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Short communication

Soybean crops may benefit from forest pollinators

Monasterolo M.[a,*], Musicante M.L.[b,1], Valladares G.R[c,2], Salvo A.[c,2]

[a] Cátedra de Botánica General, Facultad de Agronomía, Universidad de Buenos Aires, Av. San Martín 4453, C1417DSE Buenos Aires, Argentina
[b] Universidad Nacional de Chilecito-La Rioja, 9 de Julio No 22, Ciudad de Chilecito C.P F5360CKB, Argentina
[c] Centro de Investigaciones Entomológicas de Córdoba, Instituto Multidisciplinario de Biología Vegetal CONICET and Facultad de Ciencias Exactas Físicas y Naturales, Universidad Nacional de Córdoba, Avda. Vélez Sarsfield 1611, X 5016GCA Córdoba, Argentina

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ABSTRACT

Increasing evidence indicates that pollinator diversity and pollination services are highly threatened by the destruction and fragmentation of natural habitats and the intensification of agricultural landscapes. Here we analyze the bee visiting ensemble on soybean flowers and the effects of pollinator visits on soybean reproductive success, within a fragmented Chaco forest landscape embedded in a soybean matrix in central Argentina. We assessed visitation rates in relation to distance from the forest (5, 50 and 100 m) compared soybean bee assemblages with those on wild flowers in the nearby forest fragments, and carried out an exclosure experiment in order to assess the contribution of insect visits to soybean reproductive success. We also analyzed the relationship between visitor body size and the distance from the forest to the visited flower. Five species belonging to two families of bees were observed visiting soybean flowers. The bee species observed on soybean were well represented in the forest, and *Apis mellifera* was the most abundant species, visiting soybean flowers at all studied distances from the forest. Instead, wild visitors displayed a turnover of species throughout those distances, with smaller species being restricted to the forest proximity and replaced by larger ones toward the interior of the crop. Total visitation rates were significantly and negatively affected by distance to the forest. All plant productivity variables measured in the exclosure experiments were significantly improved in exposed flowers, duplicating the values observed without pollinators. The present study offers preliminary evidence linking forest proximity to higher visitation rates and presence of wild pollinators on soybean flowers thus providing for the first time, evidence of the forest role as pollinator donor for the soybean crop. It also shows that pollinator activity matters for this crop, leading to increased soybean yield. Further research on this topic is necessary in order to provide informed guidelines to enhance soybean production while simultaneously promoting natural habitat conservation.

1. Introduction

Forests and other natural habitats are being converted into agricultural lands at extraordinarily high rates, with dramatic effects on biodiversity and, ultimately, on ecosystem services (Palmer et al., 2004). Pollination is a crucial ecosystem service, with nearly 90% of the world's wild plants (Ollerton et al., 2011), over 70% of the major crops and at least one third of the global food production (Klein et al., 2007) depending on animal pollination. Moreover, although many animal-pollinated wild plants can self-pollinate to some degree, all rely on pollinators in the long term for genetic exchange among individuals (Winfree et al., 2011).

Increasing evidence indicates that pollinator diversity and pollination services are highly threatened by the destruction and fragmentation of natural habitats and the intensification of agricultural landscapes (Potts et al., 2010). Forests and other natural areas near agricultural systems usually support a variety of wild pollinators, with an important and well documented movement toward the cultivated land (see review in Blitzer et al., 2012). The exchange of insects between crops and natural environments has received much attention in fragmented habitats, where the increased extent of edges facilitates dispersal of organisms across habitats. The “spillover” of insects to either side of the edges can strongly affect the dynamics of ecological processes in such environments (Rand et al., 2006). Moreover, pollinator richness, visitation rates and pollination on crops have been shown to decline with increasing distance from natural

* Corresponding author. Tel.: +54 11 4 524 8069.
E-mail addresses: marcosmonasterolom@gmail.com (M. Monasterolo), mmusicante@undec.edu.ar (M.L. Musicante), gvalladares@efn.uncor.edu (G.R. Valladares), asalvo@com.uncor.edu (A. Salvo).
[1] Tel.: +54 3825 427200/01/02/03.
[2] Tel.: +54 351 4334141.

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habitats (Ricketts et al., 2008; Carvalheiro et al., 2010). Given the mounting environmental conflict between conservation and agriculture, the consequences of pollinator spill-over between natural and managed systems need to be better understood (Blitzer et al., 2012), in order to predict future changes in pollinators, animal-pollinated plants and resulting pollination services (Potts et al., 2010).

