



Exotic plants promote pollination niche overlap in an agroecosystem



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ABSTRACT

Agricultural land management modifies ecosystem structure and functioning in natural landscapes. Pollinators are a key functional group that may suffer from such intensification. Here we evaluate how agricultural land management influences the diversity of pollen transported by pollinators and the pollination niche overlap among plants. We described pollen transport networks (which allow assessing the contribution of pollinators to the flow of pollen among plants) in agricultural and restored fragments in three sites representative of the pampas region of Argentina. We analyzed diversity of pollen transported by pollinators and the pollination niche overlap among plants in both types of fragments with general and generalized linear mixed models. The agricultural fragments were associated to increased diversity of transported pollen and pollination niche overlap among plants. Greater pollination niche overlap in agricultural fragments was associated with increased abundance of exotic plants. Our results indicate that agricultural intensification has significantly increased the diversity of pollen and the pollination niche overlap in natural communities by promoting exotic plants and generalized plant-pollinator interactions. Strategies to encourage improvements in the quality of pollination in agroecosystems could range from controlling the levels of exotic species to mechanisms that promote increased diversity of native plants.

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1. Introduction

Over the last three centuries the intensification in agricultural land management produced a profound transformation of earth's surface (Ellis et al., 2010). Agricultural land management may greatly influence the structure of ecological communities and the functioning of ecosystems in natural landscapes (Kremen et al., 2007; Marrero et al., 2014; Kremen and M'Gonigle, 2015). Animal pollinators, which play a key ecological role in many ecosystems, are being greatly influenced by such intensification. Their pollination service may be affected by changes in pollen flow and pollination quantity and quality (i.e., the amount and type of pollen reaching floral stigmas, Larson et al., 2006; Garibaldi et al., 2011, 2014; Marrero et al., 2016). In addition, agricultural land

management can favor exotic plants (Marrero et al., 2014), which usually compete strongly with natives (Bjerknes et al., 2007; Muñoz and Cavieres, 2008; Stout and Morales, 2009; Morales and Traveset, 2009; Montero-Castaño and Vilà, 2012; Gómez et al., 2014).

Although exotic plants could be the only resource for pollinators in some agroecosystems (Nicholls and Altieri, 2013), little is known about their potential effects on other plants in the community. Exotic plants can disrupt mutualistic interactions between native plants and their pollinators and thus influence plant fitness (Traveset and Richardson, 2014). Grass et al. (2013) found increased pollinator visitation rates on native plants and decreased visitation to exotic plants with increasing exotic abundance and land-use intensity in agroecosystems. In addition, the functional diversity of pollinators in agroecosystems decreases with increasing relative exotic plant abundance, affecting pollination and the stability of plant-pollinator assemblages (Grass et al., 2014). However, nothing is known about the effects that agricultural land management and the presence of exotic plants have on pollen transport in agroecosystems.

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Limited space on the pollinator's body might restrict transported pollen loads, so that adding pollen of one species reduces the amount of pollen of another species (Mitchell et al., 2009). By negatively affecting specialist pollinators and promoting generalized pollinators that carry multi-specific pollen (Kremen et al., 2007; Fischer and Lindenmayer, 2007; Grass et al., 2013; Marrero et al., 2014; Weiner et al., 2014; Vanbergen, 2014; but see Vázquez and Simberloff, 2002), agricultural land management may lead to increased deposition of heterospecific pollen in floral stigmas (Marrero et al., 2016), increasing the pollination niche overlap among plants (Mitchell et al., 2009) and ultimately hampering fruit and seed production (Morales and Traveset, 2008; Ashman and Arceo-Gómez, 2013; Arceo-Gómez and Ashman, 2011a,b, 2016). Exotic species are often supergeneralists (Aizen et al., 2008; Vilà et al., 2009; Traveset and Richardson, 2014) with broad niches (Vázquez, 2006), which could lead to increased overlap in the pollination niche among plants in the invaded communities. High levels of pollination niche overlap might affect plant reproduction in general and even the yield of crops. For example, Montero-Castaño et al. (2016) showed that some mass flowering crops can influence pollinator patterns in the surrounding landscape by competing with native plants for generalist pollinators.

