fencerows delimiting patches occupied with annual crops (i.e. metres of fence-

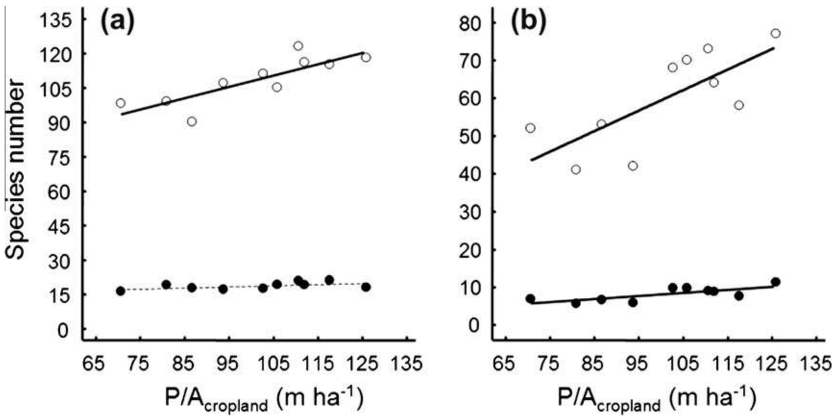

Fig. 2. Plant species number in fencerow (a) and cropped field (b) habitats as a function of landscape perimeter/area ratio for cropland ($P/A_{cropland}$, m ha^{-1}). Alpha and gamma diversities are shown by filled and empty symbols, respectively. Solid lines are fitted linear models ($P < 0.05$); dotted lines depict non significant trends. For full statistics, see Table 1.

rows per ha of cropland). The modified Shannon diversity index ($e^{H'}$) was computed from the proportional area occupied by the three land-cover types (cropland, pasture land and riparian zones) in each circle (Magurran, 2004).

To generate a continuous gradient of agricultural intensification, all surveyed fields were ranked according to the values of $A_{cropland}$ of their surrounding landscape circles, and were subsequently arranged in 10 groups, each including 22–23 fields. Fields occurring within a given group were located, on average, within ~5 km distance from one another and were generally managed by the same farmer. Thus, fields within a group were assumed to share the same species pool (i.e. fields could be potentially connected by plant dispersal forming a 'meta-community', see Leibold et al., 2004). Further, we assumed a common flora (native and exotic) for the whole study area (Parodi, 1930; de la Fuente et al., 1999; Poggio et al., 2004).

We finally chose $P/A_{cropland}$ to study the relationship between species richness and landscape complexity because this metric better reflects the extent of the fencerow network, which in turn is negatively correlated with percent cropland area (% $A_{cropland}$, $r = -0.64$, $F_{1,220} = 156.4$, $P < 0.0001$), and is positively associated with habitat diversity ($e^{H'}$, $r = 0.67$, $F_{1,220} = 182.8$, $P < 0.0001$). Thus, decreased values of $P/A_{cropland}$ may reflect a reduction in fencerow density as the area cultivated with annual crops increases by field expansion, while it may also reflect an increase in land-cover heterogeneity (e.g. due to presence of riparian corridors), which often precludes the expansion of cultivated area.

2.4. Relationship between plant diversity and landscape complexity

Landscape (gamma diversity) and field-scale (alpha diversity) plant species richness were calculated for each group of fields along the landscape complexity gradient. For each group, gamma diversity was estimated by the total number of plant species encountered in those fields, while alpha diversity was the mean species richness per field. Species turnover (beta diversity) among fields within a group was additively obtained as the difference between gamma and alpha diversities (Allan, 1975; Lande, 1996; Wagner et al., 2000). In addition, plant species were classified according to their origin (exotics and natives) and life history (annuals and perennials); biennial species were scarce and grouped with the perennials. Only those species originally belonging to the Pampean Phytogeographic District, which comprises the whole study region, were considered as natives (Parodi, 1930). Cosmopolitan species were included with the exotics. Species were further grouped by dispersal mode as wind-dispersed (anemochory), animal dispersed (endozoochory and epizoochory), and non-specialised dispersal (barochory).

