Soybean biotic pollination and its relationship to linear forest fragments of subtropical dry Chaco

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Abstract

The delivery of ecosystem services, such as biotic pollination is a benefit that nature provides us. Pollinators increase the quantity, quality and stability of crops for food production. Previous works show that proximity to natural habitats increases crop production through the delivery of pollination services. However, similar researches in subtropical regions is largely lacking. In this study we evaluated the role of linear forest fragments (LFFs) on the provision of biotic pollination service to soybean crops (*Glycine max*) and explored whether this service changes with increasing distance to LFFs in subtropical dry Chaco (Argentina). In three agricultural farms and testing two soybean varieties, we covered plots of $0.75\,m^2$ with soybean plants and compared them with equally sized open plots. Plots were placed near (60 m) and far (600 m) from LFFs. We found that plants from the open treatment produced 32% more pods, 41% more seeds and had 42% higher yield (kg/ha) than plants from the covered plots. The difference between open and covered plots in seeds and yield did not change significantly with the distance to LFFs, but the number of pods, contrary to what we expected, was higher far from LFFs. Our findings highlight the possible impact of pollinators on soybean yield in both varieties tested here; but the proximity to LFFs was not directly related to a larger difference in production. Observed patterns are explained by edge effects and competition between soybean plants and trees near LFFs, combined with an underestimation of the distance from the natural hives to which honeybees can efficiently exploit the crops. In this subtropical region, soybean expansion is the most important driver of land cover change and this study represents a first step towards a better understanding of the functioning of these remnants of natural areas within the agricultural land in the region of dry Chaco forests.

Introduction

Ecosystem services are benefits that humans obtain from nature (Millennium Ecosystem Assessment 2005), many of which are strengthened by biodiversity (Díaz et al. 2005; Kremen 2005). The mitigation of climate change through carbon sequestration and storage by trees (Bunker et al. 2005), the regulation and pest control by birds (Philpott et al. 2009) and the biotic pollination by insects and vertebrates (Ollerton, Winfree, & Tarrant 2011) are examples of services provided by natural habitats through biodiversity. The conversion and degradation of natural ecosystems for agricultural, livestock

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and urban land uses (Foley et al. 2005; FAO 2007) imposes a major threat to biodiversity and ecosystem services from local to worldwide scales (Newbold et al. 2015). In the current context of increasing food demands due to accelerated rates of human population growth, it is vital to understand the functional role of natural vegetation remnants that persist in transformed landscapes. Several studies assessed the provision of ecosystem services by isolated large and small habitat fragments in agroecosystems worldwide (Tscharntke, Klein, Kruess, Steffan-Dewenter, & Thies 2005; Ferraz et al. 2014; Mitchell, Bennett, & Gonzalez 2014; Decocq et al. 2016). Additionally, ecosystem services provided by hedgerows, defined as continuous or closely spaced lines of shrubs and trees (Dondina, Kataoka, Orioli, & Bani 2016), common in anthropogenic landscapes of temperate regions (Dainese, Montecchiari, Sitzia, Sigura, & Marini 2017; Van Vooren et al. 2017) have also received much attention. Another common habitat type more frequently used in tropical and subtropical transformed regions are forest strips or linear forest fragments (hereafter, LFF) (Núñez Regueiro et al. 2015), however, they have been poorly studied in relation to their role in the provision of ecosystem services.

In many agricultural landscapes of the world natural habitats are only represented by linear elements like hedgerows or linear forest fragments. These habitat types share certain common features as their configuration (length is much greater than width), but they also have some dissimilarities. Although hedgerows (e.g., shelter belts, fencerows) may be residuals of native woodlands, they are in most cases, human-made features or new plantations with different management strategies, presenting large differences in their internal structure and quality (Baudry, Bunce, & Burel 2000; Dondina et al. 2016). LFFs, on the other hand, are natural vegetation left in the landscape during land conversion, with a species composition and structure similar to the original forest (Núñez Regueiro et al. 2015). Both hedgerows and LFFs can function as wildlife corridors by connecting larger forest fragments (Davies & Pullin 2007; Lees & Peres 2007; Hawes, Barlow, Gardner, & Peres, 2008; Sreekar, Mohan, Daas, Agarwal, & Vivek 2013) or as windbreaks, controlling soil erosion on adjacent crop and pasture fields (Areskoug 2001; Böhm, Kanzler, & Freese 2014). Hedgerows have also been shown to enhance pollinator abundance in adjacent fields (Hannon & Sisk 2009; Morandin & Kremen 2013; Sardiñas & Kremen 2015). However, it is unknown whether natural habitats such as LFF provide similar pollination services in agricultural landscapes.

