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REVIEW PAPER

Effects of agriculture expansion and intensification on the vertebrate and invertebrate diversity in the Pampas of Argentina

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Abstract In this paper we summarize for the first time the effects of agriculture expansion and intensification on animal diversity in the Pampas of Argentina and discuss research needs for biodiversity conservation in the area. The Pampas experienced little human intervention until the last decades of the 19th century. Agriculture expanded quickly during the 20th century, transforming grasslands into cropland and pasture lands and converting the landscape into a mosaic of natural fragments, agricultural fields, and linear habitats. In the 1980s, agriculture intensification and replacement of cattle grazing-cropping systems by continuous cropping promoted a renewed homogenisation of the most productive areas. Birds and carnivores were more strongly affected than rodents and insects, but responses varied within groups: (a) the geographic ranges and/or abundances of many native species were reduced, including those of carnivores, herbivores, and specialist species (grassland-adapted birds and rodents, and probably specialized pollinators), sometimes leading to regional extinction (birds and large carnivores), (b) other native species were unaffected (birds) or benefited (bird, rodent and possibly generalist pollinator and crop-associated insect species), (c) novel species were introduced, thus increasing species richness of most groups (26% of non-rodent mammals, 11.1% of rodents, 6.2% of birds, 0.8% of pollinators). Much taxonomic and ecological work is still needed to understand Pampean animal biodiversity, to understand how agriculturization is affecting it, and to identify appropriate conservation actions. Networks of Important Bird Areas and Valuable Grassland Areas harbor a balanced representation of Pampean biodiversity and, if adequately protected, may provide valuable research sites, but complementary work should be carried out on agriculturized areas.

Keywords Birds · Grasslands · Insects · Other vertebrates · Pollinators · Rodents

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Introduction

Loss of biodiversity as a result of agricultural expansion and intensification

The fate of a substantial part of terrestrial biodiversity will depend on their capacity to exist within agroecosystems. This is due to their vast and expanding geographical extent and the intrinsic environmental disturbance associated with them (Tilman et al. 2001). Conversion of natural habitats to agriculture has induced changes in global, regional, and local patterns of species composition, abundance, and biodiversity in various ecosystems, even though effects vary considerably among taxa (Robinson and Sutherland 2002; Kim and Byrne 2006; Tylianakis et al. 2007). These changes generally contributed to biotic homogenization through colonization by non-native species, followed by extinction of native species. Altered landscape structure has also led to biotic homogenization which affects important ecological traits that shape species composition in local communities, such as mobility and habitat specificity. Thus, land use change is likely to cause biodiversity loss across various kinds of ecosystems worldwide (Ekroos et al. 2010).

The natural component in most agroecosystems is retained in a network of fragments embedded in a matrix of fields assigned to farming or pastures (Marshall and Moonen 2002; Oesterheld et al. 2005). The natural or semi-natural remnants may function as biodiversity refuges (Le Cœur et al. 2002; Marshall and Moonen 2002; Marshall et al. 2003). Linear fragments can act as corridors connecting larger remnant patches, thus potentially attenuating the negative consequences of fragmentation (Tewksbury et al. 2002; Haddad et al. 2003; Fried et al. 2005; Saarinen et al. 2005; Townsend and Levey 2005), one of which is loss of interspecific interactions. These are less easily detected than extinction of particular taxa, but their consequences for biodiversity are no less real, because trophic networks are strongly associated with the stability and functioning of the ecosystems in which they occur (Melián and Bascompte 2002; Ives and Cardinale 2004; Montoya et al. 2006).

The Pampas example

The Río de la Plata grasslands are part of the most extensive biogeographic unit of the prairie biome in South America, and constitute one of the most important grasslands in the world (Bilenca and Miñarro 2004; Baldi and Paruelo 2008). Covering 75 million ha, these grasslands include part of south-east Brazil, central and north-east Argentina, south-east Paraguay, and Uruguay (Soriano et al. 1991; Di Giacomo and Krapovickas 2003). Its two subregions, the “Pampas” in the temperate area, and the “Campos” in the subtropical part (Soriano et al. 1991; Krapovickas and Di Giacomo 1998) (Fig. 1) differ geologically. The Pampas developed on a 300–1500 m deep layer of loess and clay sediments accumulated on a crystalline structure, while in the Campos the crystalline basement is much closer to the surface (Bilenca and Miñarro 2004). Pampean soils are mainly Mollisols, associated with Alfisols and Vertisols towards the east and with Entisols towards the west (Soriano et al. 1991). The mean annual temperature varies from 20°C in the north to 13°C in the south, and the annual precipitation varies from 1800 mm in the northeast to 400 mm in the southwest (Baldi and Paruelo 2008). In the Pampas, 90% of the original grasslands have been converted into fields used for agriculture or cattle-raising. The subtropical Campos retain their original physiognomy to a much higher degree (Overbeck et al. 2007), although a rapid replacement with *Pinus* and *Eucalyptus* afforestations is currently taking place there (Di Giacomo and Krapovickas 2001; Baldi and Paruelo 2008).

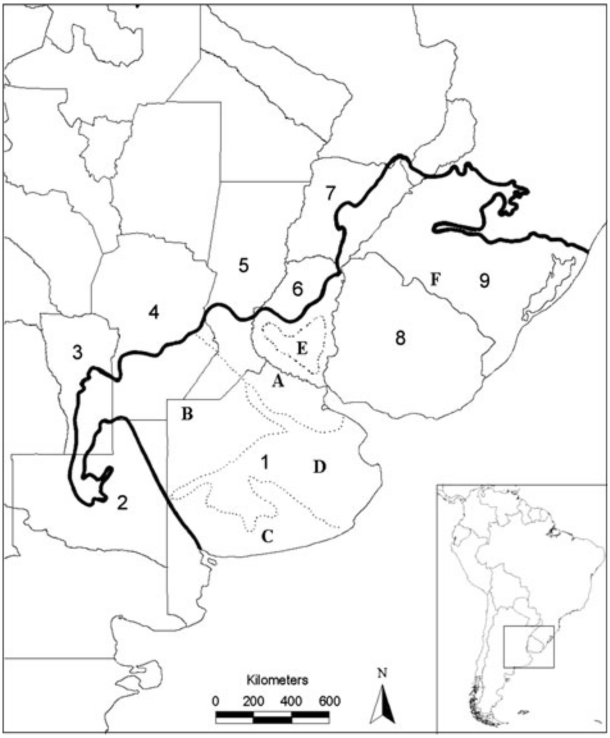

Fig. 1 The Río de la Plata grasslands (area encircled by *thick line*). Subdivisions are limited by *dotted lines* and identified by *capital letters*; political units are limited by *thin lines* and identified by *numerals*. *A* Rolling Pampa, *B* Inland Pampa, *C* Southern Pampa, *D* Flooding Pampa, *E* Mesopotamic Pampa, *F* Campos. *1–7* Argentina's provinces: *1* Buenos Aires, *2* La Pampa, *3* San Luis, *4* Córdoba, *5* Santa Fe, *6* Entre Ríos, *7* Corrientes. *8* Uruguay, *9* Brazil (state of Rio Grande do Sul). Pampean limits taken from Soriano et al. (1991) and Hall et al. (1992)