Here we evaluate how agricultural land management influences pollen transport by pollinators in the Argentine Pampas, a highly transformed region that has experienced a strong intensification of agricultural land management during the last two centuries (Medan et al., 2011). Although data are available on plant-pollinator interactions and composition of stigmatic pollen loads in this system (Marrero et al., 2014, 2016), some studies suggest that the analyses of pollen transported by pollinators could contribute to a better understanding of the effects of agricultural intensification. For example, the deposition of heterospecific pollen on stigmas was shown to be unrelated to the interspecific movements of pollinators and their degree of specialization (Fang and Huang, 2016). Moreover, in a community the plants that act as heterospecific pollen donors are not the same that act as receptors (Fang and Huang, 2013). We can thus expect that the diversity of pollen transported by pollinators and the pollination niche overlap among plants are also greater in agricultural land management. Teasing apart these effects of agricultural land management on pollen transport by pollinators and the resulting niche overlap among plants is essential for a mechanistic understanding of the effects of agricultural practices on pollination services. To this end, we studied the pollen transport networks, which quantify the interactions between plants and pollinators through the amount of pollen grains transported by pollinators (Forup and Memmott, 2005). This type of networks represents a useful approach to study pollination niches of plants, providing information about which pollinator species carry pollen of which plant species, and are thus more accurate than visitation networks to study pollen flow in communities (Forup and Memmott, 2005).

We compared pollen transport networks from fragments under agricultural management (agricultural fragments) with fragments where these practices had been abandoned for several years or were under conservation-aimed land management (restored fragments). We hypothesized that, by promoting the invasion by exotic plants and the predominance of generalized plant-pollinator interactions, agricultural land management would lead to increase diversity of pollen transported by pollinators and increased pollination niche overlap among coexisting plants. Thus, we predicted that (i) agricultural fragments would have greater diversity of pollen transported by floral visitors, (ii) agricultural fragments would have greater pollination niche overlap among plants, and (iii) pollination niche overlap would be positively related to the presence of exotic species.

2. Materials and methods

2.1. Study sites

The study was carried out at three sites along a 700 km transect located at 36°S in Buenos Aires and La Pampa provinces, Argentina. From east to west, the sites were located in Estancia Las Chilcas (hereafter referred to as 'LC'), Estancia San Claudio ('SC') and Estancia Anquilóo ('AN') (see Supporting information for a detailed description of the study sites). The predominant land use varied among sites as a function of precipitation and soil types (see Fig. S1 in Supporting information). In LC, extensive cattle production on semi-natural pastures was predominant and no agrochemical or farm machinery was used during this study. The main entomophilous crop found at this site was bird's-foot trefoil (*Lotus tenuis*). In SC, cropping is predominant under a mixed farming system (although there was extensive cattle production), where herbicides and pesticides are frequently and intensively used. The main crops found at this site were soybean (*Glycine max*), maize (*Zea mays*) and, to a lesser extent, sunflower (*Helianthus annuus*) and alfalfa (*Medicago sativa*). Lastly, production in AN was mixed farming, with a predominance of extensive cattle production and controlled grazing. Here, the agricultural fragments were sown with alfalfa and weeping lovegrass (*Eragrostis curvula*) as forage.

In LC and SC, restored fragments were enclosures with permanent fences which have not been cultivated or grazed for the last 3 and 20 years, respectively. In AN, restored fragments were sites with a conservation-aimed land management where cattle have been absent from September until April during the last 30 years, the time of the year when sampling was carried out. In these fragments, farm managers conserved the woody elements of the vegetation intentionally, including many entomophilous species (*Prosopis caldenia*, *Condalia microphylla* and *Geoffroea decorticans*, among others), although cattle trampling may have affected the entomophilous herbaceous plants. It is important to emphasize that woodland clearance traditionally has been the greatest modification undertaken by human beings in this region, thus making access for cattle easier and obtaining larger grazing areas (González-Roglich et al., 2012).