Alpha, beta, and gamma plant diversities were computed separately for fencerow and crop habitats and were related to landscape complexity, as measured by the average $P/A_{cropland}$ of each group of fields. Statistical relationships were tested through simple least-squares regression using Table Curve 2D for Windows v 2.03 (Jandle Scientific, San Rafael, California, USA). We implemented a false discovery rate (FDR) procedure to control for spurious significant results (at $\alpha < 0.05$), which may arise from multiple tests performed on the same data (Benjamini and Hochberg, 1995; Verhoeven et al., 2005). This procedure provides an easily interpretable means for controlling type I errors and for simultaneously reducing type II errors (Verhoeven et al., 2005). Calculations were performed using the spreadsheet provided by Verhoeven et al. (2005).

3. Results

A total of 221 species were recorded throughout the study area, representing 86.4% of the total estimated species richness. Total plant richness was 206 species for fencerows and 124 species for cropped fields, which corresponded to 82% and 88% of the estimated total species richness for each habitat, respectively. These figures indicate that our sampling effort was adequate for inclusion of most of the flora present in the study farmland mosaics. Mean species richness was 19 (95% CI = 0.9) for fencerows and 8 (95% CI = 0.7) for crop fields. Total richness of native plants was 83 and 42 species in fencerow and crop field samples, while exotic plant richness totalised 123 and 82 species in fencerows and crop fields, respectively. When species were grouped according to life

Table 1
Summary of regression analyses of gamma, alpha, and beta diversities of plant species in fencerows and crop fields as a function of the landscape perimeter-area ratio for cropland ($P/A_{cropland}$, m ha^{-1}).

	Fencerow			Crop field		
	Gamma	Alpha	Beta	Gamma	Alpha	Beta
Slope	0.49	0.05	0.44	0.54	0.08	0.46
Intercept	58.6	13.6	11.8	5.1	−0.16	5.3
R^2	0.686	0.306	0.646	0.556	0.568	0.546
$F_{(1,8)}$	17.46	3.53	14.62	10.02	10.54	9.63
P-value	0.0031	0.0972	0.0051	0.0133	0.0118	0.0146

history, there were 104 annuals, 97 perennials and five biennials in fencerows, and 79 annuals, 47 perennials and only one biennial species in field centres.

Gamma diversity of both fencerows and cropped fields increased with landscape complexity (Fig. 2, Table 1). However, alpha diversity of fencerows and fields responded differently along the complexity gradient. Whilst alpha diversity in cropped fields increased in more heterogeneous landscapes, that of fencerows did not show a definite statistical trend with landscape complexity ($P = 0.097$; Fig. 2, Table 1). Beta diversity, which is graphically represented by the difference between gamma and alpha diversities at each level of landscape complexity (Fig. 2), increased in both fence-

