1	Forest cover and proximity decrease herbivory and increase crop yield via enhanced natural
2	enemies in soybean fields
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25 Abstract

 Non-crop habitats are essential for sustaining biodiversity of beneficial arthropods in agricultural landscapes, which can increase ecosystem services provision and crop yield. However, their effects on specific crop systems are less clear, such as soybean in South America, where the responses of pests and natural enemies to landscape structure have only recently been studied.

Here, we analyzed how native forest fragments at local and landscape scales influenced
 arthropod communities, herbivory, and yield in soybean fields in central Argentina. To do
 this, we selected soybean fields located in agricultural landscapes with varying proportions
 of forest cover. At two distances (10 and 100m) from a focal forest fragment, we sampled
 natural enemy and herbivore arthropods, and measured soybean herbivory and yield. We
 focused on herbivore diversity, abundance of key soybean pests in the region (caterpillars
 and stink bugs), and their generalist and specialist natural enemies.

Higher abundance of predators, lower herbivory rates, and increased yield were found near
 forests, while overall forest cover in the landscape was positively related with parasitoid
 and stink bug abundance, soybean yield, and negatively with herbivory. Moreover, yield was
 positively linked to richness and abundance of generalist and specialist enemies and
 independent of herbivory according to piecewise Structural Equation Models.

43 4. Synthesis and applications. Our results show positive effects of native forests on biodiversity
and yield in soybean crops, highlighting the need for conservation of forest fragments in
agricultural landscapes. Moreover, the relation between natural enemies and crop yield
suggests that Chaco forests support a diverse and abundant community of natural enemies
that can provide sustained levels of ecosystem services and result in positive effects for
farmers.

49 Resumen

1. Los ambientes no cultivados son esenciales para mantener la biodiversidad de artrópodos
 benéficos en los paisajes agrícolas, lo que puede aumentar la provisión de servicios
 ecosistémicos y el rendimiento de los cultivos. Sin embargo, sus efectos en algunos sistemas
 de cultivos son poco claros, como es el caso de la soja en América del Sur, donde las
 respuestas de las plagas y los enemigos naturales a la estructura del paisaje se han
 estudiado recientemente.

56 2. En este trabajo, analizamos cómo los fragmentos de bosque Chaqueño a escala local y de paisaje influyeron en las comunidades de artrópodos, la herbivoría y el rendimiento en los 57 58 campos de soja en el centro de Argentina. Para este fin, seleccionamos campos de soja 59 ubicados en paisajes agrícolas con proporciones variables de cobertura de bosque nativo. A 60 dos distancias (10 y 100 m) de un fragmento de bosque focal, tomamos muestras de artrópodos enemigos naturales y herbívoros, y medimos la herbivoría y el rendimiento de 61 62 la soja. Nos enfocamos en la diversidad de herbívoros, la abundancia de plagas clave de soja 63 en la región (orugas y chinches) y sus enemigos naturales generalistas y especialistas.

3. Se encontró una mayor abundancia de predadores, tasas de herbivoría más bajas y un
mayor rendimiento cerca de los bosques, mientras que la cobertura de bosque en el paisaje
se relacionó positivamente con la abundancia de parasitoides y chinches, el rendimiento de
la soja y negativamente con la herbivoría. Además, el rendimiento se relacionó
positivamente con la riqueza y abundancia de enemigos generalistas y especialistas, y fue
independiente de la herbivoría según modelos de ecuaciones estructurales.

Síntesis y aplicaciones. Nuestros resultados muestran efectos positivos de los bosques
 nativos sobre la biodiversidad y el rendimiento de los cultivos de soja, destacando la
 necesidad de conservar fragmentos de bosque Chaqueño en paisajes agrícolas. Además, la

73	relación entre los enemigos naturales y el rendimiento de los cultivos sugiere que los
74	bosques del Chaco apoyan una comunidad diversa y abundante de enemigos naturales que
75	pueden proporcionar niveles sostenidos de servicios ecosistémicos y tener efectos positivos
76	para los agricultores.
77	
78	Keywords
79	Biological control; cascading effects; caterpillars; <i>Glycine max</i> ; parasitoids; predators; soybean yield;
80	stink bugs
81	
82	Introduction
83	Several well-documented changes in agricultural landscapes are linked to agricultural
84	intensification, including the transformation of small arable fields into larger fields cultivated with
85	only a few crop species, excessive use of chemical inputs, and the loss of non-crop habitats due to
86	land clearing (Emmerson et al., 2016; Kremen, 2015; Tscharntke, Klein, Kruess, Steffan-Dewenter, &
87	Thies, 2005). As a consequence, agricultural landscapes often sustain species poor and
88	homogeneous biological communities (Gossner et al., 2016). Biodiversity conservation as well as
89	agricultural production can be negatively affected in extremely simplified landscapes and
90	alternative approaches are needed to integrate these objectives (Fischer et al., 2014).
91	Natural enemies of crop pests, including predators and parasitoids, provide the valuable
92	ecosystem service of biological control (Losey & Vaughan, 2006) and are responsible for keeping up
93	to 50% of pest populations below critical levels at which they can reduce yield (Pimentel & Burgess,
94	2014). Most species of natural enemies depend on the presence of natural habitats near agricultural
95	fields to obtain additional resources such as alternative prey or hosts, floral resources,
96	overwintering sites and refuges (Bianchi, Booij, & Tscharntke, 2006; Gurr, Wratten, Landis, & You,

97 2017; Landis, Wratten, & Gurr, 2000). Hence, many studies have found that natural enemy diversity 98 and/or abundance decreases in simplified landscapes with few non-crop habitats (Chaplin-Kramer, 99 O'Rourke, Blitzer, & Kremen, 2011), resulting in lower levels of pest control and higher prevalence 100 of pests (Rusch et al., 2016; Veres, Petit, Conord, & Lavigne, 2013). Furthermore, landscape 101 simplification can indirectly influence crop yields through cascading effects that affect ecosystem 102 service providers (Dainese et al., 2019; Grab, Poveda, Danforth, & Loeb, 2018; Liere et al., 2015). 103 Nevertheless, there are exceptions where natural habitats do not enhance biological control 104 (Tscharntke et al., 2016) and pests can also benefit from the presence of non-crop habitats (Perez-105 Alvarez, Nault, & Poveda, 2018; Veres et al., 2013), resulting in diverse effects on pests and crop 106 yield (Karp et al., 2018). Moreover, the influence of non-crop habitats is not homogeneous across 107 arable fields but depends on their proximity. Although natural enemies generally benefit from the 108 proximity of non-crop patches (Bianchi et al., 2006; González, Salvo, & Valladares, 2015, 2017), 109 herbivore and yield responses can vary (Bortolotto et al., 2015; Carvalheiro et al., 2011; Karp et al., 110 2018; Mitchell, Bennett, & Gonzalez, 2014a, 2014b; Raatz et al., 2019).