The original Pampas

The Pampas once covered most of the province of Buenos Aires and parts of the provinces of Entre Ríos, Santa Fe, Córdoba, La Pampa and San Luis in Argentina. Several subunits are recognized on the basis of geomorphology, drainage, geology, physiography, soils and vegetation: Rolling Pampa, Inland Pampa (further divided into Flat Pampa and Western Pampa), Southern Pampa, Flooding Pampa and Mesopotamic Pampa (Fig. 1) (Soriano et al. 1991). As far back as the Quaternary the entire region was covered by grasslands dominated by mesothermic species, trees being almost completely absent. Mammals were represented by ca. 60 spp., among these large-bodied carnivores (Puma *Puma concolor*, Jaguar *Panthera onca*), large herbivores (Pampas Deer *Ozotoceros bezoarticus*, Marsh Deer *Blastocerus dichotomus* and Guanaco *Lama guanicoe*), bats, armadillos, and several rodents, while birds were mainly ground-dwelling species (Soriano et al. 1991; Ghersa and León 2001; Chebez 2008). Only small groups of indigenous nomadic people inhabited the area before Europeans brought horses and cattle by the mid 16th century. While the indigenous people had probably used fire to facilitate hunting, it is assumed that both the fire and grazing regimes would have changed greatly since the introduction of livestock as well as the use of fires to herd the cattle and horses around 1600 (Soriano et al. 1991).

Agriculture expansion phase

Since the beginning of the 20th century grasslands have been transformed at high rates into cropland and managed pasture, affecting both landscape structure and land use patterns (Viglizzo et al. 2001; Paruelo et al. 2005; Martínez-Ghersa and Ghersa 2005). In the 1880s land cultivated with annual crops (mainly wheat, corn and flax) occupied <10% of the land in half of the region, while the rest was exclusively covered by natural grasslands. By about 1930 croplands covered between 20 and 60%, depending on the Pampean subunit considered. These figures (by then including sunflower and sorghum) climbed to 40–60% by the late 1980s (Soriano et al. 1991; Hall et al. 1992; Viglizzo et al. 2001; Baldi and Paruelo 2008). The original landscape had thus become a heterogeneous mosaic with a few isolated fragments of natural habitat. It consisted of many pastures and cultivated fields, and a network of linear habitats developed along the crop field margins, roadsides, riversides, and fencerows. This supported a mixed vegetation dominated by herbaceous species from the native grasslands together with introduced (herbaceous and non herbaceous) weedy and invasive plants (Viglizzo et al. 2001; Ghersa et al. 2002).

Intensification phase

From the late 1980s, technology (adoption of no-tillage techniques and genetically modified cultivars) and market conditions (global increase in soybean demand) (Baldi and Paruelo 2008) led to an intensification of agriculture with rapid replacement of mixed cattle grazing-cropping systems with continuous cropping, and an increase of field sizes. The landscape of the Southern, Rolling, and Flat Inland Pampas developed into homogeneous cropland. For instance, ca. 75% of the Flat Inland and Rolling Pampas were croplands in 2002–2004 (Paruelo et al. 2006; Baldi and Paruelo 2008), and taking only the province of Buenos Aires into account, the soybean harvested area increased from 1,400 ha in 1971 to 5,109,041 ha in 2009 (SAGPYA 2009). Along with this process, many wire fences and hedgerows were removed to enlarge fields, and natural grassland, roadsides, riversides and woodlot areas were cultivated. Thus the overall proportion of non-cultivated area further decreased, as did the diversity of crops and management practices (Aizen et al. 2009). The biodiversity within fields also decreased (de la Fuente 2010). Only the Mesopotamic, Flooding, and Western Inland Pampas are still dominated by grassland devoted to cattle raising (85.1% of the area of the Flooding Pampa was assigned to this use in 2002–2004) (Paruelo et al. 2006; Baldi and Paruelo 2008).

It is expected that intensification will continue in the future unless there is government intervention, or market factors that are promoting soybean crop expansion change. Moreover, it is likely that use of transgenic cultivars will increase as new transgenic forms become available.

Threats to animal biodiversity

The impact of agricultural intensification on animal organisms has received much attention worldwide but is not yet fully understood. Population decline and species extinction have been reported for a numbers of birds and butterflies (Robinson and Sutherland 2002; Thomas et al. 2004; Butler et al. 2007). Some authors (Kremen et al. 2007; Potts et al. 2010) assert that native pollinators are undergoing a worldwide decay; although, Westphal et al. (2003) and Winfree et al. (2007) find opposite results. Rodents (usually monitored in agricultural landscapes because of their behaviour as pests, Stenseth et al. 2003; Singleton et al. 2005; Brown et al. 2007) are being given particular attention because of their contribution to the complexity of food webs (Ellis et al. 1998; Parera 2002; Millán de la Peña et al. 2003; Butet et al. 2006; Michel et al. 2006).

In the Pampas, agriculturization threatens native animals through destruction, fragmentation and/or loss of quality of original habitat, the introduction of competing animals, and direct human impact (hunting and pesticide spraying). Consequences have varied in severity among animal groups (Table 1) reaching regional extinction in the cases of iconic species like the Puma and Jaguar.

Conservation initiatives

Concerns about the conservation of the native Pampean biota has concentrated on birds and large herbivores. A listing of 'Important Bird Areas' (IBAs) for Argentina was released in 2005 (Di Giacomo 2005), and Bilenca and Miñarro (2004) identified 'Valuable Grassland Areas' (VGAs), defined as 'sizeable portions of natural grassland in good conservation status' distributed across the Pampas. If the VGA and IBA sets are superimposed, a total of 41 different sites result (Table 2), with a combined area over one order of magnitude greater than that currently protected in the Pampean region (only 0.3% of the original area is currently protected; Krapovickas and Di Giacomo 1998). The remaining populations of Pampas Deer are under protection in the Flooding Pampa (Merino et al. 1997) and progress has been made in the conservation of grassland birds, including coordinated efforts of researchers, non-government organizations, and landowners also in the Flooding Pampa (Marino 2008). The Swainson's Hawk *Buteo swainsoni*, the decline of which during the mid 90s emerged as a paramount example of improper usage of pesticides in the Pampas (Goldstein et al. 1996), is showing some recovery after efforts aimed at extension, education and research (Sarasola et al. 2007).