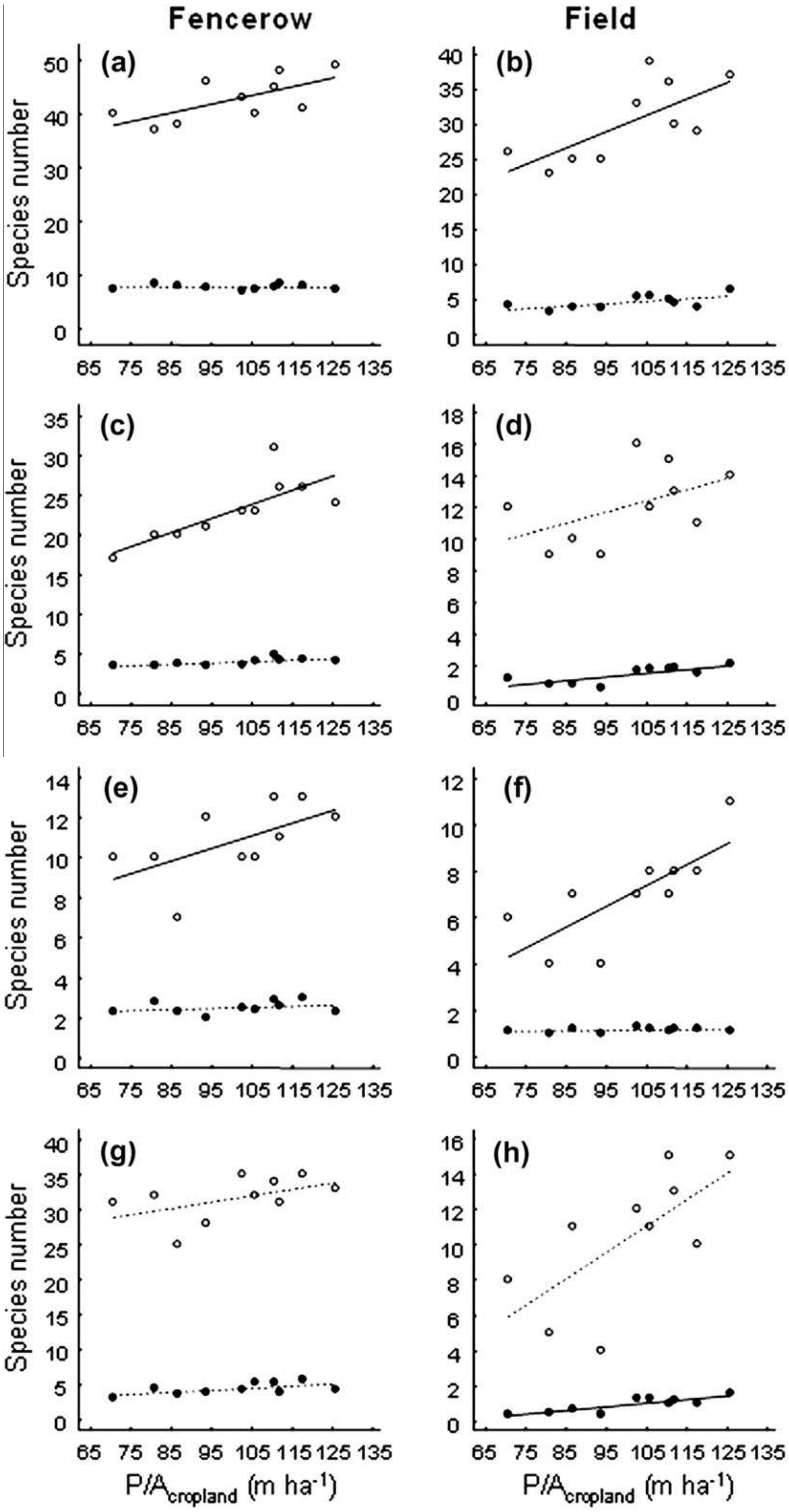

Fig. 3. Species number, according to their life cycle and origin, as a function of the landscape perimeter/area ratio for cropland ($P/A_{cropland}$, m ha^{-1}). Species groups are exotic annuals (a and b) and perennials (c and d), native annuals (e and f), and perennials (g and h). Alpha and gamma diversities are shown by filled and empty symbols, respectively. Solid lines are fitted linear models ($P < 0.05$); dotted lines depict non significant trends. For full statistics, see Table 2.

Table 2
Summary of regression analyses of gamma, alpha, and beta diversities of plant species in fencerows and crop fields as a function of the landscape perimeter-area ratio for cropland ($P/A_{cropland}$, m ha^{-1}). Species are grouped according to their origin (exotics and natives) and life history (annuals and predominantly perennials). For each variable, *P*-values shown in bold type were lower than the threshold values corresponding to a False Discovery rate (FDR) level of 0.05.

	Fencerow				Crop field			
	Exotics		Natives		Exotics		Natives	
	Annuals	Perennials	Annuals	Perennials	Annuals	Perennials	Annuals	Perennials
Gamma								
Slope	0.16	0.18	0.06	0.09	0.23	0.07	0.09	0.15
R^2	0.448	0.615	0.363	0.253	0.511	0.253	0.578	0.471
$F_{(1,8)}$	6.49	12.78	4.56	2.71	8.37	2.71	10.94	7.11
P-value	0.0343	**0.0072**	0.0652	0.1381	**0.0201**	0.1386	**0.0107**	**0.0285**
Alpha								
Slope	-3.1×10^{-3}	0.02	5.3×10^{-3}	0.03	0.04	0.02	1.8×10^{-3}	0.02
R^2	0.013	0.483	0.086	0.374	0.408	0.580	0.110	0.714
$F_{(1,8)}$	0.11	7.47	0.75	4.77	5.50	11.02	0.99	19.92
P-value	0.7534	0.0257	0.4108	0.0605	0.0470	**0.0105**	0.3494	**0.0021**
Beta								
Slope	0.16	0.16	0.06	0.06	0.20	0.05	0.09	0.13
R^2	0.444	0.618	0.334	0.162	0.505	0.162	0.581	0.427
$F_{(1,8)}$	6.39	12.92	4.01	1.55	8.17	1.55	11.08	5.96
P-value	0.0354	**0.0070**	0.0803	0.2488	0.0212	0.2486	**0.0104**	0.0405