Soybean (*Glycine max* L. Merril) is currently the most important seed legume worldwide, contributing 25% of the global edible oil and about two-thirds of protein concentrate for livestock feeding (Agarwal et al., 2013). Despite its relevance, information on soybean pollination ecology across countries and varieties is still scarce (Chacoff, 2010). Although primarily self-compatible, soybean flowers display anatomic traits predicted in insect pollinated plants, such as nectar guides and floral nectaries (Palmer et al., 2009). It increasingly appears that the impact of flower-visiting insects has been underestimated, with evidence that insects such as honey bees contribute to cross pollination (Yoshimura, 2011). With a "modest dependence" on pollinators (Klein et al., 2007), soybean production has been shown to increase in presence of foraging *Apis mellifera* (Moreti et al., 1998; Chiari et al., 2005, 2008).

On the other hand, although soybean flowers offer low-quality nectar and may, thus, not be particularly attractive for bees (Erickson, 1975), their high density in crop fields may attract pollinators from nearby natural environments (Chiari et al., 2005). In fact, soybean flowers have proved the main source of pollen (Free, 1993) and nectar resources (Santos et al., 2013) for some beehives.

Here, we analyze the bee visiting ensemble on soybean flowers and the effects of pollinator visits on soybean reproductive success, within a fragmented Chaco forest landscape in Central Argentina. Soybean is the main export from Argentina, which is the third largest soybean exporter worldwide (Calvo et al., 2011). By analysing visit rates in relation to distance from the forest, and by comparing soybean bee assemblages with those on wild flowers in the nearby forest fragments, we hoped to provide for the first time, evidence of the forest role as pollinator donor for the soybean crop. We expected bee richness and visitation rates to decrease and to be restricted to larger species (body size being a good estimator of bee foraging distance, e.g., Greenleaf et al., 2007), on flowers located further away from the forest. Moreover, we expected lower reproductive success on soybean flowers experimentally isolated from pollinators.

2. Materials and methods

2.1. Study area

The Chaco Serrano district belongs to the most extensive dry forest in South America, with 750 mm annual rainfall concentrated mostly in the warm season (October–April), and mean temperatures between 26 °C (maximum) and 10 °C (minimum) (Luti et al., 1979). The native vegetation comprises an open tree stratum (up to 15 m high), 1–3 m high shrubs covering 10–80% of the ground, a herbaceous layer (up to 95% cover), and many vines and epiphytes (Cabido et al., 1991). This vegetation is currently restricted to isolated patches of native vegetation within an intensely managed agricultural matrix, largely dominated by wheat in winter and soy in summer. Within a fragmented Chaco Serrano landscape in Central Argentina (31°10′ – 31°30′ S and 64°00′ – 64°30′ W) we selected from satellite images (QuickBird, October 2010), nine landscapes circles (500 m diameter) including on average 32.66% (SE = 7.33) natural vegetation cover. At the time of the study, the transgenic soybean variety ALM 3830 was cultivated in the area.

During December 2010–January 2011, hymenopteran visits to soybean flowers were observed on each landscape circle (further referred to as "sites") at three distances from the forest edge: 5, 50 and 100 m. At each distance, all visits by hymenopteran insects were recorded during a 10-min interval in two linear plots, interval in each of two lineal plots 50 cm in length along a row of soybean plants, i.e., one hour per site and sampling date. Each site (with two plots at three distances from the forest) was observed four times during the flowering period (total 4 h per site), under similar weather conditions (moderately windy and sunny days). Attending to possible differential preferences in visitation time across bee species half of the observations on each site was made in the morning (8:30–12:30 h) and the other half in the afternoon (14:00–18:00 h). Moreover, insects visiting soybean flowers were collected and taken to the laboratory, where they were identified, and their wing and body length were measured with a calibrated ocular micrometer at 2.5× (±0,01 mm).

The pollinator ensemble observed on soybean, was compared with a regional database compiling flower-visitor records from 45 h of observation per site in nine forest areas (Musicante, 2013) in order to corroborate the species occurrence in the forest. The number of other *Fabaceae* species available in the forest, provided also by the same database, was considered to detect possible interaction preferences.