111 The diversity and structure of natural enemy communities can influence biological control 112 of pests in agricultural landscapes. On one hand, diverse landscapes can support a higher species 113 richness of natural enemies that result in an increased pest control, as proposed by the insurance 114 hypothesis (Tscharntke et al., 2007). On the other hand, pest control can be more strongly 115 influenced by the abundance of the main pests and their generalist and specialist natural enemies, 116 given that abundance of key species is sometimes more relevant for ecosystem services than total 117 species richness (Snyder, 2019; Straub & Snyder, 2006; Winfree, Fox, Williams, Reilly, & Cariveau, 118 2015).

Soybean (*Glycine max* L.) is an important global crop, covering more than 125 million
 hectares mainly in South and North America (USDA, 2019). During 1995-2011, soybean production

121 doubled, leading to the displacement of other crops and the loss of natural habitats in the USA 122 (Wright & Wimberly, 2013), Argentina (Phélinas & Choumert, 2017), and Brazil (Morton et al., 2006). 123 Soybean fields located in simplified landscapes are associated with lower diversity of natural 124 enemies and pest control levels (Gardiner et al., 2009; González, Salvo, & Valladares, 2015, 2017; 125 Mitchell et al., 2014a). The consequences for soybean yield were investigated in North America, 126 where landscape diversity led to higher yields by an increase in biological control of the soybean 127 aphid by generalist predators (Liere et al., 2015), although yields decreased near forest fragments 128 (Mitchell et al., 2014a, 2014b). In South America, the soybean aphid is not present, but stink bugs 129 (Hemiptera, Pentatomidae) and lepidopteran larvae (mainly from Erebidae and Noctuidae) are the 130 key pests among a diverse pest assemblage (Bortolotto et al., 2015; González et al., 2017). 131 Lepidopteran caterpillars consume leaves throughout the crop cycle, whereas both stink bugs and 132 some caterpillars feed on pods and seeds, causing serious yield losses (Bortolotto et al., 2015; 133 Turnipseed & Kogan, 1976). However, the relative impact of these pests on yield remains unknown. 134 Natural enemies of both pest groups include generalist predators such as true bugs (Orius spp., 135 Geocoris spp., Podisus spp.), ladybeetles, and ants (e.g. Solenopsis spp., Pheidole spp.), and specialist 136 parasitoids of stink bugs (mainly wasps from the families Encyrtidae, Scelionidae, and 137 Trichogrammatidae and tachinid flies) and caterpillars (Braconidae, Encyrtidae, and Ichneumonidae; 138 Tillman, 2010). The impact of parasitoids and predators on stink bug eggs can be high but varies 139 among studies (González et al., 2017; Olson & Ruberson, 2012; Tillman, 2011; Yeargan, 1979), while 140 the impact on stink bug adults and caterpillars is poorly understood. Moreover, whether non-crop 141 habitats influence stink bug and caterpillar populations, the control exerted by natural enemies, or 142 the relative importance of predators and parasitoids and the consequences for crop yield is 143 unknown.

144 Here, we investigated the influence of native forests on soybean herbivores, their generalist 145 and specialist natural enemies, herbivory by chewing insects, and soybean yield. Specifically, we 146 tested the direct effects of forests at landscape (forest cover) and local (forest proximity) scales in 147 agricultural landscapes of central Argentina. Furthermore, we explored causal paths for the indirect 148 effects of natural habitats on soybean yield mediated by natural enemies, herbivores, and herbivory 149 using piecewise structural equation models to test two main hypotheses based on the effects of 150 species richness of enemies and pests and on the abundances of specific groups. Considering that 151 natural enemies frequently benefit from non-crop habitats (Bianchi et al., 2006), we expected to 152 find higher diversity and abundance of predators and parasitoids in landscapes with higher forest 153 cover and in parts of fields closest to forest patches. Furthermore, we predicted that natural 154 enemies will lead to improved pest suppression, lower herbivory, and higher yield of soybean plants 155 located near forests and in landscapes with higher forest cover.

156

157 Materials and Methods

158 Study sites

The study was performed during the 2015-2016 summer season in central Argentina, in an agricultural region near Córdoba city (31° 10' to 31° 42' S, 64° 12' to 64° 26' W). This area is characterized by extensive fields of annual crops (mainly soybean, but also maize and wheat) and forest remnants of different sizes. The original vegetation of the region is the Chaco Serrano forest (Cabido, Carranza, Acosta, & Páez, 1991). Chaco forests suffered high rates of deforestation between 2000 and 2010 (Aide et al., 2013), in coincidence with an increase of 78% of soybean production (Phélinas & Choumert, 2017).

Based on satellite images and field inspections, twelve landscape circles with varying amounts of soybean fields and forest fragments directly adjacent to soybean fields were selected 168 (Fig. 1a; see Table S1 in Supporting Information). The center of each circle was located on a forest-169 soybean boundary. The minimum distance between landscapes was 1.58 km (mean = 28.21 km; SD 170 = 19.92 km) and all the forest fragments were isolated for at least 40 years. Forest cover was 171 calculated at three scales (concentric circles of 0.5, 1, and 1.5 km diameter surrounding the focal 172 fields; Fig. 1b, c), and ranged from 1.3 to 71.3% at 0.5 km, 2.2 to 67.2% at 1 km, and 1.5 to 66.5% at 173 1.5 km. These scales were selected based on previous studies that detected effects of landscape 174 variables on ecosystem functioning (Thies, Steffan-Dewenter, & Tscharntke, 2003, 2008) and 175 soybean arthropods (González, Salvo, & Valladares, 2015, 2017). Sampling was carried out within 176 the soybean fields at two distances, 10 m and 100 m from the forest edge (Fig. 1d). When more than 177 one forest fragment was present near the landscape center, the sampling distances of 10 and 100 178 m were calculated with reference to the central focal fragment, and the remaining fragments were 179 always at larger distances. All fields were cultivated using no-till and conventional pest management 180 practices (i.e. herbicides and fungicides) were applied. Arthropod sampling was always performed 181 at least two weeks after any application and occurred throughout the flowering, pod-filling and 182 ripening phases of soybean (see details below and in Fig. S1).