At each site, two restored and two agricultural fragments of 1 ha each one were selected (except for LC, where only one appropriate restored area was found; see Marrero et al., 2014 for more details on the study sites). The restored and agricultural fragments in each site were located at least 500 m apart in order to guarantee their independence. Although some bee species are known to fly much larger distances (Beekman and Ratnieks, 2000), smaller bees and/or some flies (which dominated our visitor assemblages) typically fly distances shorter than 500 m (Zurbuchen et al., 2010; Rader et al., 2011). Unlike the cattle production sites (LC and AN), the field margins in SC (4% of total area) were included in the cropping areas as they are a landscape elements of the agroecosystem and are generally considered to be important biodiversity reservoirs (Olson and Wäckers, 2007; Torretta and Poggio, 2013; Hodara and Poggio, 2016). Although our study fragments were located in three distant areas with rather different plant and pollinator assemblages, the structure of the plant-pollinator networks (e.g., overall generalization) was similar among fragments (Marrero et al., 2014). For this reason we think that fragments from different sites can be used as replicates to carry out this study.

2.2. Floral visitors and vegetation surveys

Monthly samplings in the eleven fragments were performed from November to March (2010–2011). Two 50 m × 2 m transects were placed randomly in each fragment to estimate the abundance of flowers or inflorescences of entomophilous plants and their

floral visitors (for a similar approach see [Memmott, 1999](#); [Marrero et al., 2014](#)). Each transect was sampled twice: the first time to count the units of floral attraction (hereafter UFA, i.e. individual flowers or inflorescences) found in a 2 m wide strip (1 m on either side of a linear transect), and the second time to catch all the floral visitors seen in the same strip, by walking at a pace of 10 m/min. This procedure was performed randomly in one transect before noon (from 10:00–12:00) and another in the afternoon (14:00–17:00). The transects established in the agricultural fragments included the crop species. In each transect, flowers of all plant species in bloom were collected to build a palynological reference collection. Floral visitors were caught with a net, sacrificed in a killing jar and separated individually (wrapped in a piece of paper) to prevent contact among specimens and pollinic contamination. Specimens were mounted with special care to avoid loss of the pollen transported on their bodies and later identified in the laboratory to the lowest taxonomic level possible. Specimens were grouped into morphospecies when they could not be identified to the species level. All insects found foraging on individual flowers or inflorescences were considered as floral visitors. The material collected (floral visitors and plants) is stored in the Faculty of Agronomy, University of Buenos Aires.

2.3. Pollinic analysis

To obtain samples of pollen loads from the bodies of floral visitors, we used small cubes (ca. 18 mm³) of gelatine-glycerin with safranin under a binocular microscope in the laboratory ([Kearns and Inouye, 1993](#)). The cubes were rubbed on the bodies of the floral visitors, taking care not to pass over parts of the body with pollen that was not available for pollination (e.g. scopa in female bees). The gelatine-glycerine cube impregnated with pollen was then melted on a microscopic slide and covered with a coverslip ([Kearns and Inouye, 1993](#)). The 576 preparations (171 from LC, 223 from SC and 182 from AN), obtained from 117 floral visitor species, were analyzed under an optic microscope (400×). The pollen preparations were compared with a reference collection of 141 entomophilous plant species found at the three study sites, in order to identify the pollen loads transported by the pollinators (see [Marrero et al., 2014](#)). In preparations containing less than 2000 grains of a given pollen species all grains were counted, but if number of pollen grains was higher only one every two stripes were observed, so that only 50% of the preparation was analyzed (see [Bosch et al., 2009](#); for a similar approach). To estimate the total number of grains for each species, the mean number of that species' grains per stripe was multiplied by the total number of stripes in the preparation. The presence in a preparation of 10 or more grains of a given species was considered as proof of the pollinator's visit to that species ([Bosch et al., 2009](#)). Several pairs or groups of phylogenetically related plant species (*Conium maculatum* and *Ammi* spp.; *Carduus acanthoides* and *Cirsium vulgare*; *Eryngium horridum* and *Eryngium elegans*; *Lactuca* sp. and *Sonchus* sp.; *Hypochaeris* sp. and *Crepis* sp.; *Baccharis ulicina* and *Baccharis gilliesii*) were treated as pollen complexes, as the similarity of their pollen grains made it impossible to differentiate among them under the conditions of observation used.