Visitation rate was estimated as: [(visitor number/open flowers in the patch)/observation time] × 1000, as widely used in the relevant literature contributions (Vázquez et al., 2005). Visitation rates were calculated: (a) for each pollinator species in soybean (this study) and in the forest (data from Musicante, 2013); (b) for soybean plants at each distance to the forest in each site, summing up all visiting pollinator species.

2.2 Exclosure experiment

This experiment was carried out in order to assess the contribution of insect visits to soybean reproductive success. Ten plants, at least 10 m apart from each other and at 5 m from the forest edge, were randomly selected in each site. On each plant, 6 floral buds were marked and on three of them pollinators were excluded by enclosing the buds in voile bags. After a month, all mature fruits developed from marked flowers were harvested and carried to the laboratory to be measured and weighed, and to estimate variables indicative of plant productivity: percentage of aborted flowers, number of seeds per fruit, weight of fruits and seeds and reproductive success (Dafni et al., 2005). Relative reproductive success was estimated as (no. fruits/no. flowers) × (mean no. seeds per fruit/mean no. ovules per flower). The mean number of ovules per flower was previously estimated by counting ovules in ten randomly selected soybean flowers per site, which were excised before opening and conserved in alcohol 70%.

2.3. Data analysis

Variations in pollinator richness and visitation rates were analyzed by means of linear mixed models (LME) with distance to forest as fixed factor and site as random. Prior to these analyses, Mantel tests were performed to check for spatial effects of site location on the response variables. Euclidean distance matrices of visitation rates and visitor species richness were compared with the geographic distance matrix (latitude and longitude at the site center point).

Visitation rates displayed by the visitor species observed in soybean and in the forest were compared by means of *G*-test, in order to check for differential activity in relation to habitat type. Spearman's rank correlations between femur or wing length of each native visitor and the distance from the forest to the flower it visited were also performed, in order to explore possible dispersal limitations for forest species to visit soybean flowers.

Data obtained from the exclosure experiment (percentage of aborted flowers, weight of fruits and seeds and reproductive success) were also analysed through LME, with exclosure treatment as fixed factor (two levels) and site as random factor.

Response variables were log transformed before data analysis. All analyses were done in SPSS Statistics 17.0.

3. Results

From a total of 36 h of observations, just 27 insect visits were recorded on soybean flowers. Five species belonging to two families of bees, *Apidae* and *Halictidae*, were identified (Table 1). On soybean flowers, the number of visits was an order of magnitude lower (soybean = 0.66 specimens/h; forest = 6.51 specimens/h) and involved nearly half the number of species (soybean = 0.14 species/h; forest = 0.37 species/h) in comparison with observations from the forest (Fig. 1A).

The bee species observed on soybean were well represented in the forest (Fig. 1A), but their relative abundance differed between these habitats: *Apis mellifera* (domestic bee) was more abundant than expected in the forest, whereas *Augochloropsis* sp. 1 and *Lasioglossum* sp. 1 were observed more frequently on soybean flowers than would be expected from a random distribution (G-test = 8.82, df = 4, P = 0.047). *Lasioglossum* sp. 1 was even more generalist (visiting 45 plant species in the forest) than the domestic bee (38 species), whereas the other three wild visitors showed noticeably narrower ranges (Table 1).

Apis mellifera was the most abundant species, accounting for over 50% of all flower visits recorded, both on soybean and in the forest (Fig. 1A) and, although its visitation rates were substantially lower in the crop (Table 1), it was the only visitor found on soybean at all distances from the forest (Fig. 1B). A turnover of native species was observed along the gradient of distance, with *Lasioglossum* sp. 1 being even more abundant than honey bees on soybean flowers nearer the forest (Fig. 1B).

Visitor richness in soybean samples varied between 0 and 2 ($X = 0.63 \pm 0.13$), without significant influence of the distance to the forest (linear mixed model, F = 2.245, df = 2,16, P = 0.13). As distance from the forest increased, larger native bees were observed on soybean flowers (Spearman's rank correlation, femur length r = 0.86, P = 0.02; wing length r = 0.85, P = 0.02) (Fig. 2A and B). Moreover, visitation rates were significantly and negatively affected by distance to the forest (linear mixed model, F = 5.022, df = 2,24, P = 0.015), with flowers situated at 5 m from the forest receiving at least three times more visits than those at longer distances (Fig. 2C). Pollinator visitation rates at each site fluctuated between 0 and 2.50, with an average of 0.25 (±0.08) pollinators/flower/hour, independently of the geographic location of the study sites (Mantel test, $P > 0.05$).

