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Native marsupial acts as an in situ biological control agent of the main soybean pest (*Euschistus heros*) in the Neotropics

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Abstract

Natural predators of agricultural pests are known to help increase crop yields and are considered an alternative to chemical insecticides. We investigated the role of the gracile mouse opossum *Gracilinanus agilis* for controlling a soybean pest, the brown stink bug *Euschistus heros*. We tested the hypothesis that this bug disperses to natural forest environments of the Brazilian savanna (Cerrado) during the soybean off-season and that *G. agilis* acts as a relevant predator of this insect. We also quantified and valued *G. agilis* predation on *E. heros* independently in five forest areas located at different distances from a soybean crop. The isotope ratios (δ^{13} C and δ^{15} N) of *E. heros* remains found in predator fecal samples collected during the soybean off-season were more similar to *E. heros* collected in the crop than to samples collected during the growing season. *Gracilinanus agilis* predation on *E. heros* in forest and crop. This inverse relationship indicates that the potential role of mouse opossums for pest control depends on the proximity of natural forests to crops. We estimated that the ecosystem service provided by this marsupial may reach up to US\$ 31.08 ha⁻¹ year⁻¹ of native forest, which may represent tens of millions of dollars per year considering the amount of native vegetation within farmlands in the Cerrado. These results highlight the relevance of natural vegetation conservation near crops for the maintenance of agricultural pest control.

Keywords Cerrado · Ecosystem service · Predation · Small mammal · Stink bug · Economic valuation

Introduction

The high efficiency of modern agriculture in food production based on the widespread use of synthetic pesticides causes multiple negative impacts on biodiversity and ecosystems,

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in addition to increasing production costs and impacting human health (Pimentel and Burguess 2014; Tilman et al. 2001). For instance, costs with pesticides totaled more than \$39.4 billion in 2007 (Grube et al. 2011). Natural enemies, however, can be up to tenfold more effective than synthetic pesticides in pest control (Pimentel and Burguess 2014). The current knowledge on the effective pest control provided by native species, especially in tropical ecosystems (Veres et al. 2013), is still incipient but this service was preliminarily valued from \$54 billion to \$1 trillion year⁻¹ (Naylor and Ehrlich 1997). Pest control provision and other ecosystem services, however, have been severely reduced due to global land use changes (Costanza et al. 2014). For taking actions against reduction on the losses of pest control services, it is necessary the identification of species involved in predator-prey interactions and the understanding of their spatial and temporal dynamics. Moreover, the economic valuation of relevant pest control services is highly desirable. All these actions are necessary for predicting outputs of ecosystem services

and improving the adequate management of ecosystems and natural resources (Power 2010).

Pest control services may be enhanced by the conservation and management of natural habitats (e.g., landscape composition and strucuture; Veres et al. 2013; Werling and Gratton 2010), which in turn, potentially increase the diversity of pest natural enemies (Greenop et al. 2018). In fact, the advantages of the maintenance of non-crop native natural habitats surrounding crops for pest control have been well documented (Chaplin-Kramer et al. 2013). This practice would reduce habitat simplification and disruption of connectivity between natural and agricultural areas caused by large monocultures. In cropping systems in Europe and North America, for instance, landscape homogenization of the landscape resulting from removal of natural environments has led to a loss of 46% of pest control provided by natural enemies (Rusch et al. 2016). Pest control services may be enhanced by the maintenance of non-crop native habitats, which increase niche complementarity of predators and allow them to forage at different places and times, attacking different pest species (Ives et al. 2005; Snyder 2019). In some cases, however, conservation of natural habitats negatively affects pest suppression, through a reduction in intraguild predation (Janssen et al. 2007). Moreover, there are several factors at landscape scale (e.g., proximity of non-crop enemy-suitable natural habitats to crops, proportion of these habitats in the landscapes surrounding crops), whose role in pest control is still not well understood (Karp et al. 2018). These factors in general affect positively enemy activity but also, in some cases, even enhance pest survivorship (Chaplin-Kramer et al. 2013). Therefore, identifying the ecological factors that predict the role of natural habitats on the pest control services remains a major challenge.

One of the most important crops worldwide that might benefit from natural pest control is the soybean crop (Hartman et al. 2011), the fourth largest agricultural input in the world considering the planted area (FAO 2018). About 27% of this area is composed by crops cultivated in Brazil, the second largest soybean producer worldwide (CONAB 2020). These soybean crops are attacked by a diverse fauna of herbivorous insects but the stink bugs (Hemiptera: Pentatomidae) are the most relevant pests during the reproductive phase of soybean (O'Neal and Johnson 2010). In South America, the brown stink bug *Euschistus heros* is the main phytophagous hemipteran species that causes injuries in soybean plants (Panizzi et al. 2012), leading to 30% damage to both the quality and quantity of available soybean cultures if no control measures are taken (Nunes and Corrêa-Ferreira 2002).

The main pest management strategies for controlling *E. heros* consist of the use of pesticides when pest densities reach certain threshold levels, and the use of biological control agents such as parasitoid wasps and pathogens (bacteria, viruses, and fungi) (O'Neal and Johnson 2010). This bug is

also consumed by native animals such as the gracile mouse opossum *Gracilinanus agilis*. This marsupial was the first vertebrate reported as a potential predator of brown stink bugs in savanna woodlands in the Brazilian savanna (Camargo et al. 2014). This consumption occurs in native forests during the soybean off-season, suggesting a dispersal of *E. heros* from the soybean crop to natural environments when there is no soybean available after the harvest. This potential dispersal, however, has not been properly investigated, since the source of the bugs consumed by the marsupials is still unknown (Camargo et al. 2014).

Understanding the predation dynamics of E. heros by G. agilis can be important for preserving pest control services, highlighting the relevance of the conservation of natural vegetation near crops and helping decision-makers for farm management and pest control solutions based on ecological processes (Bianchi et al. 2008; Chaplin-Kramer et al. 2013). This knowledge can be even more relevant considering the high destruction rates of the Cerrado (Strassburg et al. 2017), since the maintenance of natural environments for biological control purposes could also contribute to sustaining the biodiversity and related services as a whole (Nelson et al. 2009). An extinction model integrating predator-prey dynamics with an economic model of three natural predators of pear psylla (Cacopsylla pyri) at farm level, for example, showed a relevant reduction of net farm income up to thousands euros per hectare (Daniels et al. 2017). Therefore, conserving natural habitats adjacent to plantations could reduce production costs through pest regulation by natural predators (Chaplin-Kramer et al. 2013; Gardiner et al. 2009).