Many crops around the world benefit from biotic pollination provided by large fragments of natural vegetation remaining within transformed landscapes (Tscharntke et al. 2005; Morandin & Winston 2006; Chaplin-Kramer, Tuxen-Bettman, & Kremen 2011). Recent studies highlighted the importance of the distance to forest fragments in determining the frequency, effectiveness and stability of the pollination service in tropical and temperate regions (reviewed by Garibaldi et al. 2011). At small distances from natural

habitats, animal pollination in the agricultural field is guaranteed but its frequency decays exponentially when distances increase (Ricketts et al. 2008). When natural habitats are close to crops in agricultural landscapes, pollinators can obtain nesting resources from them while surrounding crops may offer abundant floral resources, at least for some period of time (Kremen et al. 2007; Ricketts et al. 2008). Pollination service improves production on 75% of the most important global food crops (Klein et al. 2007); unfortunately, insect pollinators are suffering regional declines in many parts of the world due to degradation and loss of terrestrial ecosystems (reviewed by Goulson, Nicholls, Botías, & Rotheray, 2015).

In subtropical dry forests of Argentina, Bolivia and Paraguay land conversion promoted one of the highest global rates of deforestation between 2000 and 2012 (Hansen et al. 2013). The expansion of cattle ranching and the large-scale soybean (*Glycine max*) production (Vallejos et al. 2015) were the main factors responsible for this regional land cover change. In Northern Argentina, these land uses expanded rapidly during the past three decades transforming the predominantly wooded landscape to mosaics of forest patches within an agricultural and/or livestock matrix (Gasparri, Grau, & Gutiérrez Angonese 2013). As a consequence, national and provincial laws emerged to regulate and promote the rational use and conservation of native forests (Coria & Navall 2009). They demand agricultural landowners to leave linear fragments of native dry forests to convert a new crop field (i.e., near 5 ha of linear forest for every 100 ha of cultivated land) as a mitigation action for the forest cover lost. This legislation, when fulfilled, turned LFF into a common element of the landscape. Unfortunately, their inefficiency as connector elements of forest patches at landscape scale (Ginzburg, Torrella, & Adámoli 2012) indicated by their poor use by native medium and large mammals (Núñez Regueiro et al. 2015), suggests that they did not work as well as expected. Despite these results, recent field observations within LFFs of native trees (e.g. *Ziziphus mistol* and *Caesalpinia paraguariensis*) occupied entirely by honeybees (*P. Zelaya*, *personal observations*), motivated further investigations focused on their possible role as pollinator sources to a mass flowering crop such as soybean.

Although soybean is recognized as an auto-pollinated species, several studies showed that production of seeds and yield are enhanced if the flowers are visited by native pollinators or even through the introduction of honeybees (*Apis mellifera*) (Chiari et al. 2005, 2008; Milfont, Rocha, Lima, & Freitas 2013; Monasterolo, Musicante, Valladares, & Salvo 2015). In this study, we examined: (a) the role of LFFs in the provision of pollination services to two soybean varieties and (b) whether this biotic pollination service decreases as distance to LFFs increases. We expected that plants exposed to pollinators would show an enhanced production compared

to plants excluded from pollinators, and that this difference would be larger in the proximity to LFFs.