rows and cropped fields as landscapes became increasingly complex (Table 1).

In fencerow habitats, gamma diversity of exotic perennials, but not of annuals, increased with landscape complexity, whereas that of native annuals and perennials did not change significantly with farmland complexity (Fig. 3e and g, Table 2). In cropped fields, however, gamma diversity of exotic perennials remained unchanged, whereas that of both exotic and native annuals increased with farmland heterogeneity (Fig. 3, Table 2). Interestingly, the gamma diversity of native perennials, mostly representing species from the pristine Pampa grassland, also significantly increased in field centres as landscapes became more complex (Fig. 3h, Table 2). In contrast, the alpha diversity of all plant groupings in fencerows was not influenced by landscape complexity. Alpha diversity of both exotic and native perennials increased in cropped fields along the farmland complexity gradient (Fig. 3, Table 2). Only the beta diversity of exotic perennials increased in fencerows, whereas that of native annuals increased in cropped fields (Fig. 3, Table 2).

Gamma and alpha diversities of barochorous species showed different patterns for fencerows and cropped fields as farmland complexity increased. Gamma diversity of fencerows increased but alpha diversity did not vary (Fig. 4a, Table 3), while the opposite occurred within crop fields (Fig. 4b, Table 3). For species dispersed by anemochory and epizoochory, only gamma diversity of fencerows increased with landscape complexity (Fig. 4c–f, Table 3). Both gamma and alpha diversity of endozoochorous species increased with landscape complexity in cropped fields but remained unchanged in fencerows (Fig. 4g and h). Beta diversity of barochorous and epizoochorous species in fencerows significantly increased with landscape complexity (Fig. 4a and e), whereas that of anemochorous and endozoochorous species showed no clear trend (Fig. 4c and g). Beta diversity in cropped fields did not significantly vary with farmland complexity for any of the four dispersal modes (Fig. 4).

4. Discussion

Overall, plant species richness in both fencerow and crop fields was positively associated with farmland complexity at the landscape (gamma) scale. Since we surveyed agricultural fields comprising various winter and summer crops, our results widen the scope of the relationships between plant diversity and landscape complexity previously established for cropping systems in Europe (Gabriel et al., 2005, 2006; Roschewitz et al., 2005; Marshall, 2009). Patterns reported here support the notion that structurally complex farmland mosaics may contribute to maintain plant biodiversity, even in intensively managed agro-ecosystems (Burel et al., 1998; Benton et al., 2003; Tscharntke et al., 2005). However, gradients in gamma diversity were differentially driven by spatial species turnover and local richness depending on the habitat type. Whilst plant diversity in cropped fields increased with farmland complexity as a result of greater beta and alpha diversities, fencerow plant diversity increased in more complex landscapes mostly due to higher species turnover among sites. This finding suggests that the size of plant diversity reservoirs would be controlled by differently scaled processes in cropped fields and non-cultivated linear habitats associated with fencerows.

Fencerows harboured higher plant diversity than cropped fields at both local and landscape scales (Fig. 2, Table 1). This is noteworthy considering that fence strips occupy much smaller proportional areas than cultivated fields. Moreover, the higher plant diversity sustained by fencerows would also reflect their lower perturbation level and higher habitat heterogeneity compared with crop fields. Higher plant richness in linear farmland patches such as hedgerows was observed at field and landscape scales in Europe (Marshall, 1989; Burel and Baudry, 1995; Wilson and Aebischer, 1995; Burel et al., 1998; Wagner et al., 2000) and North America (Forman and Baudry, 1984; Jobin et al., 1997; Boutin and Jobin, 1998; de Blois et al., 2002). Our results provide novel evidence for the role of fencerows as plant diversity reservoirs in the South American Pampas, where extensive landscapes originally occupied by mesic grasslands were turned into one of the largest agricultural regions of the world (León et al., 1984; Hall et al., 1992).