In the present study, we quantified and valued the natural pest control service performed by the marsupial G. agilis through predation on the brown stink bug E. heros. For this purpose, we analyzed the spatiotemporal predation dynamics of *E. heros* by quantifying the occurrence of this soybean pest in fecal samples of G. agilis in five distinct forest habitats in an anthropic landscape in the Cerrado. We also relied on stable isotope analysis, using the ratios of δ^{13} C and δ^{15} N, to determine the origin of the brown stink bugs found in the forests. Our objectives were (1) to confirm whether there is a seasonal dispersal of E. heros from a soybean crop to forest environments of the Cerrado; (2) to describe the spatiotemporal predation dynamics of G. agilis on E. heros in forest environments; and (3) to value the potential natural pest control performed by G. agilis populations in forest environments near a soybean crop.

Considering our objectives, we expected that (1) individuals of *E. heros* disperse from the soybean crop to forest environments during the soybean off-season, when food resources for this insect are in shortage (Camargo et al. 2014). Therefore, we predicted that during the soybean off-season, predation by opossums is more frequent than during the soybean growing season. Additionally, since our

expectation lays on the dispersal of *E. heros* from the soybean crop to natural environments, we predicted (2) that the isotopic signatures of these insects found in forests during the soybean off-season are more similar to *E. heros* collected in the soybean crop than to those insects collected in the forests during the growing season. This would indicate that the source of *E. heros* individuals found in the forests during the soybean off-season is the soybean crop. Moreover, we expected (3) a negative relationship between the distance from forest environments to the soybean crop and the proportion of individuals in *G. agilis* populations preying upon *E. heros*. In cases where natural environments are closer to the soybean crop (the potential source of these insects), *G. agilis* predation on *E. heros* is more frequent due to the higher local abundances of this agricultural pest in forests.

Methods

Studied species

Euschistus heros

The brown stink bug Euschistus heros (Supplementary Information, Fig. S1) is a pentatomid species native to the Neotropical region that attacks soybean in Central and South America, especially in Brazil. Compared with other sympatric stink bugs in soybean crops, E. heros has a relative abundance varying between 50 and 90% (Aquino et al. 2018; Panizzi and Lucini 2016). Its distribution in the country ranges from the south to the west, central and northeastern regions (Panizzi and Slansky Jr. 1985). The growth from the egg to the adult phase is achieved in approximately 30 days, and the lifespan of E. heros is approximately 120 days (Cividanes and Parra 1994b; Panizzi and Oliveira 1998; Villas Bôas and Panizzi 1980) being able to produce up to six generations during the soybean growing season in central Region of Brazil (Cividanes and Parra 1994a). When individuals of this species experience unfavorable conditions (e.g., food shortage), it can enter diapause or partial diapause, remaining on the soil underneath dead leaves or between grasses (Kishino and Alves 1994; Panizzi and Niva 1994; Panizzi and Hirose 1995), with reduced reproduction capacity (Borges et al. 2011; Mourão and Panizzi 2002, 2000). Individuals of E. heros may disperse to alternative host plants during the off-season such as surrounding grasses and weeds (Panizzi 1997), and other crops (Azambuja et al. 2013; Gomes et al. 2020). The current knowledge on invasiveness, impacts, and autoecology (e.g., diet, reproduction, growth, and survival) of this insect in natural environments, however, is highly scarce.

Gracilinanus agilis

The gracile mouse opossum *G. agilis* (Supplementary Information, Fig. S1) is a small (20–30 g body mass), solitary, nocturnal, and scansorial marsupial whose distribution ranges from the border of Panama with Colombia to the Northeast, Midwest, and Southeast of Brazil (Emmons and Feer 1997). Generally common in forest formations present in the Brazilian Cerrado (Nitikman and Mares 1987), *G. agilis* feeds on pioneer fruits and several orders of arthropods (mainly Hymenoptera, Coleoptera, Hemiptera, and Coleoptera), occasionally also preying upon birds (Camargo et al. 2014).

Study area

We conducted our study in the core area of the Cerrado, the second largest phytogeographic domain of South America (Ab'Sáber 1977), with 2.4 million hectares (Sano et al. 2010). The Cerrado is characterized by two well-marked seasons, a cool-dry and a warm-wet one, with the latter occurring between October and April, when 90% of the annual precipitation of 1100-1600 mm occurs (Miranda et al. 1993). Vegetation types include typical savanna habitats, grasslands, and forests, which are influenced by edaphic features (Ribeiro and Walter 1998). In Brazil, most of the soybean production comes from crops located in areas originally covered by the Cerrado (Klink and Moreira 2002; Mattos Scaramuzza et al. 2017). This Neotropical savanna has been converted in crops (mainly soybean) at high rates in the last 50 years (Klink and Machado 2005; Strassburg et al. 2017).

Our data collection was conducted near the city of Brasília (the Federal District of Brazil) between 2016 and 2018 in five distinct forest sites, four savanna woodlands (locally known as cerradão) and one gallery forest (Fig. 1). Savanna woodlands are xeromorphic forest with trees that range from 8 to 15 m and a tree layer that oscillates between 50 and 90%, encompassing about 1% of the total Cerrado area (Ribeiro and Walter 1998; Silva and Bates 2002). On the other hand, with approximately 5% of the Cerrado area, gallery forests present trees with 20 to 25 m that surround water bodies and a tree layer that ranges from 70 to 95% (Felfili et al. 2001; Ribeiro and Walter 1998). All the savanna woodland sites (SW1, SW2, SW3 and SW4) were located at the Area of Environmental Protection (APA) Gama e Cabeça-de-Veado, which covers approximately 15,000 ha of continuous Cerrado vegetation and is adjacent to a soybean crop with approximately 2,000 ha (Fig. 1). The distance of the savanna woodland sites from the soybean crop ranged from approximately 2 to 11 km (distance between soybean crop and savanna woodland sites: SW1 = 2 km, SW2 = 5 km, SW3 = 7 km, and SW4 = 11).