The problem

Conserving biodiversity in intensively managed agricultural landscapes depends on understanding and overcoming the limits to persistence of ecological communities and constituent species (Prober and Smith 2009). Within the pampas countries there is a general lack of knowledge about the impact on terrestrial biodiversity of native grassland transformation, and there is generally a poor appreciation of the importance of biodiversity conservation in temperate grasslands (Bilenca and Miñarro 2004). Most of the existing information about the effects on biodiversity of large scale transformation of native grassland has been obtained from temperate grasslands in North America (prairies), northern Europe (UK) and southern Australia (Rolls 1999, Robinson and Sutherland 2002, Brennan and Kuvlesky 2005). Most South American temperate grasslands, such as the Pampas region in South America, lack comprehensive inventories of animal biodiversity and an understanding of the effects of agricultural intensification on native fauna. Besides, there are few refereed publications about the extent of native grassland transformation in the Pampas region, much of the data being in government or consultancy reports (Bilenca and Miñarro 2004). Thus, reviews of the effects of native grassland transformation on animal biodiversity (specifically from regions that are generally underrepresented) are of great importance for future temperate ecosystem conservation, research and management.

Table 1 Threatened vertebrates of the Pampas

TAXON	Scientific name	Common name	Conservation status	Source
AN	*Argenteohyla siemersi*	–	Vulnerable	Ubeda and Grigera (2003)
AN	*Melanophryniscus stelzneri*	Red-Bellied Toad	Vulnerable	Ubeda and Grigera (2003)
AN	*Ceratophrys ornata*	Ornate Horned Frog	Near threatened	Lavilla et al. (2000)
AR	*Ozotoceros bezoarticus*	Pampas Deer	Endangered	González and Merino (2008)
AR	*Blastocerus dichotomus*	Marsh Deer	Vulnerable/ endangered	Chebez (2008); Parera (2002)
AR	*Lama guanicoe*	Guanaco	Vulnerable	Baldi et al. (2008)
AV	*Sporophila zelichi*	Zelick's Seedeater	Critically endangered	Mazar Barnett and Pearman (2001)
AV	*Alectrurus risora*	Strange-Tailed Tyrant	Regionally extinct	Di Giacomo and Di Giacomo (2004)
AV	*Numenius borealis*	Eskimo Curlew	Regionally extinct	Chebez (2008)
AV	*Rallus antarcticus*	Austral Rail	Regionally extinct	Narosky and Di Giacomo (1993); Narosky and Yzurieta (2003)
AV	*Gubernatrix cristata*	Yellow Cardinal	Endangered	Mazar Barnett and Pearman (2001)
AV	*Sporophila palustris*	Marsh Seedeater	Endangered	Mazar Barnett and Pearman (2001)
AV	*Heteroxolmis dominicana*	Black-and-White Monjita	Vulnerable	Mazar Barnett and Pearman (2001)
AV	*Sporophila cinnamomea*	Chestnut Seedeater	Vulnerable	Mazar Barnett and Pearman (2001)
AV	*Sturnella defilippi*	Pampas Meadowlark	Vulnerable	Mazar Barnett and Pearman (2001)
AV	*Xanthopsar flavus*	Saffron-Cowled Blackbird	Vulnerable	Mazar Barnett and Pearman (2001)
CA	*Chrysocyon brachyurus*	Maned Wolf	Regionally extinct	Parera (2002)
CA	*Panthera onca*	Jaguar	Regionally extinct	Chebez (2008); Parera (2002)
CA	*Procyon cancrivorus*	Crab-eating Raccoon	Regionally extinct	Parera (2002)
CA	*Puma concolor*	Puma	Regionally extinct	Chebez (2008)
CA	*Lontra longicaudis*	Neotropical Otter	Endangered	Parera (2002)
CA	*Leopardus colocolo*	Pampas Cat	Near threatened/ vulnerable	Pereira et al. (2008)
CI	*Chlamyphorus truncatus*	Lesser Fairy Armadillo	Vulnerable	Parera (2002)
CI	*Dasypus hybridus*	Southern Long-Nosed Armadillo	Near threatened	Abba et al. (2007)
CI	*Zaedyus pichiy*	Pichi	Near threatened	Parera (2002)

Table 1 continued

TAXON	Scientific name	Common name	Conservation status	Source
RO	*Ctenomys australis*	Southern Tuco-Tuco	Endangered	Lessa and Bidau (2008
RO	*Bibimys torresi*	Crimson-Nosed Rat	Vulnerable	Gómez Villafañe et al. (2005)
RO	*Dolichotis patagonum*	Patagonian Cavy	Vulnerable	Gómez Villafañe et al. (2005)
RO	*Ctenomys porteousi*	Porteous's Tuco-Tuco	Near threatened	Bidau et al. (2008)
RO	*Necromys obscurus*	Dark Bolo Mouse	Near threatened	D'elia et al. (2008)
RO	*Phyllotis bonariensis*	Buenos Aires Leaf-Eared Mouse	Near threatened	Pardiñas and Jayat (2008)
SQ	*Pristidactylus casuhatiensis*	Casuhatien Anole	Endangered	Ubeda and Grigera (2003)
SQ	*Anisolepis undulatus*	Wiegmann's Tree Lizard	Threatened	Ubeda and Grigera (2003)
SQ	*Urostrophus gallardoi*	–	Threatened	Ubeda and Grigera (2003)
SQ	*Cnemidophorus lacertoides*	South American Teiid Lizard	Vulnerable	Ubeda and Grigera (2003)
SQ	*Leptotyphlops albifrons*	Wagler's Blind Snake	Vulnerable	Lavilla et al. (2000)
SQ	*Liolaemus multimaculatus*	Sand Dune Lizard	Vulnerable	Ubeda and Grigera (2003)
SQ	*Liophis elegantissimus*	–	Vulnerable	Ubeda and Grigera (2003)
TE	*Chelonoidis donosobarrosi*	–	Threatened	Ubeda and Grigera (2003)
TE	*Trachemys scripta dorbignyi*	Black-Bellied Slider	Vulnerable	Ubeda and Grigera (2003)

Species are ordered by taxa (*AN* Anura, *AR* Artiodactyla, *AV* Aves, *RO* Rodentia, *CA* Carnivora, *CI* Cingulata, *SQ* Squamata, *TE* Testudines) then by decreasing risk category. Most sources employ IUCN conservation status categories, but Mazar Barnett and Pearman (2001) use those of BirdLife International (2000)

Table 2 Distribution of valuable grassland areas (*VGAs*) and important bird areas (*IBAs*) over the Pampean subregions of Argentina

	Mesopotamic Pampa	Rolling Pampa	Flooding Pampa	Inland Pampa	Southern Pampa
VGAs (Bilenca and Miñarro 2004)	2	6	8	6	5
IBAs (Di Giacomo 2005)	4	10	7	4	4
Total (excluding duplicate sites)	5	10	10	8	8

Thus, the objectives of this work are to summarize the available information on the effects of agriculture on biodiversity of several groups of animals (birds, rodents, other vertebrates, crop-associated insects and pollinators) and to highlight future research needs for the conservation of animal biodiversity in the Pampas of Argentina.