Interestingly, whereas gamma diversity increased with farmland complexity, alpha diversity in fencerows remained nearly constant (Fig. 2). This pattern suggests that local community factors may be constraining species richness in fencerow habitats (Cornell and Lawton, 1992; Loreau, 2000). Fencerows are narrow linear habitats, bounded on both sides by larger areas regularly disturbed by farming. Thus fencerows represent "open" habitats with the potential to be strongly influenced by immigration of seeds from adjacent cropped fields. However, the low area occupied by fencerows may set a physical limit to the number of individual plants they might contain, and thus the number of species that they can harbour (Stevens and Carson, 1999). Additionally, stand-

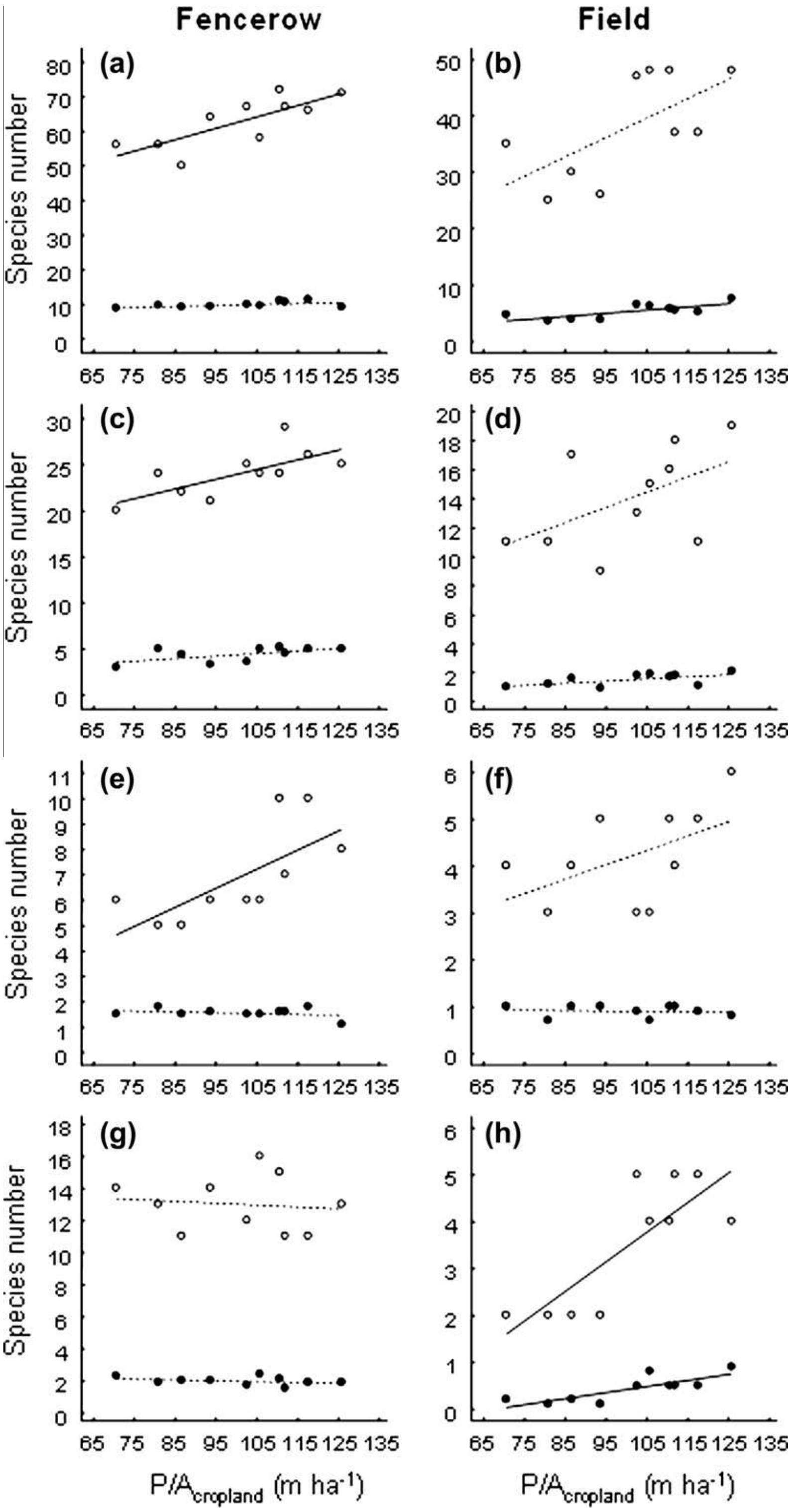

Fig. 4. Species number, according to their dispersal strategy, as a function of the landscape perimeter/area ratio for cropland ($P/A_{cropland}$, m ha^{-1}). Species groups are exotic barochory (a and b) anemochory (c and d), epizoochory (e and f), and endozoochory (g and h). Alpha and gamma diversities are shown by filled and empty symbols, respectively. Solid lines are fitted linear models ($P < 0.05$); dotted lines depict non significant trends. For full statistics, see Table 3.

ing biomass and litter accumulation by perennial vegetation in fencerows may create microsite limitations to sustain richer local plant communities. Although stochastic disturbances, such as herbicide drift, may determine the upper limit imposed by fencerow area to local richness (Loreau, 2000), the relative constancy of fencerow alpha diversity across landscapes with different levels of human intervention suggests that disturbance regimes may not substantially alter microsite availability for species establishment in these linear habitats.