183

184 Arthropod sampling

We used separate methods to obtain representative samples of flying insects moving through the crop and arthropods present on the soybean plants. Yellow pan traps were used collect parasitoids and flying herbivores and predators, while the beating-sheet method was used to sample foliage for caterpillars, stink bugs, and other predatory species.

189 Two yellow plastic pan traps (Colombraro, code 164; diameter 34 cm, depth 9.5 cm) 190 containing 3 l of water and five drops of detergent, were placed on the ground between soybean 191 rows (20 m from each other) at each site and distance from the forest. Traps were left in the field

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for 3 days at the end of soybean flowering and start of the pod-filling stage (Fig. S1; phases R2-R3 according to Fehr, Caviness, Burmood, & Pennington, 1971; starting on January 20), when most leaf and pod pests and their natural enemies are found (Bortolotto et al., 2015). The contents of the pans were then filtered, placed in plastic cups with 70% ethanol and taken to the laboratory.

196 Beating-sheet sampling was repeated twice at two different soybean stages: flowering (Fig. 197 S1; phases V6 to R1; January 5-20) and pod filling (Fig. S1; phases R5-R6; February 10-25). Soybean 198 foliage was beaten against a 1 m long white vertical beating-sheet (Drees & Rice, 1985) attached to 199 a plastic trough (11 cm diameter). Thirty repetitions per distance and site were conducted at each 200 stage. Repetitions were performed at ten sampling points, separated by 5 m. At each point, three 201 soybean rows were sampled (central and adjacent rows). Data from all the repetitions was pooled 202 to get one value per distance. All arthropods observed on the sheet were counted in the field and 203 1-5 specimens of each morphospecies were placed in plastic vials with 70% ethanol and taken to 204 the laboratory.

205 Specimens were identified to family level and assigned to feeding guilds based on dominant 206 family habits (or subfamily, for families with multiple feeding habits; Triplehorn, Johnson, & Borror, 207 2005). Depending on available keys and literature, species or morphospecies (hereafter referred to 208 as species; Obrist & Duelli, 2010) of herbivores and natural enemies including predators and 209 parasitoids were determined and used in further analyses. In order to test our hypotheses, for 210 natural enemies we combined the information from both sampling methods and calculated total 211 species richness and abundance per distance and field. Almost no soybean pests were collected with 212 yellow pan traps and thus we used only data from beating sheet sampling for this group.

213

214 Soybean herbivory and yield

215 For measurements of herbivory, leaves from 10 soybean plants 5 m distant from each other 216 (five leaves randomly selected, i.e. 50 leaves in total) per distance and site were collected. To 217 estimate accumulated leaf consumption, leaves were collected prior to their senescence, at the 218 beginning of the pod-filling stage (Fig. S1; R4-R5 phases; February 10-15). In the laboratory, digital 219 photographs over a white background with a scale were taken. We used the software ImageJ 220 (Schneider, Rasband, & Eliceiri, 2012) to measure leaf area and consumed area, and then calculated 221 the proportion of consumed leaf. For leaves with damage along the edge, the shape of the leaf was 222 digitally reconstructed based on the remaining leaflets or leaves of similar area.

In order to measure soybean seed development and yield, 10 soybean plants (5 m distant from each other) were collected from each site and distance. Plants were collected at the end of the pod/filling stage, prior to harvest (Fig. S1; R8 phase; March 1-10), taken to the laboratory, and left to dry for 10 days at room conditions. We then measured the total number of pods per plant, the number of full pods (i.e. pods containing three or four seeds completely developed), and the total seed weight per plant.

229

230 Statistical analyses

231 Direct effects of forest cover in the landscape and forest proximity on natural enemies, 232 herbivores, soybean herbivory, and yield were analyzed using Generalized Linear Mixed Models 233 (GLMMs). For natural enemies, we calculated the abundance of all predators (which tend to be 234 generalists) and specialist parasitoids of lepidopteran caterpillars and stink bugs. However, specialist 235 parasitoids of both pest groups were species-poor, so for the analyses of species richness we 236 calculated total richness of all predators and parasitoids. Forest cover, forest proximity and their 237 interaction were used as fixed factors whereas distance to forest, nested within site, was included 238 as a random variable to reflect the nested structure of the design. Arthropod richness and

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abundance and number of soybean pods were analyzed using a Poisson error distribution and a log
link function, or a negative binomial error distribution when overdispersion was detected. Herbivory
and seed weight were analyzed using a Gaussian error distribution.

242 In order to compare the effects of forest cover on our response variables at multiple levels 243 (0.5, 1.0, and 1.5 km), we first conducted simple GLMMs with forest cover at each level as the 244 predictor variable. The AICc values of these models were then compared and the level in the model 245 with the lowest value was selected for further analyses. Then, for the selected level, we compared 246 all possible models from the full model including the interaction between forest cover and proximity 247 to the null model and selected the best model for each response variable based on the lowest AICc 248 value. GLMMs were performed with the packages Ime4 (Bates, 2007) and nIme (Pinheiro, Bates, & 249 DebRoy, 2012) using the software R (version 3.5.3; R Development Core Team, 2016). Visual 250 representations of the model's predictions were produced with the package effects (Fox, Fox, & 251 John, 2003).

252 We used Piecewise Structural Equation Modelling (pSEM) to test for indirect effects of forest 253 cover and proximity on soybean yield mediated by natural enemies, herbivores, and soybean 254 herbivory. Forest cover scale for each response variable was selected based on the previous results 255 from GLMMs, although we also tested alternative models with each landscape scale level separately 256 (Table S7; Fig. S2). Similar to traditional SEMs, pSEM is a series of structured equations that unites 257 multiple predictor and response variables in a causal network or pathway. However, in pSEM each 258 equation is evaluated locally, allowing the fitting of smaller data sets and nested designs (Lefcheck, 259 2016). All quantitative variables were standardized to a mean of zero and a standard deviation of 260 one to obtain comparable estimators. Fig. 2 shows the relationships tested in this study, including 261 direct relationships between natural enemies and herbivory/yield and between herbivores and yield 262 to account for potential effects on herbivores that could not be distinguished by our samplings (for

263 example, eggs and species active at different phenological stages) and other types of plant damage 264 (produced by sucking and piercing-sucking herbivores). Correlated errors are specified when two 265 variables are presumed to be driven by similar underlying factors (Lefcheck, 2016). We included 266 them between groups of natural enemies when they improved model fit, given that they are 267 expected to respond in a similar way to forests. We tested this set of equations separately for 268 richness and abundance of arthropod groups due to the limited sample size. Starting from the sets 269 of equations showed in Fig. 2, we simplified the models by removal of non-significant paths that 270 improved model fit (Fisher's C with p > 0.05; $\Delta BIC \ge 2$). We used the Bayesian Information Criterion 271 (BIC) for model selection because it shows a better performance for complex models and low sample 272 sizes (Hertzog, 2018). Piecewise SEMs were performed with the package piecewiseSEM (Lefcheck, 273 2016).