Fig. 1 Location of the study sites in the Neotropical savanna (Cerrado), shown as a green area in Brazil's map (dark gray area) on the top left. These sites were located near the city of Brasília in the Federal District of Brazil (top right inset). The bottom map indicates the detailed location of the four sampled sites of cerradão (savanna woodland forest; SW1-SW4) at the Area of Environmental Protection (APA) Gama e Cabeça-de-Veado and the sampled gallery forest (GF). The yellow line indicates the soybean crop area located in front of the APA



The gallery forest was located adjacent and surrounded by the soybean crop, and the sampled portion of the forest was located ca. 0.1 km from the crop.

Capture procedures and fecal sample collection

In order to capture mouse opossum individuals in the savanna woodlands, we placed Sherman live traps forming grids composed of 80 to 84 capture stations spaced at 15 m intervals (grid configuration and total area covered: $SW1 = 14 \times 6$, 1.46 ha; $SW2 = 9 \times 9$, 1.44 ha; $SW3 = 9 \times 9$, 1.44 ha; and $SW4 = 10 \times 8$, 1.42 ha). In the Gallery forest (GF), we captured the animals in a grid composed of 80 capture stations (10×8 , 0.63 ha) spaced at 10 m intervals. This difference in the capture station intervals between sites was due to the shape and size of each forest. In each capture station, we installed one trap baited

with a uniform mixture of peanut butter, corn flour, mashed banana, cod liver oil, and vanilla essence. The captured individuals received numbered ear tags for further identification (National Band and Tag Co.; model 1005–1). At each site, we conducted sampling sessions during the dry season (April to September—hereafter named the soybean off-season) and in the wet season (October to March—hereafter named the soybean growing season) aiming to collect fecal samples of at least 20 *G. agilis* individuals per site. Total sample effort ranged from 480 to 2,520 trapping-nights at each site.

For each individual captured in the field, we collected the fecal samples found inside the traps or during handling of the trapped animal and stored the scats in a freezer for preservation. After each capture, the trap was cleaned or replaced with a new clean trap to avoid contamination of subsequent scat samples by other individuals captured in the same capture station. These fecal samples were washed in laboratory using a sieve mesh (0.1 mm), and with the aid of a binocular stereoscopic microscope, we searched for any E. heros remains. Most of these remains consisted of small fragments of the exoskeleton. In several samples, however, we also were able to identify intact or partially persevered structures such as wings, heads, pronotum spines, and leg parts. The identification of these remains was performed by comparing the fragments of E. heros found in the scats of G. agilis that were offered stink bugs in the laboratory (see the "Potential of predation" section for more details). As an additional reference, we also used intact E. heros individuals preserved in alcohol (Supplementary Information, Fig. S1). During the study, there were 789 captures of 183 individuals of Gracilinanus agilis (33 individuals in SW1, 51 in SW2, 40 in SW3, 32 in SW4, and 27 in GF). We collected a total of 741 fecal samples from 164 marsupials. From these samples, only one sample from each individual in each season was considered. Taking into account this criterion, we analyzed a total of 126 samples from the soybean off-season (SW1 = 17, SW2 = 34, SW3 = 33, SW4 = 20, and GF = 22) and 113 samples from the soybean growing season (SW1 = 19, SW2 = 31, SW3 = 23, SW4 = 23, and GF = 17).

Isotopic analysis

We assessed the source of stink bugs consumed by G. agilis using stable isotope analysis. We investigated the isotopic signatures (δ^{13} C and δ^{15} N) of *E. heros* remains found in the fecal samples of the marsupials captured in the native forests. We also analyzed 20 individuals of E. heros actively collected in the soybean crop during growing season, as a baseline for comparisons of the isotopic signatures. For both sample groups (remains found in G. agilis feces and bugs collected in the soybean crop), the samples were washed in distilled water, oven-dried at 60 °C for 72 h, mill-ground into a homogeneous powder, and weighed in tin capsules (minimum sample weight = 0.7 mg for fecal remains and 1.0 mg for bugs collected in the crop) on an analytical scale (0.0001 g precision). When a sample of a G. agilis individual was below the minimum required weight for the analysis, we pooled samples of other individuals from the same site and season (i.e., soybean off-season or growing season) to reach the needed minimum sample weight. With this protocol, we were able to determine whether the δ^{13} C and δ^{15} N of E. heros found in G. agilis fecal samples were similar to those of individuals feeding on soybean, which would indicate a dispersal of stink bugs from the soybean crop to forest environments. For determination of ¹³C/¹²C and ¹⁵N/¹⁴N isotope ratios of E. heros, we sent the samples to Stable Isotope Facility of the University of California, Davis, USA, or to Isotope Ecology Laboratory of the Nuclear Energy and Agriculture Center (CENA in Portuguese) at the University of São Paulo, Piracicaba, São Paulo, Brazil (see Supplementary Information for more details).

Valuation of the pest control performed by *G. agilis*

Potential of predation

To quantify the potential of predation on *E. heros* by *G. agilis* in the laboratory (ex situ), we singly offered to 11 adult opossums (five males and six females; average body mass: $24.6 \text{ g} \pm 5.4 \text{ g}$ [SD]) between 100 and 155 adult stink bugs (average body mass: $0.072 \text{ g} \pm 0.003 \text{ g}$). We obtained stink bugs to feed the mouse opossums by establishing *E. heros* colonies fed with a mixture of soybean grains, peanuts and sunflower seeds, and pea pods (Silva et al. 2008). The number of animals used for these feeding trials (11) was constrained by the availability of mouse opossums during the field activities and mainly by the number of *E. heros* in the colony. This latter also affected the number of stink bugs offered to *G. agilis* per day.

During the feeding trials, the G. agilis individuals were maintained fasting for at least 8 h, and each individual was fed with stink bugs only once in a cage with 50 cm long by 30 cm wide by 15 cm high. The cage was covered with a metal mesh preventing the stink bugs to scape. Inside the cage there were no obstacles so that the mouse opossum could freely walk to feed on the available stink bugs, with no hiding places for these insects. The trials had between 1- and 2-month intervals between June 2017 and June 2018, which corresponded to the period for obtaining the appropriated number of stink bugs to offer to a single mouse opossum. Considering that G. agilis is a nocturnal small mammal (Vieira et al. 2017), stink bugs were offered to the marsupials from 18:00 h to 07:00 h. After this feeding period, we counted the remaining E. heros individuals to determine the average number of stink bugs a marsupial can potentially prey upon in one night. None of the 11 captive G. agilis individuals consumed the totality of insects offered, indicating that they were satiated after each trial.