The increased gamma diversity of alien perennial species indicates that fencerow habitats would be increasingly stable in more complex farmland mosaics (see Fig. 2). Indeed, the frequency and intensity of fencerow disturbances associated with cropping activities in neighbouring fields can be highly variable depending on the

Table 3
Summary of regression analyses of gamma, alpha, and beta plant diversities in fencerows and crop fields as a function of the landscape perimeter-area ratio for cropland ($P/A_{cropland}$, m ha^{-1}). Species are grouped according to their dispersal modes. For each variable, *P*-values shown in bold type were lower than the threshold values corresponding to a FDR level of 0.05.

	Fencerow				Crop field			
	Barochory	Anemochory	Epizoochory	Endozoochory	Barochory	Anemochory	Epizoochory	Endozoochory
Gamma								
Slope	0.33	0.11	0.07	-1.2×10^{-3}	0.34	0.11	0.03	0.06
R^2	0.614	0.504	0.493	0.013	0.419	0.277	0.264	0.657
$F_{(1,8)}$	12.74	8.12	7.77	0.11	5.76	3.07	2.87	15.33
P-value	**0.0073**	**0.0215**	**0.0236**	0.7502	0.0432	0.1181	0.1285	**0.0044**
Alpha								
Slope	0.03	0.03	-3.5×10^{-3}	5.3×10^{-3}	0.06	1.48×10^{-3}	9.5×10^{-4}	0.01
R^2	0.303	0.340	0.095	0.123	0.554	0.367	0.018	0.662
$F_{(1,8)}$	3.48	4.11	0.84	1.13	9.92	4.64	0.14	15.66
P-value	0.0991	0.0771	0.3850	0.3198	**0.0136**	0.0634	0.7155	**0.0042**
Beta								
Slope	0.3	0.08	0.08	−0.01	0.29	0.09	0.03	0.05
R^2	0.587	0.367	0.542	0.005	0.389	0.259	0.307	0.555
$F_{(1,8)}$	11.35	4.64	9.48	0.04	5.09	2.80	3.55	9.98
P-value	**0.0098**	0.0633	**0.0151**	0.8495	0.0540	0.1328	0.0964	0.0134