These data were used to construct quantitative interaction networks. Each network was obtained from the sum of data from the same fragment, using the total number of pollen grains from one plant species transported by one species of floral visitor, instead of the frequency of visits as an indicator of the interaction value. Ten networks were built because the network in the restored fragment in LC was not included for being too small (only one plant species). Some floral visitors, such as *Oxysarcodexia varia* and *Tricharaea occidua* (in LC), *Chauliognathus scriptus* (in SC) and *Apis mellifera* (in AN), were very abundant in some transects. When this

occurred, the corporal pollen loads from only some of the recorded individuals were estimated and the mean value of transported grains was multiplied by the total number of individuals recorded in the field, including both those caught and those observed. In particular, in LC 42 individuals of *O. varia* were caught and another 50 were observed while working in the transects, and 18 individuals of *T. occidua* were caught and 76 more were observed. In SC, 27 individuals of *C. scriptus* were caught and another 20 were observed, whereas in AN, 62 individuals of *A. mellifera* were caught and another 88 were observed.

We used pollen transport networks since they provide information about the way in which the pollinators influence the pollination service of the plants they visit. This influence may be through the quantity of pollen transported, the quality of the pollen loads (diversity and specificity of the pollen transported) and the relation between the quantity of pollen grains of native and exotic species ([Lopezaraiza-Mikel et al., 2007](#)). The networks of visits are like a photograph of the interactions that occur at a given moment in a community, whereas the pollen transport networks are a summary of the interactions that occur over a given time period ([Forup and Memmott, 2005](#)).

2.4. Data analyses

To evaluate the diversity of transported pollen, we analyzed the diversity of the pollen loads per individual (prediction i). Only individuals that carried more than 10 grains of pollen were used for the analysis. The diversity of transported pollen per floral visitor was estimated by means of the inverse of Simpson's diversity index, using the *invsimpson* function (*vegan* package, [R Development Core Team, 2013](#)). Treatment effect on the values of pollen load diversity at the three study sites was analyzed with GLMM (with a Gamma distribution) using the *glmer* function (*lme4* package, [R Development Core Team, 2013](#)). In the GLMM, "treatment" (agricultural and restored fragments) was considered as fixed factor and the "site" (LC, SC and AN) as a random factor (see GLMM in Supplementary material).

In order to evaluate the effect of agricultural land management on pollination niche overlap (prediction ii), we estimated pollination niche overlap in plant species in the ten pollen transport networks using Horn's niche overlap index ([Horn, 1966](#)), a widely used index in ecology ([Krebs, 1989](#)). We estimated Horn's index with the *networklevel* function of *bipartite* package in R statistical software ([Dormann et al., 2009](#); [R Development Core Team, 2013](#)). The overlap estimation for the resource use ranges from 0 (without overlap) to 1 (total overlap) ([Dormann et al., 2009](#)). We conducted a GLMM (with a Gaussian distribution) to evaluate treatment effects on the values of pollination niche overlap. The model included a fixed factor, the "treatment" (agricultural and restored fragments), and a random factor, the "site" (LC, SC and AN) (see GLMM in Supplementary material). We used the *lmer* function (*lme4* package, [R Development Core Team, 2013](#)) since the residuals were normally distributed.