274

275 Results

276 Arthropod communities in soybean fields

277 Natural enemies were represented by 9,488 individuals (5,290 collected with yellow pan 278 traps and 4,198 with the vertical sheet) from 56 species (Table S2). Predators were slightly more 279 abundant than parasitoids (56.4% and 43.6%, respectively), but clearly more diverse (48 vs. 8 280 species). Nevertheless, the most abundant species was *Copidosoma* sp. (Hymenoptera, Encyrtidae), a caterpillar parasitoid that accounted for 29.6% of total abundance. The following dominant species 281 282 were two predators, a long-legged fly (Diptera, Dolichopodidae sp.; 15.6%) and Geocoris sp. 283 (Hemiptera, Geocoridae; 8%), and a parasitoid of stink bug eggs, Telenominae sp. (Hymenoptera, 284 Platygastridae; 7.9%).

285 Species richness of predators was not strongly affected by forest cover or proximity, 286 although there was a tendency for positive effects of both variables as shown by the AICc values of

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the models including these variables (Table S3, S4). Predator abundance was significantly higher near forest patches (Fig. 3a; Table S3), and independent of forest cover (Table S4). Parasitoid species richness was unaffected by forest proximity and cover in the landscape (Table S3, S4). Abundance of caterpillar parasitoids was positively related with forest cover, most strongly at the 0.5 km scale (Fig. 3b; Table S3). Abundance of stink bug parasitoids increased with forest cover at the 1.5 km scale (Fig. 3c; Table S3), and also, although with decreasing strength, at smaller scales (Table S4).

293 Herbivores comprised 49 species and 43,723 individuals (Table S2). Thrips were the most 294 abundant group (73% of herbivores), followed by spider mites (Tetranychus urticae; 15%) and 295 several species of lepidopteran caterpillars (Lepidoptera, Erebidae and Noctuidae; 8%). Stink bugs 296 were represented by six species and 575 individuals, with *Dichelops furcatus* (50.1% of stink bug 297 individuals) and Nezara viridula (32.9%) as dominant species. Richness of herbivores on soybean 298 plants was not related to forest cover or proximity (Table S3). Abundance of lepidopteran 299 caterpillars was higher at 100m than at 10m from the forest (Fig. 4a; Table S3). Stink bug abundance 300 increased with the proportion of forest in the landscape at 1 km (Fig. 4b; Table S3) and tended to 301 be higher at 100m from the forest, although not significantly (Table S3).

302

303 Soybean herbivory and yield

On average, soybean leaves had 11.8% (± 1.3) of their area consumed by herbivores. Herbivory was lower at 10 m from the forest (6.9 ± 0.8%) than at 100 m (16.7 ± 1.4%) and also decreased as forest cover within 1.5 km circles increased (Fig. 5a; Table S3).

Total number of soybean pods per plant was higher at 10 m from the forest than at 100 m (64.3 \pm 3.1 and 49.1 \pm 1.7, respectively) and increased with forest cover at 1.5 km, albeit not significantly (Fig. 5b; Table S3, S4). The number of full pods significantly increased with forest cover at 1.5 km and was slightly higher near forests (24.8 \pm 1.8 and 17.8 \pm 1.1 at 100 m; Fig. 5c; Table S3,

311	S4). Yield per plant was also higher at 10 m ($21.1 \pm 1.0 \text{ g}$) than at 100 m (16.1 ± 0.7) and tended to

- increase with forest cover, although not significantly (Fig. 5d; Table S3, S4).
- 313
- 314 Cascading effects on soybean yield

315 The best piecewise SEM when considering species richness of arthropods is shown in Fig. 316 5a. Forest proximity enhanced predator, parasitoid and herbivore richness, whereas forest cover 317 only modestly affected predator richness (Fig. 6a; Table S6). Herbivore richness was also positively 318 linked with parasitoid richness and negatively with predator richness. Herbivory decreased near the 319 forest and with increasing forest cover, and it was negatively linked with parasitoid richness and 320 positively with predator richness. Finally, soybean yield, measured as seed weight, was indirectly 321 linked to forest cover and proximity via positive relations with the richness of both predators and 322 parasitoids. When considering alternative models with the remaining forest cover scales the results 323 were similar, with richness of natural enemies affecting yield, although the effects of forest cover 324 on predators were not important (Fig. S2a,c,e; Table S7).

325 When evaluating cascading effects mediated by arthropod abundance, forest cover 326 enhanced the abundance of stink bug parasitoids, whereas predators were more abundant near 327 forests and caterpillars and their parasitoids far from forests (Fig. 6b; Table S6). Stink bugs were 328 negatively linked with their parasitoids, whereas caterpillars were negatively linked to predators 329 and positively with caterpillar parasitoids, albeit weakly in both cases. Herbivory was negatively 330 related to forest proximity and cover, and positively linked to the abundances of caterpillar 331 parasitoids. Soybean yield increased with the abundance of predators and stink bug parasitoids, and 332 decreased with caterpillar abundance. Alternative models with the three landscape levels were 333 similar, with variations in the associations between forest cover and arthropod groups (Fig. S2b,d,f; 334 Table S7).

335	
336	Discussion
337	Maintaining non-crop habitats in agricultural landscapes is essential for biodiversity
338	conservation and ecosystem service provision (Tscharntke et al., 2005, 2012). Nevertheless, these
339	objectives might not concur with the prime goal of farmers and other stakeholders, i.e. maximizing
340	yields and economic profit (Ahnström et al., 2009). Here, we showed that the amount of forests in
341	the landscape and their proximity to cultivated fields are linked to higher richness and abundance
342	of beneficial arthropods, lower damage to soybean plants and higher yield. Furthermore, we found
343	that forests exert positive cascading effects on soybean yield mediated by enhanced richness of
344	predators and parasitoids, and abundance of enemies of the main soybean pests. Our results
345	highlight the relevance of native forests as sources of diverse and abundant arthropod communities
346	that have a positive impact on cultivated plants.