Materials and methods

Study area

The Gran Chaco is the second largest Neotropical biome after the Amazonian rain forests, covering c. 120 million ha in Argentina, Bolivia and Paraguay (The Nature Conservancy, Fundación Vida Silvestre Argentina, Fundación para el Desarrollo Sustentable del Chaco, & Wildife Conservation Society Bolivia 2005) (Fig. 1A). This study was conducted in the semiarid sub-region of dry Chaco among Tucumán and Santiago del Estero provinces, in the northwest portion of Argentina (Fig. 1B). Dry Chaco has a subtropical seasonal climate, with a mean annual temperature ranging between 20 and 23 °C, with average temperature of 16 °C and 28 °C for the coldest (July) and hottest (January) months, respectively. Annual rainfall ranges between 400 and 900 mm, with strong monsoonal precipitation seasonality with 80% of the rainfall between November and March and with water deficit in the winter and early spring (Minetti 1999).

Experimental design and sampling sites

We carried out a field experiment on three farms (Fig. 1C) where soybean is the main annual crop and linear fragments of native forests are interspersed in the agricultural landscape. At each farm we selected 24 plots for pollination treatments, that is, there were two sites with 12 plots each consisting of a crop line of 0.5 m × 1.5 m (i.e., 0.75 m^2) f.e., (see Appendix A: Fig. 1A in Supplementary material). Twelve of these plots were located near (52.25 m ± 3.20 m) and twelve plots were located far (1051.92 m ± 400.43 m) from LFFs (Fig. 1D) f.e., (see Appendix A: Fig. 2 in Supplementary material). At each distance, we covered six of the twelve plots with a nylon mesh supported by six iron bars (120 cm tall) to exclude pollinators (hereafter: *covered treatment*) f.e., (see Appendix A: Fig. 1B in Supplementary material). Each of the six covered plots (near and far) within a farm were approximately 100 m apart from each other. The nylon mesh was set three weeks before flowering and was maintained for 100 days in the field, from January to April of 2015. The other six plots were six paired neighboring plots that had the same area and were exposed to pollinators (hereafter: *open treatment*). At the moment of crop harvest, we collected all plants from the twelve covered and the twelve open plots at each farm. None of the farms had apiculture (use bee hives), because it is not a common practice in the region, thus all flower visitors were native species and feral honeybees.

The specific plot sites were located on the farms considering the landscape context, which means that we measured the different land cover types and their proportion in the landscape within a buffer of 1 km around each set of 12 near and far plots, f.e., (see Appendix A: Table 2 in Supplementary material). Soybean crop was the dominant land use in all farms (>97% of cover), and minimum distances to the nearest forest patch or LFF (excluding the focal LFF for near treatments) were 393 m for samples near and 454 m for samples far from LFFs f.e., (see Appendix A: Table 3 in Supplementary material).

In addition, during the field experiment, we verified that plants of both covered and open treatments had not been attacked by insect herbivores or seed pests in any of their phenological stages (growing, flowering and fructification). Although we did not quantify damage, we found no sign of leaf herbivory or seed predation on soybean plants. The soybean variety DM-5.8i was cultivated on one farm (n = 24), while DM-7.8 variety (n = 48) was cultivated in the other two farms. We accidentally lost a total of 20 plots (i.e., some were stepped on by agricultural machines and others were stolen from the agricultural field), thus the total number of plots was reduced to n = 54 (n = 16, n = 24 and n = 14 in farm 1, 2 and 3, respectively).

Once harvested, we measured three reproductive variables for each plot: (1) *number of pods*: we counted the total number of pods and summed them from each plot of covered and open treatments, (2) *number of seeds*: represents the sum of seeds within a plot produced by all the pods and (3) *yield* (in kg/ha): obtained from the relation between seed weight and the area occupied by each plot expressed in hectares. We used a small thresher to obtain all soybean seeds from pods. Before weighing the seeds, we measured seed humidity of each plot with a humidity meter (*Delver HD 1021 USB*) as the content of water within seeds affects their weight. Humidity of each plot was considered in the calculation of each yield and standardized in order to obtain the weight of seeds at 13% of humidity, as this is the expected humidity that landowners use as a reference to start crop harvest.

In order to evaluate whether the nylon mesh used to cover the plants in the covered treatment affected their normal development, we chose five individuals from each covered and open plots and measured plant height (from the base to the bottom of the principal stem of the plant) and the number of knuckles of each stem.