All plant productivity variables measured in the exclosure experiments differed significantly between bagged and unbagged flowers (linear mixed model, Table 2). Flowers exposed to visitors displayed a higher number of seeds, higher fruit and seed weight, and a lower number of aborted fruits than bagged flowers (Fig. 3A–C).

4. Discussion

Recent studies have suggested that natural habitats, by harboring wild pollinators, provide a resilient and complementary pollination service leading to increased yields in nearby crops (Carvalheiro, 2011; Vanbergen and Initiative, 2013). Although the role of insect pollinators on soybean production has been generally disregarded, with producers relying on autopollination and pesticides to maintain yield levels (Milfont et al., 2013), growing evidence links improved soybean production to the activity of flower visitors (Chiari et al., 2005; Milfont et al., 2013 Santos et al., 2013). However, the contribution of natural habitats to visitors on soybean flowers remains practically ignored. The present study offers preliminary evidence linking forest proximity to higher visitation rates and presence of wild pollinators on soybean flowers in Central Argentina. It also shows that pollinator activity matters for this crop, leading to increased soybean yield.

4.1. Does the forest provide pollinators for soybean flowers?

Although we observed fewer than one visitor per hour on soybean flowers in Central Argentina, much higher visitation rates (35.6 visitors/h) were recorded in Brasil (Chiari et al., 2005) and soybean pollen was a major input (35–50%) in experimental apiaries in Uruguay (Santos et al., 2013), proving that soybean flowers can represent an attractive resource for bees. Attractiveness for insect visitors seems to depend on soybean variety, nitrogen and potassium content in the soil (Abrol and Shankar, 2012; Robacker, 1983) and various floral traits like morphology, color, scent and pollen production (Palmer et al., 2009). The use of pesticides might have also driven low visitation rates in our work, as observed in other studies using crops under realistic agricultural practices (Milfont et al., 2013).

By comparing insect visits on soybean with visits in the nearby forest, we noticed that despite receiving ten times fewer visitors than forest flowers (allowing for differences in sampling effort), the soybean assemblage appeared to be relatively rich, with forest assemblages including just over twice the number of species found in the crop, per hour of observation. Moreover, the four wild bee species observed in the crop were well represented in the forest, supporting the role of the native habitat as refuge and donor for soybean pollinators.

Apis mellifera was the most conspicuous soybean flower visitor, as observed in other studies (Erickson, 1975; Free, 1993; Chiari et al., 2005, 2008; Santos et al., 2013; Milfont et al., 2013). However, our visitor assemblages stand out for their high representation of wild species, being responsible for over 40% of the visits, in comparison with fewer than 25% in comparable studies (Chiari et al., 2005; Milfont et al., 2013; Santos et al., 2013). These

Table 1
Bee species observed on soybean crops in Central Argentina, indicating their visitation rates in soybean flowers (36 h of observation) and in flowers of Chaco Serrano forest (408 h of observation). The number of interactions observed in the natural habitat (total and in *Fabaceae* species) is also indicated.

Family	Species	Soybean	Forest		
		Visit frequency	Visit frequency	Number of total plant species visited (N = 223)	Number of *Fabaceae* plants visited (N = 12)
Apidae	*Apis mellifera* L. 1758	0,4	7	38	0
Halictidae	*Augochlora nausicaa* (Schrottky, 1909)	0,03	0,15	11	1
Halictidae	*Augochlora pohemonae*	0,03	0,22	15	0
Halictidae	*Augocloropsis* Cockerell 1935 sp. 1	0,03	0,02	9	0
Halictidae	*Lasioglossum* Curtis 1833 sp. 1	0,17	1,28	45	2