Methods

Selection of animal groups

Vertebrate taxa (birds, rodents, and others), crop-associated insects and pollinators were chosen as target groups to highlight the effects of agriculture on Pampean animal biodiversity. These groups were selected because of their ecological relevance, the availability of information, and the authors' personal background (see references).

Birds are important seed dispersers and regulators of population size of both vertebrate and invertebrate groups, and are also widely recognized as indicators of human-driven environmental disturbation. Last but not least, birds attract public interest and have a high recreational value, both for birdwatchers and hunters (Diamond and Filion 1987). Rodents regulate plant and invertebrate populations through seed and soil invertebrate consumption, while fossorial species have an important role in nutrient cycling and maintenance of soil structure. Rodents constitute the main prey for terrestrial (opossums, grisons, foxes, Pampas Cat *Leopardus colocolo* and Geoffroy's Cat *L. geoffroyi*) and avian carnivores (Barn Owls *Tyto alba*, Burrowing Owls *Athene cunicularia* and American Kestrels *Falco sparverius*). Rodent abundance thus directly influences abundance and diversity of predators (Ellis et al. 1998; Parera 2002). Moreover, some species are good indicators of human-caused environmental change. Other groups of native and exotic vertebrates were included to record nearly-lost ecological roles (large native carnivores and herbivores), because of their invasive character, or due to conservation concerns (reptiles and amphibians) (Chebez 2008).

Crop-associated insects can reflect the outcome of contrasting strategies of crop management, thus helping to monitor the effects of human activity, particularly in the phase of agriculture intensification (Büchs 2003). Pollinators have widely recognized importance for plant reproduction both in natural environments and in agroecosystems. Their service may be divided between native plant species and communities of alien weeds associated with crops, thus affecting the survival of native flora. The value of pollination as an ecosystem service has been estimated at over S1200 million annually for the whole Río de la Plata grasslands, assuming these are 20% grasslands and 80% croplands (calculation based on data from Costanza et al. 1997).

Approach

A literature search was undertaken of books, journal papers, reviews and website data, as well as published theses and congress reports. In a few instances, local experts' opinions were quoted. In the case of insects, a different approach was used to assess the consequences of agriculture disturbance, because data on the pre-disturbance status are missing. First, it was analyzed how communities associated with two crops (wheat and soybean) varied as related to cropping history and crop management practices. Sweep net captures were carried out in wheat crops during the spring of 1996 and 1997 and in soybean crops during the summers of 1999, 2001 and 2002, covering an area of ca. 5×10^4 ha in the Rolling Pampas (Fig. 1). Surveyed fields had similar soil environments but differed in their cropping history (the number of years with permanent agriculture, the identity of the preceding crop, and crop management practices). Soybean fields in particular differed in the presence or absence of green field margins and in the contrast with the surrounding landscape. Second, diversity of pollinators under three land use regimes was addressed: cattle grazing, cultivation with an oilseed crop (sunflower), and abandonment of agriculture. Pollinators are absent from wheat and soybean assemblages, thus the two approaches are complementary.

Results

Birds

The current richness of the avifauna of the Río de la Plata grasslands, as measured on the basis of distribution areas, varies from 350 to 250 species in NE-SW direction. Additionally, this biome offers wintering sites for several Neotropical migratory species (Di Giacomo and Krapovickas 2003). The total number of birds presently inhabiting the Pampean area is estimated at 300 species, of which about 60 are grassland specialists (Krapovickas and Di Giacomo 1998). Since there are few known extinct species (see below), a figure of around 300 species seems a reasonable estimation of the entire original Pampean avifauna.

Agricultural expansion, habitat change and human-induced disturbance affected Pampean avian biodiversity in various ways (Krapovickas and Di Giacomo 1998). Three species became regionally extinct (Table 1). The Eskimo Curlew *Numenius borealis*, was once a widely distributed summer visitor to the Pampas (Chebez 2008) but is presently on the brink of global extinction (BirdLife International 2000). For several other species, there is evidence of a reduction in population size and/or distribution (Bucher and Nores 1988; Fraga et al. 1998; Tubaro and Gabelli 1999; Fraga 2003). Ten Pampean bird taxa are currently considered as globally threatened (Birdlife International 2000) (Table 1).

The most important factor behind these changes is thought to be the loss of adequate reproductive habitat (Cozzani and Zalba 2009), due to conversion of grasslands into agricultural fields and afforestation, as well as cattle grazing and drainage of wetlands (Fraga et al. 1998; Fernández et al. 2003; Di Giacomo and Di Giacomo 2004; Gabelli et al. 2004). The regional extinction of Eskimo Curlew may be at least partly explained by habitat transformation and heavy hunting in its nesting and wintering areas (Chebez 2008). Additional causes of bird decline include illegal capture for pet trade (Saffron-cowled Blackbird *Xanthopsar flavus*, Fraga et al. 1998 and Pampas Meadowlark *Sturnella defilippi*, Tubaro and Gabelli 1999), hunting for feathers, leather and food for humans (Greater Rhea *Rhea americana*, Navarro and Martella 2008), poisoning by pesticides, as already mentioned in the case of Swainson's Hawk(Goldstein et al. 1996), and increased brood parasitism by Shiny Cowbird *Molothrus bonariensis*, a species that has been favoured by habitat transformation brought about by agricultural development (Gabelli et al. 2004).

Despite reported extinctions, the Pampean avifauna increased in richness during agriculture expansion and with an additional 20 species now present than when agriculture began. Several species (e.g., Rufous Hornero *Furnarius rufus,* Rufous-bellied Thrush *Turdus rufiventris*, and Monk Parakeet *Myopsitta monachus*), originally inhabited the xeric woods which surround the Pampas, but have since penetrated the whole region. This process followed the planting of trees for several purposes (wind breaks and shade refuges for cattle) and the massive extension of the network of wire fences (Ghersa and León 2001). Increased food availability due to afforestation and annual crops explains the expansion of certain species, including the Picazuro Pigeon *Columba picazuro* across the entire area (Narosky and Di Giacomo 1993) and the White-throated Hummingbird *Leucochloris albicollis* in the eastern areas (Montaldo 1984). Three exotic species (House Sparrow *Passer domesticus*, Rock Pigeon *Columba livia* and European Starling *Sturnus vulgaris*) are slowly diffusing from peridomestic sites to agroecosystems (Peris et al. 2005; Garaffa et al. 2009).