Data analysis

We used general linear mixed effect models (GLMMs) to explore the behavior of soybean reproduction variables under the effect of pollination treatments at two different distances to LFFs. We considered the main effects of pollination treatments (covered/open) and distances (near/far), and also their interaction. The response variables were number of pods, number of seeds and yield. Pollination treatments and distances were incorporated as fixed effects and farm identity as a random effect with plot variable nested within farm. Since all variables fitted the normality assumptions and homoscedasticity of variance and adjusted better (<AIC) than
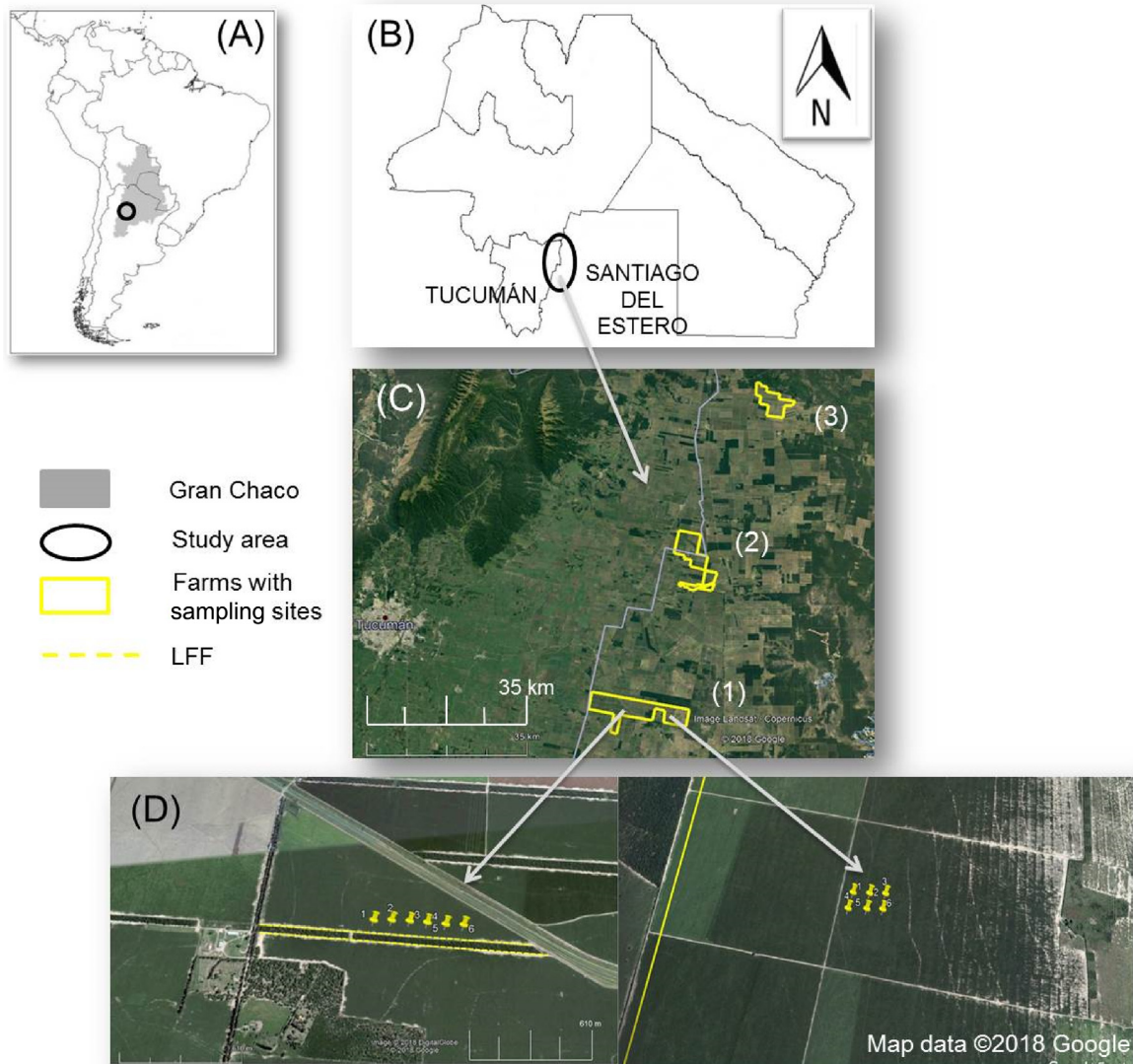
Fig. 1. Location of the study area: (A) Gran Chaco region in South America, (B) the study area in Northern Argentina, (C) The three farms selected for the experimental study and (D) Examples of the paired pollination treatment (covered/open plots) located near and far of linear forest fragment (LFF) on farm "1". (All images copyright 2018 Google Earth Pro).