This experimental protocol of stink bug offer to captive marsupials was established to determine the maximum possible number of these insects a *G. agilis* individual can eat in one night. In natural environments (in situ), however, this marsupial certainly relies on a wide range of arthropods available as food resources (Camargo et al. 2014). In order to estimate the potential number of *E. heros* actually consumed by these marsupials in their natural environments, we determined the relative consumption of stink bugs considering all arthropods found in 12 independent fecal samples of adult *G. agilis* (four males and eight females) captured in the gallery forest in May 2018. This forest was the nearest site from the

soybean crop (Fig. 1), thus, with the highest probability of the stink bug be abundantly available for the mouse opossum (i.e., according to our third hypothesis). The fecal samples collected for consumption determination of E. heros by G. agilis corresponded to a period after the soybean harvest in the property (early March), when is expected the dispersal of the stink bugs to natural areas to find food resources. In each fecal sample, we assessed the total dry mass of each invertebrate group. For that, we separated all the fragments of E. heros and other arthropods present in fecal samples of G. agilis, oven-dried the material at 60 °C for 72 h and weighed the remains of each group on an analytical scale (0.0001 g precision). Thus, multiplying the average proportion of E. heros in the diet of G. agilis (in situ) and the average number of stink bugs an individual can consume in one night (ex situ), we were able to estimate the number of E. heros preyed upon per night in natural environments.

Density of G. agilis in forest environments

To estimate the potential effect that populations of *G. agilis* can exert on the regulation of *E. heros*, we calculated the population densities of the gracile mouse opossum in each forest site. This population metric is relevant to estimate the value of the in situ natural predation performed by *G. agilis*. Since individuals are not necessarily restricted to the interior of the grid, we calculated a surrounding boundary strip that can also be used by the individuals occupying the grid. We calculated the width of this strip considering the radius (25.2 m) of a hypothetically circular home range of 0.2 ha (Ribeiro 2011; Sano 2017). We considered this enlarged area as the "effective area sampled" (Krebs et al. 2011). To calculate the population density of *G. agilis*, we divided the number of captured individuals (minimum known abundance) by the effective grid area.

Monetary value of pest control provided by G. agilis

Aiming to value the direct service potentially provided by the gracile mouse opossum as predators of the brown stink bug by reducing costs of pesticide use—*Dserv_{gmo}*, we established the following formula:

$$Dserv_{gmo} = Cost_{bug} \times Dens_{gmo} \times Cons_{bug} \times Time,$$

where $Cost_{bug}$ is the cost of bug controlling for the farmer, Den_{gmo} is the density of this marsupial (individuals per hectare, see the "Density of G. agilis in forest environments" section), $Cons_{bug}$ is the average number of *E. heros* potentially consumed per night by *G. agilis* in natural environments (see "Potential of predation" section), and *Time* is the period of time in which sanitary protection of soybean crops occurs annually (from July to September, totaling 90 days). For details, see Supplementary Information.

Additionally, we evaluated the service provided by gracile mouse opossums with their indirect regulation of E. heros populations. This service consists of the effect that G. agilis potentially exerts preying upon reproductive females of stink bug in natural environments. This predation pressure helps in suppressing population abundance of bugs in crops in the following months, during the next soybean growing season. For valuing this regulation service provided $(Rser_{gmo})$, we considered the cost of bug controlling for the farmer ($Cost_{bug}$), the number of female bugs consumed, the reproductive capacity of females, and the survival rates of E. heros eggs in natural environments (see Supplementary Information for details). All the economic values estimated in the national currency unit (i.e., Brazilian real-R\$) were converted to US dollar (US\$) according to the annual exchange rates of 2019 (1.00 US = 3.945 R), provided in the Food and Agriculture Organization of the United Nations (FAO, 2018).

Statistical analysis

In both forest types sampled (savanna woodland and gallery forest), the marsupial G. agilis is an abundant species (Alho et al. 1986; Camargo et al. 2018b; Mendonça et al. 2015) and we did not record any individual occurring in more than one site. Thus, we considered each of the five sites as independent replicates in the analyses. For the evaluation of the effect of the forest distances from the soybean crop and season (i.e., soybean growing season and off-season) on the predation of E. heros by G. agilis, we performed a generalized linear mixed model (GLMM) analysis with binomial distribution, considering the presence (assigned as 1) or absence (assigned as 0) of E. heros in each fecal sample (sampling unit). For this analysis, we used only the data from the first capture of each marsupial individual per season. We considered individual as random effect to deal with fecal samples from the same individuals collected in both seasons (31% of the samples). The explanatory variables in the model were forest distance from the soybean crop and season (soybean off-season or growing season), considered as fixed effects in the model. The GLMM was performed in the software R version 3.5.1.

We compared the similarity of the δ^{13} C and δ^{15} N signatures of *E. heros* obtained in the fecal samples of *G. agilis* during the soybean off-season and growing season with those signatures of stink bugs collected in the crop (considered as baseline). For this comparison, we first calculated the standard ellipse area corrected for small sample size (SEAc) for each group. Then, we calculated the overlap between these ellipses expressed as a proportion,

which is considered a quantitative measure of dietary similarity between populations (Jackson et al. 2012). For comparison of the overlap between ellipses, we generated posterior estimates employing the Markov Chain Monte Carlo (MCMC) method with 10,000 permutations to generate 50, 75, and 95% credible Bayesian intervals. A comparatively higher overlap between pairs of ellipses would indicate a high similarity of isotope signatures between groups, thus, a similar food resources use by E. heros. Therefore, in case of a higher ellipse overlap between the isotopic signatures of stink bugs consumed by G. agilis in natural environments and the stink bugs collected in the soybean would indicate that the E. heros source is the surrounding soybean crops. The isotopic and Bayesian analyses were performed within the software R version 3.5.1 using the SIBER package (Jackson et al. 2011).