Rodents

Until ca. 1910, i.e., before the initial expansion of agriculture in the Pampas, the most abundant rodent species were the native sigmodontines, the Pampean Grassland Rodent *Akodon azarae* and the Common Burrowing Mouse *Oxymycterus rufus*. The Dark Bolo Mouse *Necromys obscurus,* Argentine Rice Rat *Oligoryzomys flavescens,* Vesper mice *Calomys* spp. and the introduced House Mouse *Mus musculus* were rare (Crespo 1966; Dalby 1975; Bilenca and Kravetz 1995). The high homogeneity of the original grasslands caused both the low diversity and evenness of rodent species (Bilenca and Kravetz 1995). The spatial distribution and abundance of individuals of different species of rodent were regulated by interespecific competitive effects. Competitive interactions by interference for space were expressed as negative spatial associations between species, which caused interspecific segregation at the individual level (Busch and Kravetz 1992a, b; Busch et al. 2005).

The expansion of agriculture after 1910 generated a great diversity of habitats suitable for many wild species of small mammal, all of which were highly represented when densities of predators were low (Parera and Kesselman 2000). The high patchiness of landscapes increased the diversity of wild rodents (both the most common and generalist species and the rare or habitat-specialist ones). All habitats varied seasonally in structure and in both quality and amount of available resources, which induced changes in the patterns of habitat use by different species and promoted movements between habitats (Busch and Kravetz 1992a; Ellis et al. 1997). Although much of the rodent population (up to 90%) declined as a result of the direct mechanical effects of harvesting and ploughing and/or by subsequent predation after agricultural practices (de Villafañe et al. 1988), many individuals (up to 77%) survived harvest disturbance by moving from agricultural fields towards the edges (Cavia et al. 2005; Hodara and Busch 2006). Field areas could be favourable habitats at some times of the year, especially before the harvest of summer crops (de Villafañe et al. 1988; Hodara et al. 2000; Hodara and Busch 2010), but edges provided better habitat than crop fields for many small mammals due to the much lower impact of agricultural practices. In Pampean agroecosystems such linear habitats provide shelter, food, nesting sites and protection against terrestrial and avian predation pressure for a sizeable assemblage of small mammals, including at least 14 rodent species, three marsupials and one carnivore (Mills et al. 1991; Ellis et al. 1997; Miño et al. 2001).

The Pampean rodent fauna currently includes 36 species, four of which are introduced (Gómez Villafañe et al. 2005). Regarding their biology, the best known ones are five sigmodontines: Pampean Grassland Rodent, Small Vesper Mouse *Calomys laucha*, Vesper Mouse *C. musculinus*, Argentine Rice Rat, and Common Burrowing Mouse, the native caviid Brazilian Guinea Pig *Cavia aperea*, the introduced murines House Mouse, Black Rat *Rattus rattus* and Brown Rat *R. norvegicus*. The Dark Bolo Mouse, *N. benefactus*, Red Marsh Rat *Holochilus brasiliensis*, Argentine Swamp Rat *Scapteromys aquaticus* and Coney Rat *Reithrodon auritus* are native sigmodontine species less well represented in the Pampean rodent community. Pampean Grassland Rodent, Dark Bolo Mouse, Argentine Rice Rat and Brazilian Guinea Pig usually inhabit linear undisturbed habitats, although the two last species, together with Common Burrowing Mouse and Argentine Swamp Rat, are also associated with edges of water bodies. Vesper mice are numerically dominant in wheat and maize fields but avoid soybean fields (Mills et al. 1991; Busch and Kravetz 1992a; Ellis et al. 1997; Hodara et al. 2000; Busch et al. 2001). The Red Marsh Rat is associated with riparian habitats, while the Coney Rat and Dark Mouse use open habitats like pastures and grasslands (Gómez Villafañe et al. 2005). The introduced murines are mostly restricted to poultry farms and human dwellings surroundings (Gómez Villafañe et al. 2001; Miño et al. 2007), although House Mice can occasionally be found in cultivated areas as well (Busch et al. 2005).

In conclusion, what is known about patterns of habitat use and movements of Pampean rodents (Ellis et al. 1997; Cavia et al. 2005; Hodara and Busch 2006; 2010), as well as about their nesting behaviour (Hodara et al. 1997; Gómez Villafañe et al. 2005) and dietary habits (Ellis et al. 1998), indicate that the introduction of agriculture in the area has had a profound impact on the group as a whole, by affecting both shelter and food availability, and consequently reproductive success. The initial expansion phase had a generally positive influence, but the current intensification of agriculture seems to reduce diversity, favouring more common species at the expense of rare or habitat-specialist species, and density, by promoting concentration of individuals around sites of higher food availability (Miño et al. 2007).

Other vertebrates

Considering both native and introduced species, vertebrates other than birds and rodents are represented in the Pampas by ca. 123 species in ten orders, including mammals (29 spp.; Parera 2002; Chebez 2008), reptiles (49 spp.) and amphibians (35 spp.) (Lavilla et al. 2000; Ubeda and Grigera 2003). The impact of human activities on the native species has differed depending on the taxonomic and functional group to which they belong.

Large-bodied carnivores Puma, Jaguar and Maned Wolf *Chrysocyon brachyurus*, which were historically distributed across the Pampas are currently locally extinct due to the high hunting pressure to prevent livestock depredation and because of agriculture expansion (Parera 2002; Chebez 2008). Population densities of medium-bodied carnivores such as skunk *Conepatus chinga*, Pampas Fox *Pseudalopex gymnocercus*, Lesser Grison *Galictis cuja*, Geoffroy's Cat and Pampas Cat strongly decreased due to habitat fragmentation and habitat loss (Crespo 1966; Pereira et al. 2002, 2008). In comparison, populations of omnivorous mammals like armadillos (Large Hairy Armadillo *Chaetophractus villosus,* Screaming Hairy Armadillo *C. vellerosus,* Pink Fairy Armadillo *Chlamyphorus truncatus,* Southern Long-nosed Armadillo *Dasypus hybridus* and Dwarf Armadillo *Zaedyus pichiy*) and opossums (White-eared Opossum *Didelphis albiventris,* Yellow-sided Opossum *Monodelphis dimidiata* and Lutrine Opossum *Lutreolina crassicaudata*) have been less affected by agricultural intensification (Parera and Kesselman 2000; Abba et al. 2007).

Populations of three wild ungulates (Pampas Deer, Marsh Deer and Guanaco) are decreasing mainly due to habitat alteration by agriculture, tree plantations, and competition with domestic livestock. Introduced livestock have competed directly for food resources with all three species, and indirectly through the transmission of their diseases to native animals (Uhart et al. 2003; Vila et al. 2008). This has led to disruption of original geographical distributions, range reductions and local extinction (Real et al. 2003). Guanacos survive as relict populations in the Pampas' southwest (Baldi et al. 2008), and the remaining populations of Pampas Deer and Marsh Deer are small and highly isolated (e.g., a population of Pampas Deer of ca. 200 individuals which is protected within the Flooding Pampa; González and Merino 2008).