Poisson distribution, we used normal distributions of errors in the models, f.e., (see Appendix A: Table 4 in Supplementary material). We calculated the proportion of variance explained within and among soybean farms (i.e., marginal and conditional R^2, respectively), according to Nakagawa and Schielzeth (2013). In this way, we could separate the proportion of variance within farms given by local environmental variation on treatments, and the proportion of variance among farms given by environmental variation at larger spatial scales (e.g., differences in soils and farm management).

We used pairwise t-test to assess the effect of nylon mesh on plant height and number of knuckles (Sokal & Braumann 1980), and a posteriori multiple comparison test, the LSD (least significant difference) with ($\alpha = 0.05$) to get differences among treatments. All statistical tests were evaluated at the

$P < 0.05$ level of significance using R 3.0.1 (R Development Core Team 2013).

Results

Soybean reproductive variables differed between covered and open treatments and near and far distance, Fig. 2, f.e., (see Appendix A: Table 1 in Supplementary material).

Pods

The number of pods was higher in the open (mean $\pm$ SE $= 846.70 \pm 58$) than in the covered treatment (mean $\pm$ SE $= 641.59 \pm 38$), which means that plants
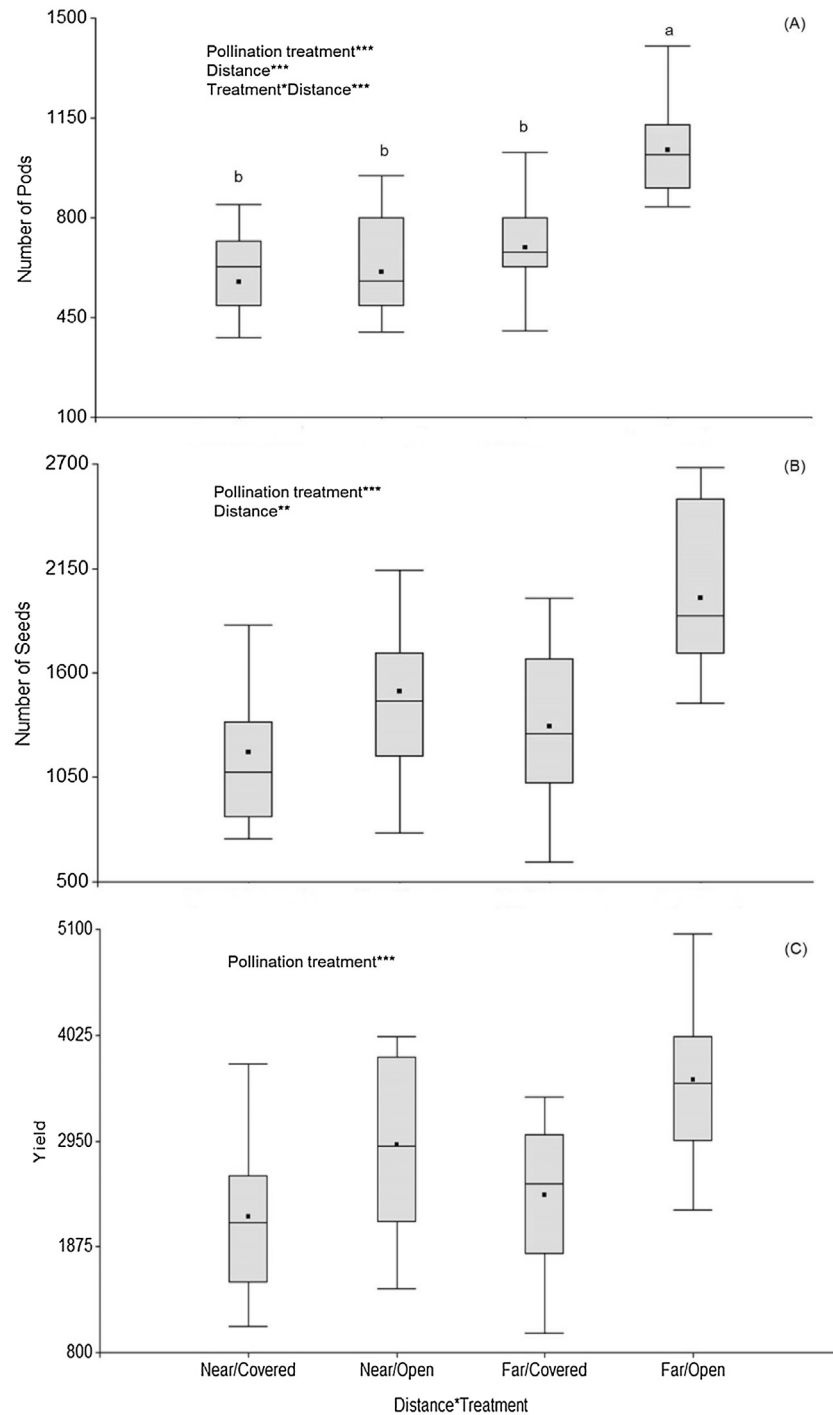
Fig. 2. Soybean reproductive variables. Box plots showing means ± SE of Pods (A), Seeds (B) and Yield (C) under covered and open pollination treatments, placed near and far from linear forest fragments and their interaction. Statistical differences are shown with a posteriori multiple comparison test (the LSD, least significant difference). P < 0.05**, P < 0.0001***.