347

348 Arthropod communities in soybean fields

349 Natural enemy abundance benefitted from forest fragments albeit the responses differed 350 among groups. In the case of predators, only forest proximity was important, which could be linked 351 to the limited dispersal of many ground-dwelling spiders, small true bugs, and carabids, which leads 352 to short-distance spillover towards fields (González et al., 2017; Knapp, Seidl, Knappová, Macek, & 353 Saska, 2019; Mitchell et al., 2014a). The abundance of caterpillar and stink bug parasitoids increased 354 with forest cover but were not affected by forest proximity. The dominant caterpillar parasitoids, 355 encyrtid wasps, can overwinter within forest fragments and attack alternative hosts before moving 356 to the crop (Tabuchi et al., 2014). Stink bug parasitoids, which were numerically dominated by small-357 sized species that parasite eggs, are also known to be benefitted by forest amount (González et al., 2017). Therefore, landscapes with higher amounts of forest can represent larger sources of 358

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359 parasitoids for adjacent crops, which then can move within the soybean fields throughout the 360 season and parasite their hosts at similar rates across a distance gradient (Lowenstein, Andrews, 361 Hilton, Kaiser, & Wiman, 2019). 362 Neither forest cover nor proximity affected herbivore richness, although contrasting effects 363 were found for the abundances of the key soybean pests. Caterpillars were more abundant far from 364 the forest, suggesting that top-down control from predators could be reducing their populations 365 near forest fragments (Mitchell et al., 2014a). Instead, stink bug abundance increased with forest 366 cover in the landscape, which could be linked to resource dilution effects, where a negative 367 relationship is found between herbivore abundance and host plant availability (Otway, Hector, & 368 Lawton, 2005; Schneider, Krauss, Riedinger, Holzschuh, & Steffan-Dewenter, 2015). In forest-369 dominated landscapes, soybean represents a small portion of the landscapes and then stink bugs 370 would concentrate in the available fields, whereas in simplified landscapes soybean is widely 371 available and the pest population would be diluted within soybean fields. Moreover, a higher forest 372 cover could benefit stink bugs through an increase in overwintering sites such as trees and debris 373 (Todd, 1989) and this could enhance the concentration on soybean fields surrounded by more 374 forest.

375

376 Soybean herbivory and yield

Herbivory on soybean plants was strongly affected by forest cover and proximity, showing a clear benefit of forest presence. Leaf damage in plants located at 100 meters from the forest duplicated the damage at 10 meters, and a similar increase was observed from landscapes with low to high forest cover. The higher abundance of caterpillars far from the forest is likely to be causing more damage far from the forest, whereas the increase of caterpillar parasitoids with forest cover might have led to a top-down control of plant damage at the landscape scale. Furthermore, the

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383 movement of generalist lepidopteran adults out of the forests and towards soybean increases in 384 landscapes dominated by soybean (González, Salvo, Defagó, & Valladares, 2016), which could lead 385 to higher oviposition rates in landscapes with low forest cover and higher herbivory in soybean 386 plants.

387 We also detected positive effects of forests on soybean yield, with variations in the relative 388 importance of forest cover and proximity depending on yield measurements. Besides the potential effects mediated by arthropods, which are discussed in the following section, forests can also 389 390 enhance yield through improved pollination. Although soybean is a self-pollinating crop, insect 391 pollination can increase yield (Zelaya, Chacoff, Aragón, & Blendinger, 2018). Forest proximity has 392 been linked to higher visitation rates by pollinators and increased soybean productivity in central 393 Argentina (Monasterolo, Musicante, Valladares, & Salvo, 2015), and these effects could be 394 magnified with increasing amounts of non-crop habitats (Benjamin, Reilly, & Winfree, 2014). 395 Therefore, forest cover and proximity may enhance crop yield through a synergic interaction 396 between richer communities of natural enemies and pollinators (Gagic, Marcora, & Howie, 2019).

397

398 Cascading effects on soybean yield

399 Our analyses of indirect effects of forest cover and proximity on yield pointed at an increase 400 of both species richness and abundance of natural enemies as the most important mechanisms 401 through which soybean yield is enhanced in this system. Furthermore, forest proximity can play a 402 stronger role in enhancing enemy richness and predator abundance, whereas forest cover is 403 important for boosting abundance of specialist parasitoids. Top-down effects of natural enemies on 404 soybean yield were previously described in the USA, where predator abundance decreased soybean 405 aphid (Costamanga, Landis, & Difonzo, 2007; Liere et al., 2015). However, the soybean pest 406 assemblage in South America includes several herbivores other than aphids (Bortolotto et al., 2015; 407 González et al., 2017) and therefore a diverse community of enemies could be necessary to provide 408 effective control. For example, enhanced control of stink bug eggs required both parasitoids and 409 predators in landscapes with high forest cover (González et al., 2017). Thus, our results support the 410 role of enhanced biodiversity in sustaining ecosystem functioning (i.e., the insurance hypothesis; 411 Tscharntke et al., 2007), which is linked with higher stability and functional redundancy of 412 ecosystem services in complex landscapes (Feit, Blüthgen, Traugott, & Jonsson, 2019). A recent 413 global synthesis also highlights the relevance of species richness of natural enemies to explain the 414 influence of landscape simplification on crop productivity (Dainese et al., 2019).

On the other hand, soybean yield was positively linked to the abundance of generalist 415 416 predators and stink bug parasitoids, suggesting that the provision of ecosystem services by 417 common, abundant species (Winfree et al., 2015) can also be translated into higher yields. 418 Nevertheless, the diverse complex of soybean pests in the region might limit the potential of a single 419 abundant species to have an impact on yield. Species rich communities of ecosystem services 420 providers with high abundances of key species are linked to the provision of ecosystem services 421 (Cusser, Neff, & Jha, 2016), and therefore not only diverse but also highly abundant generalist and 422 specialist enemies are probably necessary to control soybean pests, as observed in other systems 423 (Snyder, 2019; Straub & Snyder, 2006).