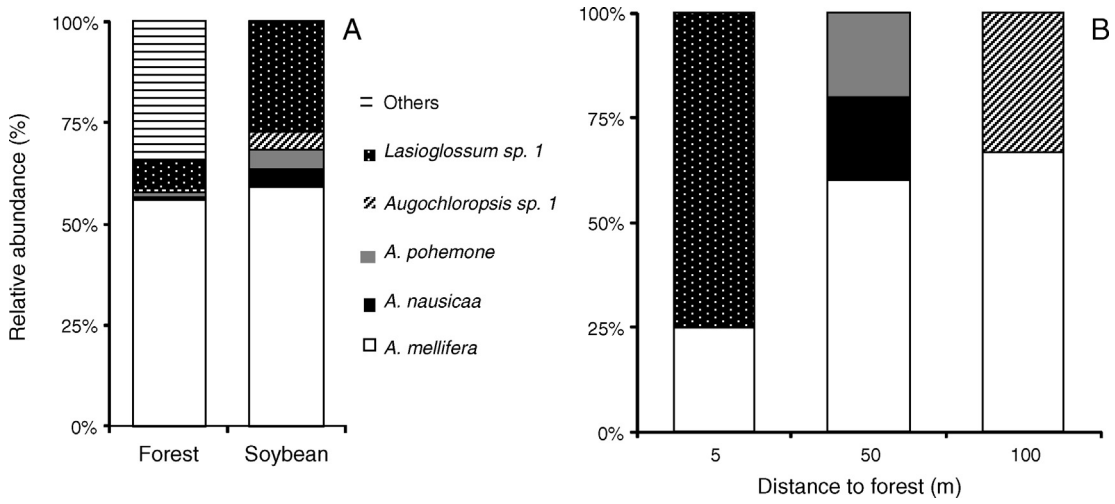

Fig. 1. Relative abundance (%) of each bee flower visiting species in (A) assemblages observed in Chaco Serrano forest (n = 405 h of observation, 2638 insects, 149 species) and soybean flowers (n = 36 h, 24 insects, 5 species) and (B) assemblages in soybean flowers at three distances from the forest (5 m: n = 8, 50 m: n = 5, 100 m: n = 3).

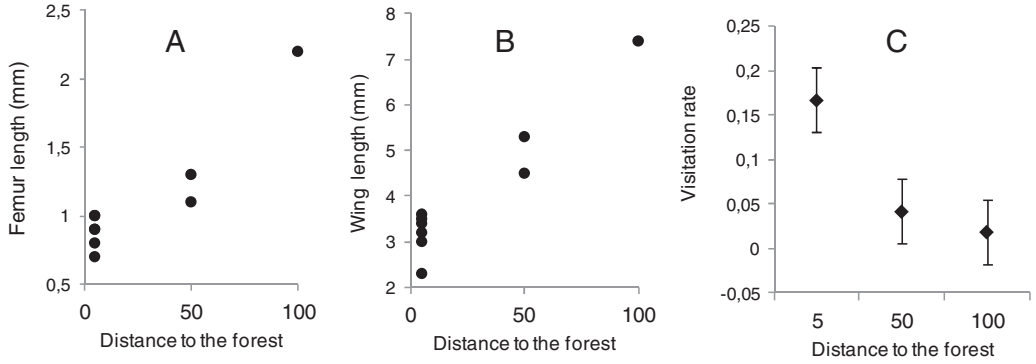

Fig. 2. Wing (A) and femur (B) length of native hymenopteran visitors, and mean (from 9 sites) visitation rates (C) in soybean flowers at three distances from forests. Vertical bars are standard errors.

wild species belong to three genera (*Augochloropsis*, *Augochlora* and *Lasioglossum*) not previously observed on soybean flowers, although insects from other *Hymenoptera* families and other insect orders have been reported on soybean flowers elsewhere (e.g., Jaycox, 1970). Remarkably, two wild species (*Augochloropsis* sp. and *Lasioglossum* sp.) seemed to thrive in the crop, where they were relatively more common than in the forest. Wild bees appear to be less sensitive to environmental conditions than their domesticated counterparts, with effects on crop pollination rates (Brittain et al., 2013) and reinforcing the importance of natural habitat conservation to enhance the ecosystem service of pollination.

Soybean flowers showed significantly lower visitation rates at increasing distance from the forest, as observed in other crops with relation to insect sources (Carvalheiro, 2011) and supporting the possibility of a visitor spillover from the forest to the crop. Only *A. mellifera*, which is usually omnipresent in crops (Chacoff and Aizen, 2006; Santos et al., 2013), visited soybean flowers at all studied distances from the forest. Instead, wild visitors displayed a turnover of species throughout those distances, with smaller species being restricted to the forest proximity and replaced by larger ones toward the interior of the crop. Increasing body size of flower visitors with distance from the forest suggests dispersal

Table 2
Results of mixed linear model analysing the effect of pollinator exclusion on indicators of soybean production, in plants growing at 5 m from remnants of Chaco Serrano forest in Central Argentina.