landscape configuration. Farming disturbance dominates simplified agricultural landscapes, which may result in more transient and harsh fencerow environments. In intensively cropped landscapes, fencerows typically separate fields regularly cultivated with annual crops. Therefore, spontaneous vegetation established along uncultivated field margins has higher chances of being damaged by herbicide drift and may also receive greater nutrients loads from fertilisers (Jobin et al., 1997; Kleijn and Snoeijing, 1997; Boutin and Jobin, 1998; de Blois et al., 2002). In addition, fencerows in complex landscapes often divide fields utilised for varied purposes, including annual or perennial crops, pastures, woodlots, and semi-natural vegetation. Moreover, fencerows may be relatively persistent structures in more complex landscapes, as natural heterogeneity of farmland mosaics created by low-fertility soil patches and riparian zones reduces the chances of fencerow removal. Conversely, in landscapes having flat and homogeneous soil mosaics, field enlargement through fencerow removal would be a likely procedure accompanying agricultural intensification (Petit et al., 2003).

The concomitant increase of within field alpha and gamma diversities in complex farmland mosaics (Fig. 2) suggests that local species richness of the arable flora would be largely dependent upon the size of the regional species pool, rather than on biotic interactions (e.g. competition) within fields. This pattern has been referred to as 'proportional sampling' (Cornell and Lawton, 1992), and in this context suggests that, despite the prevailing unfavourable conditions imposed by farming practices, species dispersal from fencerows may contribute to sustain local plant richness within fields embedded in complex landscapes. Whilst crop fields can be considered unsuitable patches for the self-maintenance of most wild plant populations, propagule immigration from nearby 'source' habitats could determine that fields work as 'sink' habitats that help to sustain plant species diversity both locally and regionally (Shmida and Wilson, 1985; Pulliam, 1988; Leibold et al., 2004). Enrichment of local plant diversity in field edges through greater environmental heterogeneity and mass effects has been also suggested for European agro-ecosystems (Roschewitz et al., 2005; Gabriel et al., 2006).

The increased occurrence of alien and native perennial species within fields in more complex farmland mosaics (Fig. 3) may be also explained by the regular influx of propagules from neighbouring fencerows. Our results suggest that dispersal, closely interacting with habitat heterogeneity, contributes to maintaining species richness at local and landscape scales. Most native perennial species occurring within fields could neither complete their life cycles nor produce sufficient propagules to sustain self-perpetuating populations in the harsher environmental conditions imposed by farming practices. As farmland is increasingly simplified by cropland expansion, agricultural activities would expand the area of inhospitable habitat for many species, allowing persistence of fewer weed species adapted to high disturbance rates. In the Pampas, land management has shifted from traditional ploughing to no-till agriculture, which has affected the persistence of weed seeds in the soil (de la Fuente et al., 1999; Ghersa and Martinez-Ghersa, 2000). In no-tillage systems, recently dispersed seeds are concentrated near the soil surface facing higher risk of predation, and are also more exposed to unfavourable microclimatic conditions that often reduce germinability (Thompson et al., 1998; Ghersa and Martinez-Ghersa, 2000). Our findings emphasise the importance of fencerow networks not only for providing refuges to native grassland species, but also as sources of propagules that help to maintain plant richness within fields through spatial mass effects. According, some species may persist in the unfavourable environments of cropped fields through a meta-population 'rescue effect' (Brown and Kodric-Brown, 1977; Leibold et al., 2004).

In general, gamma diversity was mostly driven by changes in beta diversity as farmland landscapes became increasingly complex (Fig. 2). Such a pattern would be expected as a result of greater spatio-temporal environmental heterogeneity and higher dispersal rates among different landscape patches (Shmida and Wilson, 1985; Loreau, 2000; Kneitel and Chase, 2004). In this study, changes in habitat heterogeneity were directly reflected in the measure we used to characterise farmland complexity ($P/A_{cropland}$). In Central European farmland, beta diversity also increased in the edges of wheat fields as the surroundings became more complex; indicating that higher floristic turnover among fields resulted from greater environmental heterogeneity (Roschewitz et al., 2005; Gabriel et al., 2006). Here, we focused on fencerows instead of field edges. This is an important difference since the field edge is actually farmed, whereas fencerows, albeit to some extent disturbed by farming practices, remain uncultivated. Given this lack of cultivation and the extended distances that fencerows cover across landscapes, these networks of linear habitat would comprise a wider range of environmental heterogeneity than cropped fields. This might be especially apparent in the Rolling Pampa, where landscapes are relatively more coarse-grained and extensive than those of Central Europe due to larger fields and sparser corridor networks.