Even though forest presence was linked to improved yield and reduced herbivory on soybean at local and landscape scales, our structural models did not find any effects of herbivory on yield. Soybean plants can tolerate more than 30% defoliation without relevant yield losses, depending on the timing of the damage (Batistela et al., 2012). Therefore, the levels of herbivory detected here might be too low to affect seed production. The fact that yield was negatively linked to caterpillar abundance might reflect the consequences of pod-feeding caterpillars, which can be more damaging than defoliating caterpillars (Bortolotto et al., 2015).

431	
432	Conclusions
433	To sum up, our study provides evidence of a positive influence of native forests on natural
434	enemies and crop yield in soybean fields, whereas herbivory, an ecosystem disservice, was
435	negatively affected. Furthermore, forest effects on soybean yield were at least partly mediated by
436	the abundance and species richness of generalist and specialist natural enemies, indicating a major
437	role of biodiversity for ecosystem functioning within arable fields. In addition to stressing the
438	importance of conserving native forests in order to promote biodiversity and ecosystem services,
439	our results highlight the extension of these benefits to the agricultural systems.
440	
441	Authors' contributions
442	EG, DAL and GV designed the study; EG conducted field and laboratory work; EG and MK performed
443	statistical analysis; all authors wrote the manuscript and agreed on the final version.
444	
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456	
457	Data availability statement
458	The datasets supporting this article are available from the Dryad Digital Repository (González,
459	Landis, Knapp & Valladares, 2020).
460	
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674	Fig. captions
675	
676	Figure 1 – (a) Satellite image showing study sites in central Argentina. (b) and (c) Examples of sites with
677	varying forest cover (dark green) at 0.5, 1 and 1.5 km diameter (white circles). (d) Example of forest
678	proximity locations.
679	
680	Figure 2 - Hypothetical effects of natural enemies, herbivores, and herbivory on soybean yield tested with
681	piecewise SEMs. Models with (a) species richness and (b) abundance of arthropods were evaluated. Black
682	and red arrows indicate expected positive and negative relationships, respectively.
683	
684	Figure 3 – Effects of forest proximity and cover on natural enemy abundance. (a) Forest proximity effects on
685	predator abundance. (b) Forest cover in the landscape (0.5 km diameter) effects on abundance of caterpillar
686	parasitoids. (c) Forest cover in the landscape (1.5 km diameter) effects on abundance of stink bug
687	parasitoids. Means, slopes, and 95% CI predicted by GLMMs are shown. Solid lines and asterisks represent
688	significant effects of forest cover and proximity, respectively.
689	
690	Figure 4 – Effects of forest proximity and cover on herbivore abundance. (a) Effects of forest proximity on
691	caterpillar abundance. (b) Effects of forest cover in the landscape (1 km diameter) on stink bugs. Means,
692	slopes, and 95% CI predicted by GLMMs are shown. Solid lines and asterisks represent significant effects of
693	forest cover and proximity, respectively.

694

695 Figure 5 – Effects of forest proximity and forest cover on (a) herbivory in soybean leaves (proportion of leaf

- areas eaten), (b) total number of pods per plant, (c) number of full pods and (d) seed weight per plant.
- 697 Means, slopes, and 95% CI predicted by GLMMs are shown. Solid lines and asterisks represent significant
- 698 effects of forest cover and proximity, respectively, whereas dashed lines and dots represent marginal effects
- 699 (p<0.1).
- 700
- Figure 6 Best piecewise SEMs for (a) arthropod richness and (b) arthropod abundance effects on soybean
- herbivory and yield. Dashed lines indicate non-significant and solid lines significant relationships (thin lines:
- 703 p<0.05; thick lines: p<0.01). Black and red lines indicate positive and negative relationships, respectively.
- 704 Grey, double-headed arrows are used for correlated errors. Conditional R² values (including random effects)
- are shown for response variables. Table S6 shows detailed statistics for each model.



Figure 1 – (a) Satellite image showing study sites in central Argentina. (b) and (c) Examples of sites with varying forest cover (dark green) at 0.5, 1 and 1.5 km diameter (white circles). (d) Example of forest proximity locations.

152x113mm (300 x 300 DPI)





Figure 3 – Effects of forest proximity and cover on natural enemy abundance. (a) Forest proximity effects on predator abundance. (b) Forest cover in the landscape (0.5 km diameter) effects on abundance of caterpillar parasitoids. (c) Forest cover in the landscape (1.5 km diameter) effects on abundance of stink bug parasitoids. Means, slopes, and 95% CI predicted by GLMMs are shown. Solid lines and asterisks represent significant effects of forest cover and proximity, respectively.

476x204mm (300 x 300 DPI)



a - Abundance of caterpillars b - Abundance of stink bugs

Figure 4 – Effects of forest proximity and cover on herbivore abundance. (a) Effects of forest proximity on caterpillar abundance. (b) Effects of forest cover in the landscape (1 km diameter) on stink bugs. Means, slopes, and 95% CI predicted by GLMMs are shown. Solid lines and asterisks represent significant effects of forest cover and proximity, respectively.

476x311mm (300 x 300 DPI)



Figure 5 – Effects of forest proximity and forest cover on (a) herbivory in soybean leaves (proportion of leaf areas eaten), (b) total number of pods per plant, (c) number of full pods and (d) seed weight per plant. Means, slopes, and 95% CI predicted by GLMMs are shown. Solid lines and asterisks represent significant effects of forest cover and proximity, respectively, whereas dashed lines and dots represent marginal effects (p<0.1).</p>

476x323mm (300 x 300 DPI)



Figure 6 – Best piecewise SEMs for (a) arthropod richness and (b) arthropod abundance effects on soybean herbivory and yield. Dashed lines indicate non-significant and solid lines significant relationships (thin lines: p<0.05; thick lines: p<0.01). Black and red lines indicate positive and negative relationships, respectively. Grey, double-headed arrows are used for correlated errors. Conditional R2 values (including random effects) are shown for response variables. Table S6 shows detailed statistics for each model.

476x268mm (300 x 300 DPI)



66x89mm (300 x 300 DPI)

Site	Latitude	Longitude	Forest cover	Forest cover	Forest cover
No.			(ø 0.5 km)	(ø 1.0 km)	(ø 1.5km)
1	-31.186086°	-64.256511°	0.530	0.672	0.665
2	-31.197453°	-64.279801°	0.201	0.171	0.212
3	-31.209551°	-64.265376°	0.344	0.276	0.186
4	-31.669050°	-64.305413°	0.501	0.458	0.279
5	-31.222226°	-64.276218°	0.042	0.065	0.084
6	-31.680775°	-64.365254°	0.226	0.048	0.031
7	-31.577790°	-64.432092°	0.351	0.113	0.089
8	-31.547631°	-64.318905°	0.014	0.022	0.015
9	-31.705992°	-64.382021°	0.300	0.111	0.054
10	-31.645275°	-64.317641°	0.713	0.665	0.480
11	-31.573765°	-64.452722°	0.611	0.651	0.541
12	-31.564344°	-64.439078°	0.667	0.471	0.283

 Table S1 – Geographic location of the study sites and forest cover in the landscape scale. For each site, the geographic coordinates and forest cover at the three analyzed landscapes scales are provided.