Explanatory variable	Fixed effects	F	df	P	Mean treatment difference (SE)	Random factor	Wald's (P)
Percentage of seed abortions	Constant	1407.646	14	<0.001	0.1703	0.0000	–
	Exclusion	17.159	14	0.001	(0.0411)		
Weight of pods	Constant	83.507	7.63	<0.0001	-0.0715	0.0005	0.466
	Exclusion	8.678	7.15	0.021	(0.0242)		(>0.05)
Weight of seeds	Constant	6.745	12.8	<0.0001	−0.0489	0.0004	0.594
	Exclusion	6.051	6.05	0.031	(0.0175)		(>0.05)
Reproductive success	Constant	14.586	10.9	0.006	−0.8203	0.5001	1.194
	Exclusion	6.166	6.16	0.049	(0.3348)		(>0.05)

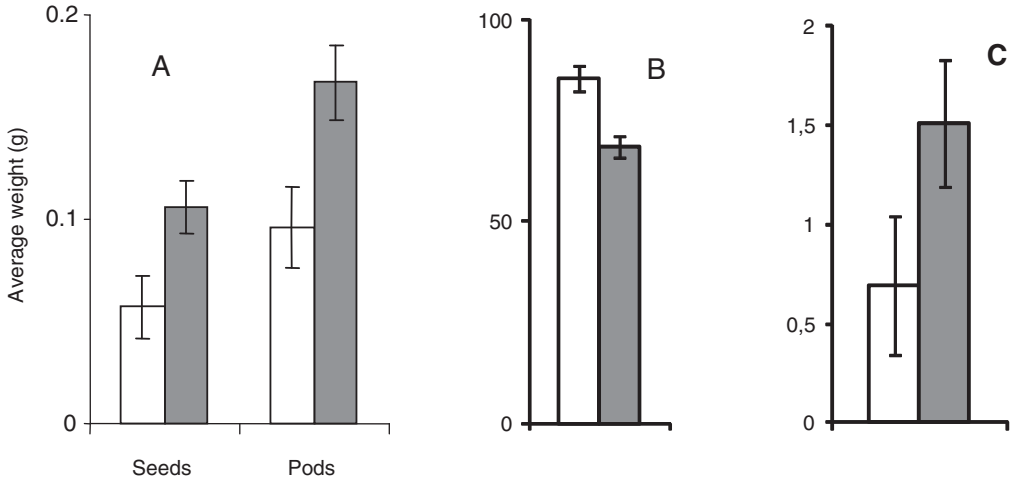

Fig. 3. Average weight of seeds and pods (A), seed abortion percentage (B) and reproductive success (C) in flowers exposed (empty bars) and not exposed (filled bars) to pollinators. Vertical bars are standard errors.

limitations and reinforces our proposition of the forest being the source of visitors for soybean flowers.

4.2. Pollinators on soybean flowers: do they matter?

All our indicators pointed to an improved production when floral visitors were allowed to reach soybean flowers. Notwithstanding the scarcity of flower visitors we observed, seed and pod weight as well as reproductive success in flowers exposed to pollinators showed twice the values from bagged flowers. These results are particularly interesting when comparing with previous studies reporting 5–95% soybean yield increments from experiments with *A. mellifera* introductions (Chiari et al., 2005 and references therein). Moreover, in our study the number of aborted flowers was reduced by 20% when pollinators were allowed, with values closely resembling those recorded by Chiari et al. (2005) where soybean abortions reached 82.90 and 53.81% in experimental plots with and without addition of bees, respectively. Our results, obtained under natural conditions, indicate that natural pollinators might effectively improve soybean productivity, and therefore should be a factor to be considered in crop management schemes.

Since the exclosure experiments were carried out at 5 m from the forest, where visitation rates were highest and mostly by *Lasioglossum* sp. 1, these results suggest that the wild bee may play an important part in local crop production by contributing to enhance soybean fruit set. Moreover, this species showed higher visitation rates in the crop than in the natural habitat, suggesting some preference for the cultivated environment, which may contribute to its positive effect on the crop and deserve further study.

5. Conclusions

Our findings emphasize the existence of positive links between natural and cultivated systems, supporting the role of forest remnants as source of flower visitors for nearby soybean crops. Furthermore, we provide evidence indicating that pollinator activity matters, leading to higher crop productivity. These results are particularly important in the context of a global decline of pollinator populations, and underline the critical need to understand the sources of pollinators and their incidence on crop production, in order to develop conservation plans to ensure the critical ecosystem service of pollination (Brittain et al., 2013).

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