Gamma diversity of anemochorous and barochorous species increased in fencerows, while gamma and alpha diversities of wind-dispersed species remained unchanged within fields (Fig. 3c and d, Table 3). These results suggest that fencerows may be functioning as seed-trapping structures in farmland mosaics of the Rolling Pampa, hence sustaining arable plant diversity at the landscape scale. Winged and plumed seeds would have greater probability to collide with and be retained by dense and tall vegetation (Bullock and Moy, 2004), such as the perennial species occurring in the intricate fencerow networks characterising complex farmland. Moreover, agricultural activities may enhance propagule mobility by secondary dispersal events, for example, through seeds retained by combine machines during crop harvest (Ballaré et al., 1987; Ghersa et al., 1993), which could be trapped in the nearby fencerow vegetation. Since fields are smaller and fencerows networks are denser in more complex farmland, barochorous species would have a greater probability of being retained by fencerow vegetation after secondary dispersal.

Gamma diversity of epizoochorous species increased in fencerows as farmland became more complex, but did not change within fields at either local or landscape scales. Conversely, alpha and gamma diversities of endozoochorous species only increased with landscape complexity within crop fields (Fig. 3). We suggest that animal activity along fencerow networks may maintain the species richness of zoochorous arable plants in farmland mosaics. Rodents and passerine birds not only eat seeds within fields but may also transport them to the vegetation along fences and field boundaries, where they find shelter (Wenny, 2001). Moreover, species richness in fencerows of endozoochorous plants would have been sustained by birds eating seeds and fruits and perching along them, as indicated by the unaffected gamma diversity of endozoochorous species when farmland was simpler (Fig. 3g). Some of these species have fleshy fruits, such as native perennial forbs in the *Solanacea* (*Physalis viscosa* and *Solanum sisymbrifolium*), or alien trees recently documented as invaders of corridor habitats (*Broussonetia papyrifera*, *Melia azedarach*, and *Morus alba*; see Ghersa et al., 2002). Our results would suggest that animal-mediated, non-random dispersal events along fencerows may be playing a key role in preventing local extinctions as landscapes are simplified by agricultural expansion.

Our results indicate that maintaining both the presence and coherence of fencerow networks is critical for sustaining farmland biodiversity, including native grass species. Native perennial grasses, because of their low dispersal rates and reduced population growth are highly susceptible to become locally extinct due to habitat loss and fragmentation (Hanski and Ovaskainen, 2002; Casagrandi and Gatto, 2002). Local extinction risks of native tussock grasses have been increased by the extensive ploughing initiated in the late 1880s (León et al., 1984), as well as through herbicide drifts at low doses (Jobin et al., 1997; Boutin and Jobin, 1998; de Blois et al., 2002). Therefore, the removal of entire fencerows could represent a major threat to the persistence of the few small populations of rare species from the native grassland that remain scattered in the farmland landscape. The ongoing intensification of agriculture clearly constraints the alternatives to conserve or even restore remnant populations of native perennial grasses (Tognetti et al., 2010). Our findings may thus contribute to inform the design and monitoring of agri-environment schemes based on the management of fencerow habitats for plant biodiversity (see Kleijn and Sutherland, 2003).

5. Conclusions

Our results emphasise that maintaining undisturbed fencerow networks may be crucial for promoting habitat complexity and plant diversity across scales in intensively managed agricultural landscapes. Fencerows not only sustained higher species richness of arable flora at local and landscape scales, but also provided refugia for rare plant species belonging to the native Pampa grassland. Moreover, fencerows may serve as sources of species for restoring the diversity of degraded plant communities in farmland mosaics. This would be the case for the species-poor weed communities of farming systems, where prevalence of no-tillage agriculture has depleted the arable flora. Farmland mosaics could be conceived as checkerboards of local plant communities in which species respond to processes operating at different spatial scales. We propose that emergent ecological processes arising from metacommunity dynamics, such as maintenance of plant richness within fields through mass effects from nearby fencerow habitats, will be inevitably lost if farmland landscapes continue to be spatially homogenised by ongoing agricultural intensification.

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