exposed to pollinators produced 32% more pods (Fig. 2A). The difference in pod number between pollination treatments far from LFF (i.e. mean open$_{far}$ − mean covered$_{far}$ = 341.87) was higher than between those plots located near (i.e. mean open$_{near}$ − mean covered$_{near}$ = 34.16). The interaction in the GLMM model (Table 1) was significant (Pollination treatment × Distance, $F = 14.89$, $P = 0.0007$), open pollinated

flowers located far from the LFFs set more pods than the ones located near (Fig. 2A).

Seeds

The number of seeds differed both between pollination treatments and distances, and the interaction was marginally

Table 1. Summary of the ANOVA from the GLMM models for the three soybean production variables where pollination treatment, distance from linear forest fragments and their interaction were considered fixed effects and farm identity a random effect with plot variable nested within farm.

Production variables	Sum Sq	DF	DenDF	F_{value}	Pr (>F)
Number of pods					
Pollination treatment	471,337	1	25.000	22.246	7.767e − 05[***]
Distance	412,384	1	23.207	19.464	0.00020[***]
Treatment × distance	315,598	1	25.000	14.896	0.00071[***]
Number of seeds					
Pollination treatment	3,346,346	1	25.000	27.249	2.111e − 05[***]
Distance	1,112,402	1	23.276	9.058	0.00620[**]
Treatment × distance	414,070	1	25.000	3.372	0.07825
Yield (kg/ha)					
Pollination treatment	12,019,139	1	25.000	25.400	3.362e − 05[***]
Distance	1,699,241	1	23.45	3.591	0.07049
Treatment × distance	652,248	1	25.000	1.3784	0.25144

[**] $P < 0.05$.
[***] $P < 0.0001$.

significant (Table 1). Plants exposed to pollinators (open treatment) produced more seeds (mean ± SE = 1776.4 ± 89) than plants excluded from them (mean ± SE = 1255.85 ± 75), Fig. 2B. This result means that plants from open plots set 41.5% more seeds than covered plots. The number of seeds increased significantly with increasing distance to LFF (Fig. 2B, GLMM model, Table 1), showing 23.35% more seeds in plots located far (mean ± SE = 1655.4 ± 96) than those located near LFF (mean ± SE = 1342.04 ± 83). The difference between open and covered treatments was slightly larger far from LFF, although the interaction term was only marginally significant (Pollination treatment × Distance, $F = 3.37$, $P = 0.07$; Fig. 2B, GLMM model, Table 1).