Amphibians and reptiles are represented in the Pampas by ca. 84 native species, many of which (9% of amphibians and 18% of reptiles, Table 1) are threatened to some extent because of habitat loss and soil and water pollution due to agricultural practices (Lavilla et al. 2000; Ubeda and Grigera 2003).

Three introduced mammals are currently considered as invasive in the Pampean region. Wild Boars *Sus scrofa* and Black Buck *Antilope cervicapra* negatively affect the Pampas Deer populations by competition for resources (Jaksic et al. 2002; Parera 2002; Chebez 2008). Wild Boars are considered as a pest because they uproot and trample agricultural fields and damage tree bark. The European hare *Lepus europaeus*, introduced in Argentina at the end of the 19th century, competes with livestock for pastures, damages grasslands, crops, and fruit, and hampers the regeneration of the native forest (Jaksic et al. 2002; Novillo and Ojeda 2008). However, this species is also beneficial to the native herbivorous fauna, because it increases the supply of prey to large predators, and consequently lowers predation pressure on native fauna (Jaksic et al. 2002; Novillo and Ojeda 2008). Hares and Wild Boars are considered a threat to cattle because both of them host several diseases (porcine fever, trichinosis and fascioliasis).

Insects

Insects are the largest group of invertebrates and the most diverse group of animals on Earth, with over a million described species, i.e., more than half of all known living organisms (Price 1997). Two insect surveys of Argentina report several thousand species in 19 orders for the whole country (Morrone and Coscarón 1998; Claps et al. 2008), despite the fact that the second of these surveys did not include the whole order Lepidoptera and some large families of Diptera, Hymenoptera and Coleoptera. Unfortunately, the geographical distribution of species are described in administrative units instead of zoogeographical ones, thus no clear characterization of the current Pampean entomofauna can be inferred from these reports, or of the pre-agriculture insect diversity in the area.

Crop insects

Fifty-three insect morphospecies were recorded for wheat and thirty for soybean, belonging to Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera, Neuroptera, Orthoptera and Thysanoptera. Wheat and soybean assemblages shared only six morphospecies belonging to Coleoptera, Diptera, Hemiptera and Neuroptera (de la Fuente et al. 2003; de la Fuente 2010). Analysis of a partial sample (60%) of the wheat insect assemblage yielded 50% herbivores and 50% non-herbivores (de la Fuente et al. 2003), while an 83% sample of the soybean assemblage yielded 60% herbivores and 40% non herbivores (de la Fuente 2010).

The richness of wheat insect communities was lower in fields with more years of continuous annual cropping after a pasture and when soybean was the preceding crop. This decreased richness was related to soil degradation promoted by agricultural intensification (de la Fuente et al. 2003). As the number of years with annual cropping increased, soil environment was impoverished by erosion and by nutrient consumption by the crop (Michelena et al. 1989). The effect of soybean as preceding crop was also related to the impoverishment of the soil caused by the number of years with annual crops (de la Fuente et al. 2003), because farmers introduce soybean in the rotation assuming that its yield is less affected by low nitrogen availability in the soil than the yield of other summer crops (Karlen et al. 1994). On the other hand, higher richness values in the insect assemblage were associated with low intensification, expressed in good soil environmental conditions and higher wheat yields. Food quality and quantity have been recognized as controlling insect richness (Howe and Westley 1988).

Soybean fields with high productivity (expressed in high NDVI, Normalized Difference Vegetation Index) and green margins had richer insect assemblages, both in number of orders and species (de la Fuente 2010). The link of NDVI with insect richness is related to availability of food quality in terms of greenness and availability of water (Bailey et al. 2004). The effect of green field margins may be associated with the diversity of habitats, which increases the species pool (Purtauf et al. 2005) and to the proximity between species refuges and the disturbed site (Weibull and Östman 2003). Non-herbivore species richness was lower when soybean fields were surrounded by other soybean fields, while herbivores were not affected by the contrast between soybean fields and their surrounding landscape (de la Fuente 2010). Agroecosystem contrasts may not impact on all species or guilds in a similar way (Tscharntke et al. 2005). Non-herbivores may have profited from contrasts because heterogeneous landscapes support alternative hosts, host plants and provide more nectar sources (Thies et al. 2003).

These surveys reveal the importance of agricultural activities in the regulation of the structure and richness of insect communities in Pampean agroecosystem. Thus, both impoverishment of the soil environment and landscape homogenization seem to be related to a reduction in the richness of crop-associated insects. Impoverishment of the soil environment is related to the number of years of continuous annual cropping, while landscape homogenization is associated with both the recent expansion of soybean crop and the low contrast between soybean crop and the surrounding landscape as well as to the absence of green field margins. Then, agriculture intensification and homogenization of crop management are expected to have reduced the original insect biodiversity at least in the central Rolling Pampas (de la Fuente 2010).

Pollinators

The importance of insect pollination in the original Pampas can be measured by the current richness of the native anthophilous entomofauna and the zoophilous flora of the Buenos Aires province which is the Pampean core district (Fig. 1). In the area, there are ca. 90 spp. of butterflies (Canals 2000) and ca. 180 spp. of grassland-typical bees (A. Roig-Alsina, pers. comm.). The proportion of bees plus butterflies in well-resolved American plant-pollinator systems is about 30% of all pollinators (Robertson 1929; Basilio et al. 2006; Torretta 2007). Then, the Buenos Aires pollinator entomofauna should be in the order of $(90 + 180)/0.3 = 900$ species. The zoophilous flora of the Buenos Aires province, excluding alien taxa and zoophilous species of two non-Pampean enclaves, amounts to ca. 900 species, equivalent to 41% of all flora (Parodi 1940; Burkart 1957; Zuloaga et al. 1999). Thus in this province alone some $900 + 900 = 1800$ native insect and plant species are linked by pollination interactions.