The δ^{15} N values of the Cerrado plants present a wide range of values (-5 to + 7.9%); Bustamante et al. 2004). On the other hand, the soybean has a δ^{15} N value of approximately 0% because of the mutualistic interaction with bacteria that fixate atmospheric nitrogen (Steele et al. 1983; Szpak et al. 2014). This value is in accordance with the general pattern for leguminous plants, with approximately 50% of the plants of this group presenting $\delta^{15}N$ values between -1.0% e +1.0% (Szpak et al. 2014). Therefore, we expected stink bugs feeding on native plants to present a higher variation in δ^{15} N values than stink bugs feeding strictly or mainly on soybean (but not necessarily differences in the mean δ^{15} N values between both groups). For ¹³C assimilation, however, we did not expect marked differences related to distinct stink bug sources. Both soybean and most of the savanna woodland plants are C3 photosynthesizers, presenting δ^{13} C ratios typically around - 28 % (Jones et al. 1979).

Considering our expectation in relation to ¹⁵ N assimilation, we evaluated the *E*. heros δ^{15} N values as a complementary approach to determine the source of the insects (i.e., whether the stink bugs consumed by opossums during the off-season were resident of natural areas or dispersed from the soybean crop). For that, we compared the within-group dispersion of δ^{15} N values among three groups of *E. heros*: (1) those found in the fecal samples of G. agilis in the forest sites during the soybean growing season (the "resident" stink bugs), (2) those found in the fecal samples from the same sites but during the off-season (the possible "newcomers"), and (3) δ^{15} N values for those stink bugs collected in the soybean crop during the soybean growing season. For this comparison, we used a permutational test for the null hypothesis of homogeneity of dispersion (PERMDISP) using Euclidian distance as dissimilarity measure (Anderson et al. 2008). This analysis would indicate whether stink bugs feeding on native plants (group 1) would present greater variation of δ^{15} N in comparison to those feeding exclusively or mostly on soybean (groups 3 and possibly 2). The PERMDISP test is robust and powerful for evaluating real differences in spread among groups (Anderson 2006).

For obtaining the mean values of predation capacity of *E. heros* by *G. agilis* per night (i.e., predation ex situ) and the proportion of the stink bug in the diet of the mouse opossum in relation to the other arthropods (predation in situ), we used the jackknife method (Tukey 1958). This procedure (see details in Supplementary Information) allowed us to obtain a distribution of means that should approach to a normal distribution, and to determine the sensitivity of the results to the addition or removal of individuals, which improved our variance estimates (Sokal and Rohlf 1995; Tukey 1958).

Results

Predation patterns in forest environments

The occurrence frequency of E. heros in fecal samples of mouse opossums was 472% higher during the soybean offseason (36.6% of 461 samples) than in the growing season (6.4% of 280 samples). During the off-season this frequency ranged from 5.4 to 65.7% in each forest site whereas during the growing season 0.0 to 8.8% of the fecal samples from each site contained remains of the stink bug. We investigated the effect of season and distance from soybean crop on the predation of E. heros by G. agilis through a GLMM and detected a higher general predation during the soybean offseason in comparison to the growing season ($\beta = 4.49 \pm 0.91$, z = 4.93, P < 0.0001), with no general effect of the distance between forest patch and the soybean crop on the predation of E. heros ($\beta = 0.06 \pm 0.12$, z = 0.55, P = 0.584). This analysis indicated, however, a significant interaction between both explanatory factors ($\beta = -0.50 \pm 0.14$ [SE], z = -3.53, P < 0.001), with a decrease in G. agilis predation on E. heros as the distance of the forests from the soybean crop increased, but only during the soybean off-season (Fig. 2).

Isotopic analysis

We analyzed 81 samples of *E. heros* remains found in fecal samples of *G. agilis* collected during the soybean off-season and nine samples from the soybean growing season. This numerical difference between samples lies in the fact that *E. heros* is much less frequent in the diet of *G. agilis* during the soybean growing season than in the off-season. Therefore, these unequal sample sizes are inherent to our study system.

The comparison of isospaces for *E. heros* originated from the three distinct sources evaluated indicated that during the soybean off-season *G. agilis* consumed stink bugs originated from crops (Fig. 3). Fragments from fecal samples obtained



Fig. 2 Results of the generalized linear model showing the relationship between the distance of the forests (savanna woodlands: SW1-SW4; gallery forest: GF) from the soybean crop and the predation probability of the gracile mouse opossum *Gracilinanus agilis* on *Euschistus heros* during the soybean off-season and growing season. Colored shaded areas indicate 95% confidence intervals

during the soybean off-season $(2.7\%^2)$, fecal samples obtained during the growing season $(3.4\%^2)$, and also stink bugs collected in the soybean crop $(2.2\%)^2$ had fairly similar sizes of their standard ellipse areas (SEAc). The overlap of these ellipses, however, varied according to the group pair considered. Despite being sampled in different times of the year, there was a high ellipse overlap (50.9%) between E. *heros* consumed during the soybean off-season (group 2) and E. heros collected directly in the crop (group 3). This overlap was 75% higher than the overlap between the two groups of E. heros sampled during the soybean growing season (29.1%): the group from forest sites (group 1) and those stink bugs collected in the crop (group 3). The overlap between isotopic ellipse areas of E. heros found in fecal samples during the soybean growing season (group 1) and in the off-season (group 2) was even lower (18.7%; Fig. 3) despite the fact that the same forest sites were sampled in both periods.