Table S2 – Species list of natural enemy and herbivore arthropods collected on soybean fields in central Argentina. For each species, the total abundance collected at 10 and 100 meters from the forest are given. For parasitoids, the host of each species is indicated in the last column. The main soybean pests in the region are highlighted in bold.

Functional	Order	Family	Species / morphospecies	∑ 10m	∑ 100m	Host
Parasitoids	Diptera	Tachinidae	Sp. 1	129	56	Caterpillars
		Tachinidae	Trichopoda sp. 1	1	1	Stink bugs
	Hymenoptera	Encyrtidae	Hexacladia sp. 1	3	0	Stink bugs
		Encyrtidae	Copidosoma sp. 1	840	1966	Caterpillars
		Chalcididae	Sp. 1	20	11	Caterpillars
		Ichneumonidae	Camplopleginae sp. 1	237	122	Caterpillars
		Scelionidae	Telenominae sp. 1	368	384	Stink bugs
Predators	Araneae	Anyphaenidae	Gayenna sp. 1	44	24	Generalist
		Anyphaenidae	Sp. 1	2	5	Generalist
		Anyphaenidae	Sp. 2	0	2	Generalist
		Anyphaenidae	Sp. 3	102	50	Generalist
		Araneidae	Argiope sp. 1	0	3	Generalist
		Araneidae	Sp. 1	18	15	Generalist
		Corinnidae	Sp. 1	43	20	Generalist
		Linyphiidae	Sp. 1	27	15	Generalist
		Linyphiidae	Sp. 2	171	110	Generalist
		Linyphiidae	Sp. 3	107	81	Generalist
		Lycosidae	Sp. 1	41	39	Generalist
		Oxyopidae	Sp. 1	66	40	Generalist
		Oxyopidae	Sp. 2	18	13	Generalist
		Oxyopidae	Sp. 3	24	10	Generalist
		Philodromidae	Fageia sp. 1	22	34	Generalist
		Salticidae	Sp. 1	93	93	Generalist
		Theridiidae	Sp. 1	67	43	Generalist
		Theridiidae	Sp. 2	1	0	Generalist
		Theridiidae	Sp. 3	69	34	Generalist
		Thomisidae	Misumenops sp. 1	8	2	Generalist
		Thomisidae	Misumenops sp. 2	172	111	Generalist
		Thomisidae	Sp. 1	100	36	Generalist
		Thomisidae	Sp. 2	14	12	Generalist
		Thomisidae	Sp. 3	1	1	Generalist
	Coleoptera	Cantharidae	Sp. 1	4	2	Generalist
		Carabidae	Calosoma sp. 1	8	2	Generalist
		Carabidae	Lebia concinna	34	17	Generalist
		Carabidae	Notiobia sp. 1	1	4	Generalist
		Coccinellidae	Eriopis connexa	24	30	Generalist
		Lampyridae	Sp. 1	2	4	Generalist
		Staphylinidae	Sp. 1	2	5	Generalist
		Staphylinidae	Sp. 2	46	20	Generalist
	Diptera	Dolichopodidae	Sp. 1	1032	451	Generalist
		Syrphidae	Sp. 1	3	0	Generalist

	Hemiptera	Anthocoridae	Orius sp. 1	92	48	Generalist
		Enicocephalidae	Sp. 1	6	2	Generalist
		Geocoridae	Geocoris sp. 1	479	327	Generalist
		Nabidae	Nabis sp. 1	188	198	Generalist
		Pentatomidae	Podisus sp. 1	25	11	Generalist
		Reduviidae	Sp. 1	33	22	Generalist
	Hymenoptera	Sphecidae	Sp. 1	2	1	Generalist
		Vespidae	Sp. 1	3	0	Generalist
	Mantodea	Mantidae	Sp. 1	11	2	Generalist
	Mesostigmata	Phytoseiidae	Sp. 1	24	10	Generalist
	Neuroptera	Chrysopidae	Sp. 1	117	104	Generalist
	Orthoptera	Tettigoniidae	Sp. 1	6	8	Generalist
Herbivores	Coleoptera	Curculionidae	Sp. 1	52	34	-
		Elateridae	Sp. 1	41	55	-
		Chrysomelidae	Botanochara angulata	1	0	-
		Chrysomelidae	Bruchinae sp. 1	6	13	-
		Chrysomelidae	Diabrotica speciosa	54	19	-
		Chrysomelidae	Charidotella sp. 1	3	6	-
		Chrysomelidae	Sp. 1	9	7	-
		Chrysomelidae	Sp. 2	5	6	-
		Chrysomelidae	Sp. 3	21	25	-
		Chrysomelidae	Sp. 4	6	5	-
		Lagriidae	Lagria villosa	156	219	-
		Meloidae	Epicauta adspersa	1	0	-
		Melyridae	Astylus atromaculatus	30	47	-
		Nitidulidae	Sp. 1	12	0	-
	Hemiptera	Aleyrodidae	Sp. 1	39	22	-
		Aphididae	Sp. 1	24	17	-
		Aphididae	Sp. 2	1	1	-
		Cercopidae	Sp. 1	121	86	-
		Cicadellidae	Sp. 1	119	99	-
		Coreidae	Sp. 1	29	12	-
		Derbydae	Sp. 1	2	1	-
		Lygaeidae	Nysius sp. 1	5	7	-
		Lygaeidae	Sp. 1	2	0	-
		Membracidae	Sp. 1	18	24	-
		Miridae	Sp .1	1	1	-
		Pentatomidae	Dichelops furcatus	135	153	-
		Pentatomidae	Edessa meditabunda	11	10	-
		Pentatomidae	Chinavia hilaris	5	10	-
		Pentatomidae	Nezara viridula	77	112	-
		Pentatomidae	Sp. 1	3	3	-
		Pentatomidae	Sp. 2	18	38	-
		Pseudococcidae	Pseudococcus sp. 1	3	16	-
		Pseudococcidae	Sp. 1	4	17	-
		Pseudococcidae	Sp. 2	1	1	-