The introduction of alien species (cattle and weeds) into the Pampas affected native pollination partners and their interactions, as revealed by the analysis of present pollination webs. Results differ if sites are assigned to cattle grazing on native pastures, or to continuous cropping. In a site of the first type located in the Flooding Pampa, Roitman (1998) described a pollination web dominated by interactions between native insects and native plants (Table 3). Here, a significant 2.5 fold increase in pollinator availability was found inside 15-year-old cattle exclosures, as compared to the heavily grazed surroundings. Females of a specialist pollinator (the ground-nesting, oil-collecting apid bee *Chalepogenus roitmani*) were recorded visiting flowers of the perennial herb *Cypella herbertii* only inside the cattle-free enclosures, and were never seen outside. The scarcity or even total absence of pollinators outside the enclosures was attributed to the lower availability of

Table 3 Composition of five assemblages of pollinators and their host plants surveyed in the Pampean area, and distribution of their interactions according to the partners' geographical origin

Data source/Pampean subdivision	No. of native/alien		No. of interactions (%)			
			Of native pollinators with		Of alien pollinators with	
	Pollinators	Plants	Native plants	Alien plants	Native plants	Alien plants
Roitman (1998)/Flooding Pampa	13/1	6/3	21 (65.6)	10 (31.3)	1 (3.1)	0 (0.0)
Chamer et al. (2003)/Inland Pampa	39/1	3/7	9 (13.0)	59 (84.0)	0 (0.0)	2 (3.0)
Torretta (2007)/all subdivisions except Mesopotamic Pampa	128/6	39/42	95 (33.7)	153 (54.2)	14 (4.9)	20 (7.0)
Fernández Corujo et al. (2009) (1-year-old enclosure)/Inland Pampa	99/2	14/20	68 (21.9)	228 (73.5)	3 (0.9)	11 (3.5)
Fernández Corujo et al. (2009) (40-year-old enclosure)/Inland Pampa	81/2	14/9	126 (70.4)	46 (25.7)	3 (1.7)	4 (2.2)

For further details see text

nesting sites (due to soil compaction and vegetation changes) caused by cattle trampling. Later studies in the area suggested that pollinator shortage, together with reduced seed set when self-pollinated, puts *C. herbertii* at reproductive risk under severe grazing (Devoto and Medan 2004, 2008).

In contrast, areas under intense agriculture in the Inland Pampa showed pollination webs dominated by interactions between native insects and alien weeds, while native plants played a secondary role as food plants (Table 3). In a sunflower field Chamer et al. (2003) found that 84% of the interactions were of the native-alien type, and Torretta (2007) found 54.2% of native-alien vs. 33.7% of native–native interactions after sampling sunflower fields in nearly all Pampean subunits. In these sites, native pollinators could have native plants as a secondary option. Cilla et al. (2007) showed that adult females of native *Melissodes* bees initially transported virtually pure sunflower pollen to their nests, but resorted to native plants at the end of the crop flowering period. When alien weeds gradually disappeared in sites where agriculture was abandoned, native pollinators switched to native plants (Fernández Corujo et al. 2009).

The pollinators introduced into the Pampas are the European Honey Bee *Apis mellifera*, the recently naturalised alfalfa leafcutter bee, *Megachile rotundata* (A. Roig-Alsina, pers. comm.), three syrphid flies and two muscoid flies (Torretta 2007). Although few, these species can be involved in up to 12% of all interactions in Pampean pollination webs (Table 3).

Discussion

We have presented the available information on the effects of agriculturization of the Pampas on several animal groups. To the best of our knowledge, this is the first attempt to assess the effects of agriculture on vertebrate and invertebrate animals of this region simultaneously. In the following paragraphs we (a) point out to causes and extent of changes experienced by populations of Pampean animals during agriculture expansion and intensification, (b) indicate past and present research vacancy areas, and (c) identify future actions needed to complete the evaluation of Pampean animal biodiversity and to develop conservation programs.

Causes and extent of changes

Biodiversity decline under agriculture is primarily caused by direct losses of native vegetation through clearing, with remaining native biodiversity further impacted by the introduction of livestock, soil cultivation, use of fertilizers and introduction of alien species (Prober and Smith 2009). All these causes have been present or are still in action in Pampean agriculture, as well as derived causes like habitat fragmentation and reduced landscape heterogeneity. Interestingly, the presence in the Pampas of large herbivores and predators may have buffered impacts on biodiversity. Grazing and trampling by native Guanacos and Pampas Deer was an existing pressure on soils and the associated fauna when cattle and horses were introduced (although the formers' grazing pressure may have been limited; Ghersa and León 2001). Thus, the introduced species may have only intensified the effect. Similarly the suppression of top predators (Jaguar and Puma) by hunting and other factors may have been balanced in the impact exerted on their prey (the smaller vertebrates) by habitat destruction and hunting by people.

Agriculture expansion

This first phase witnessed regional extinctions (some birds and large carnivores) and a reduction in the ranges and/or abundances of many other animals, including smaller carnivores, herbivores, and particular habitat-specialist or feeding-specialist taxa (grassland-adapted birds and rodents, and specialized pollinators) due to reduction and/or loss of connectivity of habitats suitable for survival and reproduction. Increased landscape heterogeneity and habitat disturbance had neutral effects for some birds, armadillos and opossums, and was favourable for other birds, rodents and possibly generalist pollinators and crop-associated insects, all of which became more abundant locally and/or increased their geographical ranges.

A study by Filloy and Bellocq (2007) clearly shows these variable responses for birds. These authors studied a 300 km long gradient in increasing agricultural intensity extending from the heavily cultivated Rolling Pampa into the mainly grazed Flooding Pampa. Out of the 43 most frequent bird species, 30.2% increased their abundance as crop density dropped, 11.6% became less abundant, and 53.6% were unaffected or showed other response patterns.

The extinction of the largest carnivores elevated native birds of prey and smaller carnivores (opossums, foxes, and grisons) to the top of the food chain. Birds of prey are ecologically important because they control both insect and rodent populations, including pest grasshopper species and human disease-transmitting mice. However, they are particularly sensitive to human activities. This is evidenced by the case of Swainson's Hawk, a migratory species that breeds in the Northern Hemisphere and overwinters in the Pampas, which is slowly recovering after having been greatly reduced by pesticide poisoning. Moreover, broad home ranges and low densities make birds of prey susceptible to fragmentation and habitat loss (Trejo et al. 2007).

The introduction of new animals from other American biomes and from the Old World was an important driver of change during this phase. Even if the effects of domestic cattle are ignored aside, introductions were proportionally higher for non-rodent mammals (10 spp., or 26% of current fauna) than for rodents (4 spp., 11.1%), birds (20 spp., 6.2%), pollinators (7 spp., ca. 0.8%) and other terrestrial vertebrates (no introductions). However, only a few of those species seriously interfered with native animals, including domestic cattle, wild boars, Black Bucks and hares, the European Starling and the European Honey Bee.

Domestic cattle may have caused a deterioration in nesting conditions for ground-nesting native insects, subsequently affecting plants to which they are linked through mutualistic relationships, as suggested by the *Chalepogenus*-*Cypella* example. This case also illustrates the vulnerability of specialized mutualisms. In mutualistic networks, species with few links (i.e., specialists) have a greater probability of becoming extinct than those with many links (generalists) (Memmott et al. 2004; Burgos et al. 2007). Oligolectic bees are considered to be under higher risk of endangerment or extinction than generalist bees for genetic and demographic reasons, and less likely to be able to adapt to changing environmental conditions (Packer et al. 2005). For instance, Gess and Gess (1993) showed that excessive stocking rates, heavy selective browsing or grazing, and excessive trampling adversely affected the diversity of the bee fauna in South Africa. In the same region, seed set failure was observed for six specialist plant species depending on the oligolectic oil bee *Rediviva peringueyi,* in sites where the bee was absent (Pauw 2007).