The comparison of the δ^{15} N values obtained from the three distinct groups also supported the assumption that stink bugs occurring in the forests sites during the soybean off-season originated from the soybean crops. Samples from scat remains obtained in forests during soybean off-season (group 2) and those obtained from stink bugs collected in the crop (group 3) had similar isotopic patterns considering the δ^{15} N values (off-season: mean \pm SD = 2.44 \pm 0.65%, range = 0.17 to 4.88%; crop bugs: mean \pm SD = 1.98 \pm 0.73%, range = 0.86 to 3.87%). This similarity would be expected in case that bugs consumed by *G. agilis* in the forests during

the off-season originated from the crops. Both these groups were very distinct (in average at least 111% higher) in comparison to the samples from scat remains obtained in native forests during the soybean growing season (group 1; mean \pm SD = 0.94 \pm 1.63%, range = -1.57 to 2.97%). The comparison of the within-group dispersion of E. heros δ^{15} N values indicated significant differences among groups (PER-MDISP; $F_{2,107} = 13.245$, P < 0.001). A posteriori comparisons indicated no significant difference (P=0.82) between samples from scat remains obtained in the forests during the soybean off-season (group 2) and those from stink bugs collected in the crop during the growing season (group 3). On the other hand, we found significant differences between stink bug samples from scat remains obtained in the forests during the soybean growing season (group 1) and each one of the other two groups (P < 0.001 for both comparisons). The δ^{15} N of stink bugs collected from fecal samples during the soybean off-season (group 2) in each forest site showed similar values among each other and also when compared with stink bugs collected in the soybean crop (see Supplementary Information, Fig. S2). However, the few samples obtained in distant forests (>5 km from the soybean crop) seemed to present a trend of relatively more dispersed $\delta^{15}N$ values (Fig. S2).

These differences in δ^{15} N values among the three groups, however, were not observed when considering the δ^{13} C values. Isotopic signatures were similar considering the *E. heros* remains found in the fecal samples of *G. agilis* during the soybean offseason (average ± SD: δ^{13} C = $-26.2 \pm 1.3\%_{o}$, range = -21.4to $-29.0\%_{o}$) and growing season (δ^{13} C = $-27.0 \pm 0.8\%_{o}$, range = -25.8 to $-28.2\%_{o}$), and for those stink bugs collected directly from the soybean crop (δ^{13} C = $-26.2 \pm 0.9\%_{o}$, range = -24.8 to $-28.6\%_{o}$).

Ecosystem service valuation provided by G. agilis

In the laboratory experiment, we verified that the gracile mouse opossums eats an average of 101.64 stink bugs per night (jackknife confidence interval $[SE_j]=9.72$). Additionally, the proportion of *E. heros* in relation to the other arthropods found in 12 fecal samples of *G. agilis* was $22.49 \pm 4.57\%$ (mean $\pm SE_j$). Therefore, we estimated that in natural environments, an individual of *G. agilis* eats 22.85 ± 5.13 (SE) stink bugs on average per night (= $Cons_{bug}$).

According to the captures of *G. agilis* obtained in the field, we calculated that this marsupial presents a mean density (*Dens*_{gmo}) of 18.07 ± 3.05 (SE) individuals/ha in savanna woodlands and 13.00 individuals/ha in the gallery forest. Therefore, the estimated number of bugs consumed in one night by *G. agilis* individuals (*Cons*_{bug}) was 412.89 ± 115.93 (SE) stink bugs per hectare in savanna woodlands and 297.16 \pm 66.70 (SE) stink bugs per hectare in gallery forests, which represent $37,159.90 \pm 10,433.27$ (SE) stink bugs

Fig. 3 a Results for δ^{13} C and δ^{15} N signatures of *Euschistus* heros fragments obtained from three distinct sources: 1) found in fecal samples of G. agilis captured in forest environments (savanna woodland and gallery forest) during the soybean off-season, 2) found in fecal samples of G. agilis captured in these same environments during growing season, and 3) from stink bugs collected directly in the soybean crop during growing season. Colored shaded ellipses show the standard ellipse areas corrected for small sample sizes (SEAc). Dots represent the mean values of δ^{13} C and δ^{15} N signatures for each group, and vertical and horizontal lines indicate standard deviations. **b** Bayesian credible intervals (50%, 75%, and 95%) of the posterior estimates generated using the Markov chain Monte Carlo method with 10,000 permutations of the overlap between SEAc ellipses (shown in panel "a"). OS = soybean off-season, GS = soybean growing season, SB = soybean crop. Yellow dots represent the mean value of the posterior estimates and the purple dots represent the observed overlap between ellipses



per hectare in savanna woodlands and $26,744.84 \pm 6,002.78$ (SE) per hectare in the gallery forest during the soybean off-season. Considering that a stink bug costs US\$ 0.0008 to the farmer (See Supplementary Information), the direct monetary value of the ecosystem service provided by *G*.

agilis in the predation of *E. heros* (*Dserv_{gmo}*) would be US\$ $31.08 \pm US$ \$ 8.73 (SE) ha⁻¹ year⁻¹ in savanna woodlands and US\$ $22.37 \pm US$ \$ 5.02 (SE) ha⁻¹ year⁻¹ in the gallery forest.

The potential value of the ecosystem service provided by *G. agilis*, however, is much higher. Each opossum is able to

consume 11.43 ± 2.56 (SE) females of this insect per night (=*Cons_{fem}*), which represents, in only one day of foraging, a suppression of 922.88 ± 340.42 (SE) eggs that would be laid in the soybean crop. Considering this daily number of eggs potentially suppressed, the indirect regulation provided

by *G. agilis* because of the predation of *E. heros* reproductive females ($Rser_{gmo}$) reaches US\$ 1,255.011±US \$509.05 (SE) ha⁻¹ year⁻¹ for savanna woodlands and US\$ 903.26/ha±US\$ 333.19 (SE) ha⁻¹ year⁻¹ for gallery forests (Fig. 4). See Supplementary Information for details.



Fig. 4 Schematic representation of the ecosystem service provided by the gracile mouse opossum (*Gracilinanus agilis*) as predator of the main soybean pest the brown stink bug (*Euschistus heros*). Brown stink bugs may occur in high densities in soybean crops during growing season (**a**). These insects move from the soybean crops to neighboring native forests during the off-season (when there is no soybean available in the crops) where they are heavily preyed upon by the mouse opossums (**b**). In the following growing season, remaining stink bugs return to the crops (**c**). Also indicated are the estimated values for the services provided by the marsupial, including both direct ecosystem service (i.e., reduction in bug control costs caused by direct *G. agilis* predation on insects) and indirect ecosystem services (i.e., reduction in bug population size due to suppression of potentially reproductive females). Variation in the estimated values of the ecosystem services is caused by changes in marsupial densities according to forest type (savanna woodlands or gallery forests, see text for details). Considering the total area of native forests within farms in the Brazilian savanna (Cerrado), the indirect service (stink bug population suppression) provided by *G. agilis* as predator of *E. heros* in this region may reach approximately US\$ 158.8 million for savanna woodlands and US\$ 571.3 million for gallery forests per year