The pollination niche overlap in plants and its relationship with the geographic origin of the plants (prediction iii) was evaluated using a one-by-one elimination procedure of each plant species. Specifically, the value of niche overlap was estimated by subtracting the overlap for the entire community from the value of the niche overlap calculated after removing, with replacement, each plant from the community (See Fig. S2 in Supporting information). The value of the difference was divided by the value of the niche overlap in the original network in order to standardize the resulting data, obtaining a proportional difference (proportional contribution of overlap [i.e., contribution of species *i* = (total overlap – overlap after removing species *i*)/total overlap]) (see Supporting information for a detailed explanation). Thus, the value

obtained represents the relative contribution of each plant species to the niche overlap in the network. These relative contributions to niche overlap can take negative or positive values. A negative value indicates that the removal of a particular species increases niche overlap in the community. The geographic origin of plants and treatment effects on proportions of the overlap contribution were analyzed with GLMMs (with a Gaussian distribution). The models included two main fixed factors: “treatment” (agricultural and restored fragments), and “geographic origin of the plants” (exotic and native), and a random factor, “site” (LC, SC and AN). We used the lmer function in the lme4 package of R statistical software (R Development Core Team, 2013). The GLMMs included the interaction terms between the fixed factors (see GLMM in Supplementary material). The best-fitting model was that with the lowest AIC (Akaike Information Criterion).

3. Results

Overall, ca. 748,000 pollen grains were recorded, belonging to 54 plant species or species complexes (20 species in LC, 21 in SC and 27 in AN), some of which were recorded at more than one sampling site. The pollen transport networks were built with pollen transport data from 540 individual insects (162 from LC, 204 from SC and 174 from AN) belonging to 117 species of floral visitors (14 in LC, 56 in SC and 58 in AN) (see Table S1 in Supporting information). The 36 remaining individuals transported less than 10 pollen grains, and were thus excluded from the analyses.

3.1. Diversity of transported pollen

The diversity of pollen transported by individual flower visitors was greater in agricultural fragments than in restored fragments ($T=4.784$, $p=0.0001$, see GLMM output in Supplementary material) (Fig. 1). Although plant richness was also greater in agricultural than in restored fragments ($T=-5.094$, $p<0.0001$),

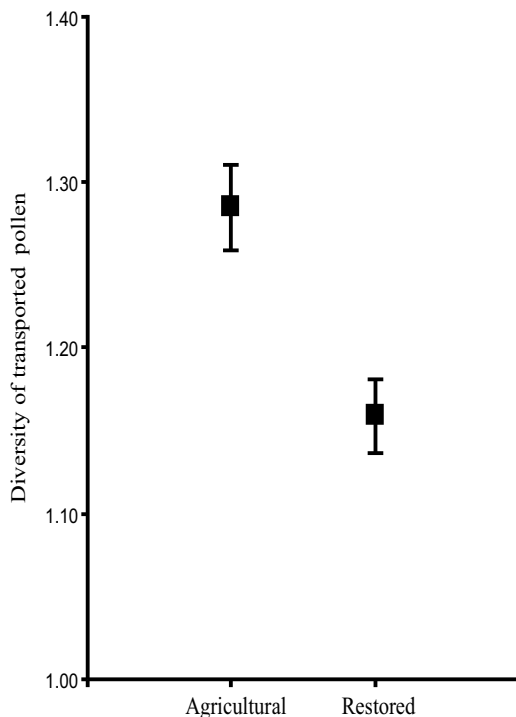


Fig. 1. Mean diversity of pollen transported (\pm standard error) by individual floral visitors in agricultural and restored fragments at the three study sites (LC, SC and AN) in the Pampean region.

richness level was unrelated to the diversity of pollen transported by pollinators (Spearman's $r=-0.02$).

3.2. Niche overlap in agricultural and restored fragments

The pollination niche overlap in agricultural fragments was greater than in restored fragments ($T=-2.478$, $p=0.0132$, see GLMM output in Supplementary material). The pollination niche was 57% more overlapping in agricultural than in restored fragments (Fig. 2).

3.3. Exotic plant effects

Exotic plant species contributed greatly to pollination niche overlap, generating the greatest differences in the simulated removal of plants ($T=-2.978$, $p=0.029$; see GLMM output in Supplementary material): while the presence of exotic plant species led to a threefold increase in pollination niche overlap, the presence of native species led to a slight decrease in pollination niche overlap (Fig. 3).