Although the European Starling has recently appeared in the Pampas, it is a case deserving careful monitoring because of the harm it has caused in other places where it was introduced. In the United States this species competes successfully with native cavity-nesting birds such as woodpeckers, and its damage to agriculture has been estimated at $800 million annually (Pimentel et al. 2000).

The supergeneralist pollinator *Apis mellifera* may have impacted on Pampean pollination webs in different ways. It may have displaced native pollinators of native plants, with uncertain consequences to plants, but with almost certainly negative consequences for the pollinators (e.g., Paini and Roberts 2005). The honeybee may also have facilitated the expansion of introduced weeds by pollinating them. More interactions of alien pollinators with alien plant species than with native ones were found (Table 3). Most alien–alien interactions involved *A. mellifera* (details not shown). A study carried out elsewhere in Argentina explained similar results through a strong preference of *A. mellifera* for alien plant species (Morales and Aizen 2002). Groups of introduced species interacting more with each other than they would randomly do, have been termed 'invader complexes of mutualists' (*sensu* Olesen et al. 2002) and may have an important role in the establishment of weed communities in Pampean agroecosystems, one which was hitherto not examined. Even in the absence of competitive interactions with native pollinators, the honeybee may have altered the balance within plant communities through differential pollination of some native plants at the expense of others, which in turn may have triggered a cascade of destabilizing effects through the ecosystem.

Agriculture intensification

With the possible exception of pollinators, the second phase of agricultural intensificationwas detrimental for most Pampean animal groups, due to its associated loss of undisturbed habitats, increased landscape homogenisation, and use of chemicals. Direct evidence of negative effects of intensification was found for rodents (Zaccagnini and Calamari 2001; Millán de la Peña et al. 2003; Fraschina et al. 2009) and crop-associated insects (de la Fuente et al. 2010).

Loss of ecological heterogeneity directly affects the diversity, abundance, and distribution of small mammals (Todd et al. 2000; Jacob 2003; Millán de la Peña et al. 2003), particularly the rare or habitat-specialist species. Those Pampean species associated with grassland remnants and linear undisturbed habitats were affected by the loss of sites for nesting and digging shelters (Hodara et al. 1997; Gómez Villafañe et al. 2005). Increased usage of pesticides indirectly damaged rodents by reducing food availability through depletion of invertebrate prey, vegetation cover and weed seeds (Zaccagnini and Calamari 2001; Bennett et al. 2005).

Declines in Pampean bird populations due to intensification are also suspected (Filloy and Bellocq 2007) on the basis of data from other agricultural systems. In the UK, Butler et al. (2007) reported a ca. 50% reduction in the populations of bird species typical of agricultural areas from 1970 to the present, and in the US, Peterjohn and Sauer (1999) found that 75% of grassland-adapted bird species suffered population reductions from 1963 to 1993. The latter data are particularly significant given the existence of functional similarities between the North American temperate grasslands and the Pampean grasslands (Paruelo et al. 1995, 1998).

On the contrary, native pollinators may have benefited from the vast expanses of resource-rich crops, like sunflower and canola, available during the intensification phase. Increased food availability was a possible cause of the unexpected abundance and richness of bees reported by Winfree et al. (2007) in human-transformed areas of the eastern US, compared with nearby forested heath areas, which constitute the bees' original habitat, where abundance of most bee species decreased. In the Pampas both the structure of surveyed plant-pollinator webs (Chamer et al. 2003; Torretta 2007) and data from their nesting biology (Cilla et al. 2007) indicate that many native pollinators became opportunistically linked to alien plants. The extent to which this process disrupted pre-agricultural webs, with possible damage to both native plants and some native pollinators, is unknown. The slow return of native–native interactions after suppression of agriculture (Fernández Corujo et al. 2009) suggests that the process is at least partially reversible in protected environments.

Research gaps areas and their implications for conservation

This review revealed that knowledge of Pampean animal biodiversity is still very incomplete. While diversity of vertebrates is relatively well known, data on their distribution and abundance are fragmentary or non-existent. The lack of historical distributional records makes it difficult to establish how landscape transformation has changed species diversity, ranges and abundances. Despite several contributions (Tubaro and Gabelli 1999; Fernández et al. 2003; Fraga 2003; Cozzani et al. 2004) there is no single Pampean bird species for which the biology is completely understood. Since feeding behavior is unknown for most species, it is similarly unknown whether or not the introduction of alien species has affected the position of native species in food chains. The biology of the less abundant rodent species and their present distributions are also poorly known, as is their resilience under agricultural intensification. Further population surveys and ecological research on the native large herbivores are also needed.

Large taxonomic efforts are still required to attain a satisfactory knowledge of the diversity and distribution of terrestrial invertebrates in the area. The approximate number of species in large insect orders like Coleoptera, Hymenoptera, Diptera and Lepidoptera is still unknown. These efforts should include (i) increased training of specialists in taxonomy of all animal taxa, (ii) systematic sampling to supplement museum collections in every

Pampean subunit, particularly the areas under higher risk of losing diversity; those currently under agriculture intensification should be surveyed first, (iii) characterization of groups involved in key ecosystem roles like predators, pollinators, and others. Until these gaps are filled, local and regional species losses will go undetected, and identification of appropriate conservation areas will be difficult.

The proposed studies of Pampean animal biodiversity could be conducted at the sites summarized in Table 2. The results would be especially valuable for Rolling Pampa, Inland Pampa and Southern Pampa, since the original faunal diversity of these subunits persists only partially in the agricultural matrix. Contrasts between areas which never experienced anthropogenic alteration, or areas that have recovered after long-term suppression of agriculture, and corresponding human-used areas could provide a measure of the human impact, also helping to assess the value of conservation protocols applied on agricultural areas. It is worth noting that undisturbed landscape fragments may also conserve the original mutualistic interaction networks, as well as plant and animal species rarely or never recorded in agricultural fields. Unfortunately, many of the sites containing grassland remnants are located on private land and are waiting for legal protection to assure their permanence.

Researchers can play an important role in the future by providing a reliable picture of Pampean animal biodiversity, and by designing tools for stabilizing or, at least, minimizing, inevitable impacts on it (see e.g., Hopwood 2008; Noordijk et al. 2009; Cerezo et al. 2010). Governments and the society as a whole should devote efforts to reverse, at least in part, biodiversity loss through education, funding and implementation of long-term policies. The application of 'Best Management Practices' to maintain raptors in rural environments is an example of such successful cooperation (Demarchi and Bentley 2005).

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