Discussion

We detected that the main soybean pest of the Neotropics Euschistus heros occurs in forest environments (savanna woodlands and gallery forests) surrounding soybean crops during the soybean off-season. During this time period, we detected high predation rates of this pest by the forestdweller gracile mouse opossum Gracilinanus agilis. The E. heros remains found in fecal samples of G. agilis showed a high similarity in their isotopic signatures (δ^{13} C and δ^{15} N) with stink bugs collected in the crop. These patterns indicate that soybean crop is the source of these insects consumed by G. agilis in crop surrounding forests during the off-season. Our valuation estimates for the potential service provided by G. agilis (i.e., E. heros predation) in forest environments are up to ca. US\$ 31 ha⁻¹ year⁻¹. This economic value may reach ca. US\$ 1,255 ha⁻¹ year⁻¹, considering the eggs potentially laid by females.

Our results strongly suggest that E. heros disperse to natural environments when their primary food resource (i.e., soybean) is in shortage. This inference relies on two main pieces of evidence: 1) the isotopic analysis showed a high similarity between isotopic signatures of stink bugs preyed upon by G. agilis in forest environments during the off-season and the stink bugs feeding on the soybean in the crop, and 2) the high predation rates only during the off-season in forests near the soybean crop, indicating that, when soybean was not available, E. heros was more abundant in these sites than in those located far from the crop. Moreover, the low similarity between the forest samples of the growing season and the stink bugs collected directly in the soybean crop indicates that the few E. heros individuals in the forest environments were probably resident and relied on a wide range of forest plants as food resources. This was confirmed by our results comparing the $\delta^{15}N$ values between E. heros samples from distinct sources. Samples of the growing season differed from the samples of the off-season and from the stink bugs collected in the soybean crop. Additionally, the δ^{15} N values of the growing season samples presented higher variation in comparison to the other two groups, as expected for insects feeding on native plants of the Cerrado vegetation (Bustamante et al. 2004). The δ^{15} N of both the other two groups (i.e., stink bugs found in the feces of G. agilis during the soybean off-season and those collected directly in the soybean crop during growing season) presented less within-group variation, probably because these insects fed mostly or exclusively on soybeans. The relatively dispersed and higher δ^{15} N values from samples of the off-season in more distant forests (\geq 5 km) could indicate that the stink bugs are residents (i.e., are not migrants from the soybean crop) or else a mix of resident and migrant individuals (Fig. S2). An appropriate analysis in this sense, however, is unachievable with our data because predation rates drastically drops with distance from the crop, and the number of samples is very limited in the more distant forests.

Our findings suggesting the dispersal of *E. heros* to native forests during the soybean off-season have not been reported previously in the scientific literature. In fact, attempts to capture the stink bug with pheromone-baited traps or beating cloths in our study areas (data not shown) and other natural environments of the Cerrado (person. obs., RAL) have been shown to be ineffective. This suggests that it is intrinsically difficult to detect *E. heros* in natural environments. Two distinct—but not mutually exclusive—reasons can explain that. The reduced (or completely interrupted) reproductive activity of *E. heros* during this period (Borges et al. 2011) and the choice of hiding places (used as shelter) by these bugs with difficult access for the human collectors (e.g., canopy trees) but that *G. agilis* can reach.

Available data indicates that after harvest, when soybean or other legumes are not available, *E. heros* can disperse to peripheral alternative host plants, such as the African invasive molasses grass *Melinis minutiflora*, the weeds *Acanthospermum hispidium* and *Amaranthus retroflexus*, and native fruits of Solanaceae plants (Medeiros and Megier 2009; Panizzi 1997). Contrary to this former belief of low or no dispersal at all, our results indicated that *E. heros* not only disperses to natural forests surrounding soybean crops during the soybean off-season but also that this dispersal may occur to forests located as far as ca. 5 km from the soybean crop.

We found that G. agilis has a high potential capacity of predation upon E. heros, being able to eat ca. 100 stink bugs per night (whose total wet mass represents approximately 30% of the marsupial body mass). As for other small-sized didelphids (Astúa de Moraes and Santori 2003; Santori et al. 2012), G. agilis is classified as an omnivorous species that may feed heavily on fruits (Astúa de Moraes and Santori 2003) but also presents high rates of insectivory (as indicated by field studies; see Bocchiglieri et al. 2010; Camargo et al. 2014; Lessa and Geise 2014). Its reported feeding patterns indicate the opportunistic behavior of G. agilis and its potential for consuming certain food resources when they are more available in the environment, which was the case of E. heros in native forests during the soybean off-season. Moreover, G. agilis is considered the second most abundant small mammal in the Cerrado as a whole (Mendonça et al. 2018) and is often reported to be one of the most representative species in small mammal communities in forest environments within this phytogeographic domain (Andreazzi et al. 2011; Lessa and Paula 2014; Mares and Ernest 1995; Mendonça et al. 2015). Therefore, the high abundance and predation capacity of *G. agilis* in combination with the dispersal of stink bugs to natural environments makes this marsupial a relevant natural predator of this agricultural pest.

Stink bugs are potentially affected by G. agilis when their population is already declining or stable (Kishino and Alves 1994; Mourão and Panizzi 2002), considering that during the soybean off-season E. heros reduces its reproductive activity. In addition, egg parasitoids, which are considered the main control agent of E. heros, can be less effective in the field after soybean harvest (Corrêa-Ferreira et al. 1998). Therefore, G. agilis could help to avoid a stronger resurgence of *E. heros* in soybean crops (as we suggest in Fig. 4), keeping the pest densities below the economic threshold or at least retarding the population growth of the stink bug (Costamagna and Landis 2006; Gardiner et al. 2009). This could reduce costs associated to soybean quality and production (Nunes and Corrêa-Ferreira 2002) and allow less use of pesticides in the crop (Zhang and Swinton 2012). Moreover, reduction of pesticide use could lessen the negative impact on human health and ecosystems related to pesticide exposure (Naylor and Ehrlich 1997; Thomas 1999). In order to better undestand the role of G. agilis and other potential natural predators in providing pest control service to farmers, a full comprehension of the temporal dynamics of E. heros movements between crops and natural vegetation (and the reverse path) is still needed.