4. Discussion

We found that the diversity of pollen transported by floral visitors and the overlap in the pollination niche among plants were greater in agricultural fragments than in restored fragments. Exotic plant species contributed positively to the increase in pollination niche overlap, while native species contributed negatively, promoting decreased pollination niche overlap. Thus, by fostering exotic plant species and suppressing native species, agricultural practices increase the diversity of transported pollen and the pollination niche overlap among plants.

The greater diversity of pollen found in agricultural fragments could lead to two contrasting situations, but with similar detrimental effects on pollination. First, pollinators could carry lower species richness of pollen with homogeneous abundance. Alternatively, pollinators could carry greater species richness with

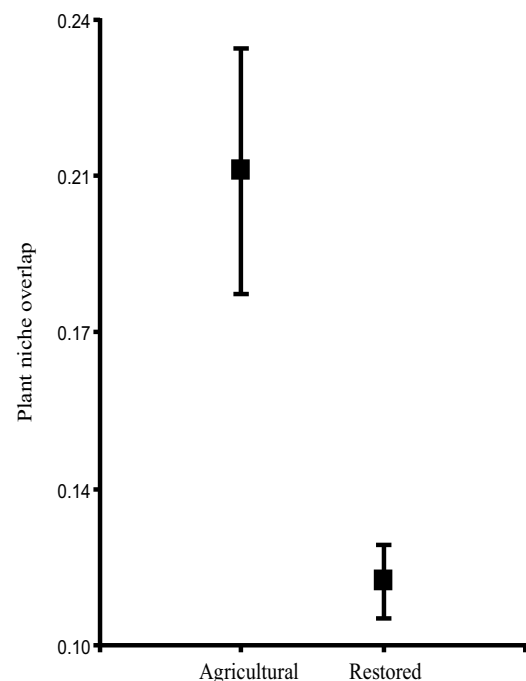


Fig. 2. Pollination niche overlap (mean \pm standard error) in agricultural and restored fragments at the three study sites (LC, SC and AN) in the Pampean region.

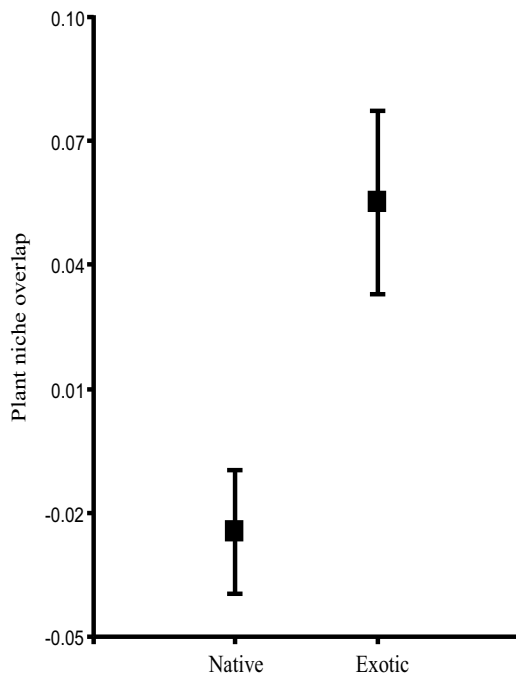


Fig. 3. Contribution of native and exotic plants species to niche overlap. The ordinates represent the difference in the niche overlap index (mean \pm standard error), estimated as the proportional difference between the niche overlap for the entire community and the niche overlap after removing each plant species [i.e., contribution of species $i = (\text{total overlap} - \text{overlap after removing species } i) / \text{total overlap}$]. A negative value indicates that the removal of a particular species increases niche overlap in the community. See Fig. S2 in Supporting information for details.

heterogeneous abundance. Either situation could lead to increased diversity of heterospecific pollen on stigmas, but not necessarily to a greater decrease in plant fitness, because multispecies effects depend on the net outcome of interactions (Arceo-Gómez and Ashman, 2011a,b). However, in a recent review Arceo-Gómez and Ashman (2016) mention that heterospecific pollen decreased plant reproduction and specially the heterospecific pollen from exotic plants tends to increase the negative effect on plant fitness. On the other hand, Grass et al. (2013) found that pollinator specialization on plants decreased within increasing relative exotic abundance and increasing land-use intensity. This result could be related to the increase of pollen diversity carried by pollinators in agricultural fragments.