Yield

The kilograms per hectare only differed significantly between pollination treatments (GLMM model, Table 1). Production in the open plots was higher (mean ± SE = 3275.31 ± 177) than in the covered plots (mean ± SE = 2301.29 ± 148), meaning a 42.3% more kg per hectare (Fig. 2C), in plots opened to biotic pollinators. Considering distance, yield was 17.3% higher in soybean plants located far from LFF than those located near but this difference was not statistical significant, neither was the interaction (GLMM model, Table 1; Fig. 2C).

Variability within and among farms was similar for all variables as marginal and conditional R^2 were 0.455 and 0.735 for pods, 0.390 and 0.541 for seeds and 0.306 and 0.531 for yield, respectively. These results showed that including farm identity as random effect and plots nested within farm enhanced the results, capturing different sources of variability from local (intra-plot variation) and larger spatial scales.

Finally, plant development was not affected by the coverage of soybean plants with the nylon mesh. Plants showed a similar height and number of knuckles in the covered and in the open treatments (height: t = 0.48, $P = 0.63$; number of knuckles: t = 0.29, $P = 0.77$).

Discussion

Linear forest fragments (LFFs) promoted by national laws are now common elements in the areas of the dry Chaco region under current anthropic use. LFFs are important relicts of native vegetation immersed in a region where the advance of the agricultural frontier triggered by soybean crops and exotic pastures for livestock, increase forest loss and fragmentation. Although LFFs have been rarely in the focus of investigations (Ginzburg et al. 2012; Núñez Regueiro et al. 2015), they may have an essential role in the provision of ecosystem services, still unexplored. In this study, we found evidence that two soybean varieties increased their yield more than 37% due to biotic pollination, although the role of LFFs as the providers of this service remains unclear and deserves more research.

Pollination service and enhancement in soybean production

We found an increase in the production of two soybean varieties (DM-5.8i and DM-7.8) attributable to the activity of pollinators, as reflected by the enhancement of almost 32% in the number of pods, 41% in the number of seeds and 42% in yield of plants exposed to pollinators. These increments in both varieties highlight the importance of pollinators to cultivated varieties in the region, and are in accordance with the increment in production (from 10 to 40%) expected for a modestly pollinator-dependent crop such as soybean (Klein

et al. 2007). Previous studies on different soybean varieties showed that production of seeds, pods and yields increase up to 50% or more when plant pollination is mediated by insects compared with the absence of pollinators (Erickson, Berger, & Shannon 1978; Chiari et al. 2005). However, this estimation has been criticized (Melathopoulos, Cutler, & Tyedmers 2015). In the Chaco Serrano of Argentina, Monasterolo et al. (2015) obtained higher numbers of seeds, pods and seed weight in plants exposed to floral visitors, compared to bagged plants using the soybean variety *ALM 3830*. Our experiments expanded on these studies by adding evidence of the positive effect of biotic pollination on soybean production, reflected by *DM 7.8* and *DM 5.8i* varieties. Thus, although the impact of animal pollination on different soybean varieties is not uniform, it is always positive and the increments in the production are not negligible (>30%). We encourage landowners to use more environment-friendly practices in the agricultural field and to maintain all kinds of natural and semi-natural vegetation that emerge in areas not occupied by crops. The availability of multiple resources (i.e., foods, shelter, nesting sites and materials, or overwintering sites) throughout the year and beyond the flowering crop season is crucial for the fate of organisms like pollinators supported in agricultural ecosystems (Schellhorn, Gagic, & Bommarco 2015).

Soybean production and distance to LFF

Production variables in open and closed treatments of both soybean varieties tended to increase with the distance to LFF. As we explain below, we propose that observed results could be explained by edge effects and competition between soybean plants and trees from LFFs, combined with an underestimation of the distance from the natural hives up to which honeybees can efficiently exploit the field crops.