We detected that gracile mouse opossums feed on pests that disperse to natural environments. This finding brings a new perspective of pest control provided by vertebrate predators. Flying vertebrates such as bats, a mammal group whose role in the biological control of agricultural pests is well established in the literature, show high predation and dispersal capacity in the landscape, including crops (Cleveland et al. 2006; Kunz et al. 2011; Rodríguez-San Pedro et al. 2020; Wanger et al. 2014). For mouse-opossums, the biological control is provided inside the native plant formations. Differently from bats, G. agilis is unlikely to exploit crops to feed on E. heros, as this opossum is highly dependent on the complexity of habitat structure (Camargo et al. 2018a; Mendonça et al. 2015) with no published record of this species occupying crops. The distancedependent predation of E. heros by G. agilis that we observed indicates the relevance of conserving forest environments near soybean crops for the maintenance of this pest control provided by the marsupial. The relevance of the distance between crops and natural vegetation to enhance pest control has also been indicated by other studies focused on evaluating the ability of natural enemy species to disperse into the agricultural environment (Henri et al. 2015; Hossain et al. 2002; Werling and Gratton 2010). However, we acknowledge that further studies including other soybean crops across the Cerrado must be conducted to verify the generalizability of our findings. This would help to provide a better understanding of the predation dynamics of *E. heros* by *G. agilis*, and the general applicability of the results in agriculture landscapes.

The forests that are more distant to the crops, however, are still useful for stink bugs control by *G. agilis*. According to our model, even in forests as far as 6 km from the nearest crop the stink bug predation during the soybean off-season would be higher than during the growing season. Moreover, forest environments of the Cerrado near soybean crops may serve as "traps" for dispersing stink bugs. This complementary function of natural forests of the Cerrado could be relevant, for example, to minimize the dispersal of individuals to other crops within an anthropic landscape still retaining patches of native forests (Ribeiro et al. 2010). The presence of forest patches increases landscape diversity, whose role in enhancing biological control services by generalist insect predators has already been shown in soybean fields in North America (Gardiner et al. 2009).

The economic value that we calculated for the predation of G. agilis on E. heros ranged from ca. US\$ 22 to US\$ 31/ ha per year during the soybean off-season. However, with the predation of female stink bugs and the eggs potentially laid (indirect suppression), these monetary values increase almost 40 times. Our results showed that predation rates of E. heros by G. agilis are dependent on the forest distance from the soybean crop. According to the available data on the total area designated for environmental preservation within farms in the Cerrado (Vilela et al. 2020), we estimate that approximately 632.5,000 ha of gallery forest and 126.5,000 ha of savanna woodland are located within soybean properties. This represents an actual economic value of approximately US\$ 3.9 million for savanna woodlands and US\$ 14.1 million for gallery forests per year, assuming that these forests are close (up to 6 km) to the soybean crops. For the indirect service (stink bug population suppression) provided by the predation of G. agilis on E. heros, this estimation is approximately US\$ 158.8 million for savanna woodlands and US\$ 571.3 million for gallery forests per year.

Our estimates indicate that gracile mouse opossums provide an impressive ecosystem service as stink bug predators in native Cerrado forests. These estimates, however, are still preliminary due to uncertainties regarding feeding ecology of *G. agilis* and basic biology of *E. heros* in natural environments, and methodological limitations. A possible lack of complete satiation of *G. agilis* in natural feeding regimes (thus resulting in less stink bugs consumed than estimated) and the difficulty to detect soft bodied arthropods in fecal samples, for example, would inflate our estimates on the predation capacity of *G. agilis* on *E. heros* in natural environments. In addition, several variables that might change the estimated figures were not considered. These variables include other potential sources of stink bug mortality than parasitoids, variation among geographically distinct areas in stink bug consumption by predators and also in parasitoid regulation. Moreover, differential contribution of females from distinct sources to the next generation of stink bugs (i.e., forest bugs vs. bugs that might have remained in the crops), and reproductive capacity of females in natural environments might also affect the final number of suppressed bugs.

There are also factors that might increase the real economic value of the biological control provided by natural predators in native Cerrado forests which we did not consider. We did not evaluate the value of crop losses to insect damage in addition to the value of expenditures on insecticide. Moreover, we based our estimates on a single species of natural predator of E. heros and in forest vegetation types that are in low proportions in relation to the other formations of the Cerrado. This bug possibly also disperses to other native vegetation types where G. agilis and other predators could act on E. heros control, such as typical savannas (cerrado senso strictu), which is estimated to comprise approximately 60% of the Cerrado area (Eiten 1972). In fact, during the soybean off-season, we recorded one stink bug in the typical savanna vegetation surrounding the SW1 site (Fig. 1), suggesting that E. heros can also use this vegetation type as refuge.

Conclusions

We showed for the first time that the main Neotropical soybean pest (the stink bug E. heros) occupies the forest environments of the Cerrado during the soybean off-season, where the marsupial G. agilis preys heavily upon the bug individuals. This predatory interaction in the forest environments, however, is distance dependent, with higher predation rates in forests closer to the crops. This pattern highlights the importance of the conservation of natural vegetation near soybean crops for the pest control provided by marsupials and likely by other natural predators that also inhabit these forests. The economic value of the pest control provided by G. agilis in Brazil savanna could reach up to tens of millions of dollars per year. In contrast to other pest control systems, where the predator feeds on the agricultural pests in the crop, this marsupial stays in the native forests. This predator preys upon a relevant agricultural pest when it disperses to the surrounding patches of native vegetation. This opens a new perspective of investigation to comprehend the services provided by wild vertebrates acting in situ in environments with pest dispersal. This comprehension comprises the evaluation of how the occurrence, size, and spatial configuration of crops and natural environments affect agricultural pest control. By understanding these factors, it would be possible to simultaneously adjust food production interests and the need to conserve biodiversity and ecosystem services, and design agricultural systems based on the ecological processes instead of relying only on external outputs.

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Declarations

Ethics approval This study was approved by the Institutional Animal Care and Use Committee of the University of Brasília (December 3, 2015).

Conflict of interest The authors declare no competing interests.

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