Our results are consistent with previous studies conducted in the same sites (Marrero et al., 2014, 2016) and suggest that the greater niche overlap observed in agricultural fragments is likely a direct result of the greater abundance of exotic plant species. Several features of exotic plants may also contribute to generate this effect. Animal-pollinated exotic plants usually produce large quantities of pollen (Chittka and Schürkens, 2001), interact preferentially with generalist pollinators (Lopezaraiza-Mikel et al., 2007), and bear flowers with highly exposed reproductive parts (Montgomery and Rathcke, 2012). These traits allow them to subtract interactions from other plants in the community (Aizen et al., 2008; Tylianakis, 2008), swamping the stigmas of native plants with heterospecific pollen (Marrero et al., 2016) and might ultimately affect their reproduction, especially when pollinators are a limiting factor (Mitchell et al., 2009).

The increase in pollination niche overlap could be related to the extinction of some specialist pollinator species in agricultural fragments. Weiner et al. (2014) show that land-use intensification

has a negative impact on the abundance of more specialized pollinators. Moreover, Brosi and Briggs (2013) show that the loss of a single pollinator species can reduce the floral fidelity of other pollinators and negatively impact plant reproductive function. They found that the suppression of a bumblebee species increases the diversity of pollen transported by other bumblebee species in a community, and it decreases the fitness in a plant species (Brosi and Briggs, 2013). On the other hand, pollination niche overlap could be related to the niche expansion of exotic plant in agricultural fragments. Niche expansion occurs because the invading species can access resources that may have otherwise been depleted or monopolized by competitors (Bolnick et al., 2010).

Our study did not evaluate the reproductive success of native plants. However, there is substantial evidence that exotic plants may disrupt the reproduction of native plants when both types of plants share pollinators in the agroecosystems (Morales and Traveset, 2008, 2009). At the same time, rare native plants with low attraction ability can obtain benefits from being close to exotic plants if these act as magnet species attracting pollinators to the neighborhood (Feinsinger, 1987; Muñoz and Cavieres, 2008). For example, Gibson et al. (2006) suggested that abundant plants in crop borders may offer resources to generalist pollinators that transport pollen of (and possibly pollinate) rare plant species. However, in our particular case the increase in the pollination niche overlap and the high diversity of the pollen transported by floral visitors probably have a negative effect on plant reproduction, mainly on that of native plants, since in our experimental sites the increases in heterospecific pollen deposition on stigmas mainly occurred in agricultural fragments and in native plant species (Marrero et al., 2016).

Strategies to encourage improvements in the quality of pollination in agroecosystems could range from controlling the levels of exotic species (Nicholls and Altieri, 2013), to mechanisms that promote increased diversity of native plants (Carreck and Williams, 2002). In Europe, sown wildflower strips are increasingly being established in agroecosystems to enhance biodiversity, especially in intensively used agricultural areas (Carvell et al., 2007; Haaland et al., 2011). In contrast, in Pampean region of Argentina, where our study was conducted, no similar actions have been established. Furthermore, we need more studies on the functionally important pollinators in agroecosystems, given that most studies focus on *Apis mellifera*, a super-generalist pollinator that contributes substantially to increase niche overlap among plants and is not necessarily an effective pollinator (Santos et al., 2012).

Our results represent a novel contribution for our understanding of the ecology of pollinator-mediated interactions among plants, and of how alien species impact agroecosystems by disrupting the functioning of interactions among native species.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.agee.2017.01.027>.

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