Firstly, the lowest production values of soybean plants located near to LFFs could result from "negative abiotic effects" of LFF acting on the nearby agricultural field. It was proposed that shrubs and pioneer species at the edge of linear fragments and planted shelterbelts compete with crop plants for water (Kowalchuk & Jong 1995; Ginzburg et al. 2012). Also, the reduction of luminosity by the shade of trees from the adjacent fragment and tree root competition appears to have a negative effect on crops (Sklenicka & Salek 2005; Ginzburg et al. 2012). Field experiments to quantify these abiotic effects of LFFs on crop production can shed light on the unexpected decrease in production in soybean plants nearer to LFFs, and its interaction with pollination.

Secondly, the unexpected higher production of plants exposed to pollinators far from LFFs can also be explained by a higher frequency of visits to soybean flowers by honeybees. Although we did not measure systematically the number and identity of flower visitors, plots near LFFs were visited by small stingless bees, whereas plots located far from LFFs were mainly visited by honeybees (*P. Zelaya, personal observations*). Honeybees can indeed forage more than 1 km to their nest (Steffan-Dewentter & Kuhn 2003). This behavior would be suggesting a spatial segregation of pollinators within crop fields to avoid competition, and in turn, that honeybees are better providers of the pollination service far from LFFs, which makes them more efficient pollinators than stingless bees. Variability in the incidence of distance to natural habitats on pollination services in agricultural fields is partly due to different life-history traits of different groups within pollinator assemblages (Liow 2001; Ricketts et al. 2008). Body size and species-specific dispersal ability are two related traits that explain that variance between the assemblage composition (Gathmann & Tscharntke 2002; Benjamin, Reilly, & Winfree 2014; Silva, Nogueira, & De Marco 2017). Honeybees are expected to be more independent of the influence of landscape structure than stingless bees when attempting to locate and reach floral resources distant from their hives (Steffan-Dewenter & Kuhn 2003; Reynolds, Smith, Reynolds, Carreck, & Osborne 2007), which encourage us to develop the competition hypothesis mentioned above. Additionally, the existence of environmental gradients affecting soybean flower traits (e.g., nectar composition) could make them more attractive to pollinators with greater foraging capacity (i.e., honeybees), leading to a higher production (Robacker, Flottum, Sammataro, & Erickson 1983). If this was the case, this could explain the larger difference in production between open and covered treatments far than near to LFF. We highlight the need of more field research on the variation in visit frequency and nectar composition of soybean flowers to better understand the effects of distance to linear forest fragments on pollinator assemblage and their pollination service.

Conclusions

Dry Chaco forests of Argentina have been under constant anthropic pressure driven by an increasing need for land to enhance soybean production, motivated mainly by growing global meat demand (Gasparri et al. 2013). These changes in land use have reduced and fragmented the natural vegetation to such an extent that in certain highly transformed areas, the native forest is only represented by LFFs. We found that soybean plants exposed to pollinators set more pods and seeds and showed an increase in yield compared to those plants that were not exposed to pollinators. Our results demonstrate that two soybean varieties commonly cultivated in Argentina benefited from open pollination treatment and production was increased. As linear forest fragments are remnants of dry Chaco native forest, with trees and many mellifluous shrubs species and cacti that can be exploited by many insect pollinator species and sites that can serve as valuable nesting sites, we expected different results to pollination treatments located near LFFs. However, in this first

evaluation, the proximity to LFFs did not have the expected effect on production of plants located near and instead higher production values were obtained in plants located far from LFFs. It would be important to increase the number of LFFs in each farm to re-evaluate the effect of proximity on production since the small number of LFFs included in this study could have contributed to the unexpected results. Additionally, future research should focus on better understanding the foraging strategies of the species involved in the service of pollination, evaluating their relationships with the resources offered within and around the LFFs. Likewise, investigating the mutual environmental effects, negative and positive between crops and these increasingly common remnants is crucial to improve the design and territorial planning of the agricultural expansion in the dry Chaco forests region.

Acknowledgments

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.baae.2018.07.004.

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