	Pyrrhocoridae	Sp. 1	1	2	-
	Rhopalidae	Sp. 1	3	1	-
	Scutelleridae	Sp. 1	0	1	-
Hymenoptera	Formicidae	Acromyrmex	7	2	-
Lepidoptera	Crambidae	Sp. 1	1	0	-
	Erebidae	Dysschema sacrifica	1	0	-
	Noctuidae	Spodoptera frugiperda	11	17	-
	Unidentified larvae	-	1271	2128	-
Orthoptera	Acrididae	Sp. 1	14	39	-
	Gryllidae	Sp. 1	18	11	-
	Proscopiidae	Sp. 1	0	1	-
Prostigmata	Tetranychidae	Tetranychus urticae	2642	4117	-
Thysanoptera	Thripidae	Caliothrips phaseoli	18201	13735	-
	Thripidae	Sp. 1	1	3	-

Table S3 – Summary of best models explaining the effects of native forests on arthropod communities, soybean herbivory, and soybean yield in central Argentina. For each response variable, the explanatory variables of the best model and their estimates (± SE) are shown.

Response variable	Explanatory variables	Estimates (± SE)
Predator richness	Null	3.23 ± 0.07 (intercept)
Predator abundance	Forest proximity	5.65 ± 0.11 (10 m)
		5.15 ± 0.09 (100 m)
Parasitoid richness	Null	1.45 ± 0.23 (intercept)
Stink bug parasitoid abundance	Forest cover (1.5 km)	2.86 ± 0.33 (intercept)
		2.50 ± 0.96 (slope)
Caterpillar parasitoid abundance	Forest cover (0.5 km)	2.27 ± 0.73 (intercept)
		4.47 ± 1.56 (slope)
Herbivore richness	Null	0.71 ± 0.29 (intercept)
Stink bug abundance	Forest cover (1 km) +	-1.44 ± 0.12 (10 m)
	forest proximity	-1.25 ± 0.34 (100 m)
		1.54 ± 0.66 (slope)
Caterpillar abundance	Forest proximity	0.09 ± 0.30 (10 m)
		0.39 ± 0.14 (100 m)
Soybean herbivory	Forest cover (1.5 km) +	0.09 ± 0.01 (10m)
	Forest proximity	0.19 ± 0.01 (100m)
		-0.10 ± 0.04 (slope)
Total number of pods per plant	Forest cover (1.5 km) +	3.87 ± 0.10 (10m)
	Forest proximity	3.66 ± 0.16 (100m)
		0.75 ± 0.45 (slope)
Number of full pods per plant	Forest cover (1.5 km) +	2.49 ± 0.14 (10m)
	Forest proximity	2.24 ± 0.21 (100m)
		1.96 ± 0.59 (slope)
Soybean yield (g per plant)	Forest cover (1.5 km) +	17.66 ± 0.92 (10m)
	forest proximity	12.60 ± 2.61 (100m)
		13.39 ± 7.74 (slope)

Table S4 – Model selection for the effects of native forests on arthropod communities, soybean herbivory, and soybean yield in central Argentina. For each response variable, the explanatory variables of each model, their AICc values and the difference in AICc between the best model are shown. The best model/s for each response variables are highlighted in bold.

Response variable	Explanatory variables	AICc	ΔΑΙCc
Predator richness	Null	131.4	0.0
	Forest cover (1.5 km)	131.8	0.4
	Forest proximity	132.1	0.6
	Forest cover + forest proximity	132.7	1.3
	Forest cover * forest proximity	136.1	4.7
Predator abundance	Forest proximity	258.3	0.0
	Forest cover + forest proximity	261.4	3.1
	Forest cover * forest proximity	263.9	5.7
	Null	270.2	11.9
	Forest cover (1.5 km)	273.1	14.8
Parasitoid richness	Null	84.6	0.0
	Forest proximity	86.6	2.0
	Forest cover (1.5 km)	86.8	2.2
	Forest cover + forest proximity	89.1	4.5
	Forest cover * forest proximity	92.4	7.8
Stink bug parasitoid	Forest cover (1.5 km)	210.5	0.0
abundance	Null	213.0	2.6
	Forest cover + forest proximity	213.6	3.1
	Forest proximity	215.8	5.3
	Forest cover * forest proximity	217.2	6.7
Caterpillar parasitoid	Forest cover (0.5 km)	242.1	0.0
abundance	Forest cover + forest proximity	244.1	2.0
	Null	245.1	3.0
	Forest cover * forest proximity	245.9	3.8
	Forest proximity	246.7	4.6
Herbivore richness	Null	4077.2	0.0
	Forest proximity	4078.4	1.2
	Forest cover (1.5 km)	4078.9	1.7
	Forest cover + forest proximity	4080.1	2.9
	Forest cover * forest proximity	4081.5	4.3
Stink bug abundance	Forest cover (1 km) + forest proximity	2608.3	0
	Forest cover	2608.7	0.4
	Forest cover * forest proximity	2608.9	0.6
	Forest proximity	2611.2	2.9
	Null	2611.6	3.3
Caterpillar abundance	Forest proximity	4301.6	0.0
	Forest cover + forest proximity	4302.2	0.6
	Forest cover * forest proximity	4302.5	0.9
		4303.4	1.8
	Forest cover (1.5 km)	4304.0	2.4
Soybean herbivory	Forest cover (1.5 km) + Forest proximity	-78,5	0.0
	Forest proximity	-76.4	2.1
	Forest cover * Forest proximity	-74.9	3.6
	Null	-53.0	25.5
	Forest cover	-52.6	25.8
Iotal number of pods	Forest cover (1.5 km) + Forest proximity	2284.0	0.0
per plant	Forest proximity	2284.5	0.5
	Forest cover	2285.4	1.4
		2285.9	1.9
	Forest cover * Forest proximity	2286.0	2.0

Number of full pods per	Forest cover (1.5 km) + Forest proximity	1760.6	0.0	
plant	Forest cover	1761.3	0.7	
	Forest cover * Forest proximity	1762.5	1.9	
	Forest proximity	1766.2	5.6	
	Null	1766.9	6.3	
Soybean yield (g per	Forest cover (1.5 km) + Forest proximity	1514.6	0.0	
plant)	Forest proximity	1515.2	0.6	
	Forest cover * Forest proximity	1516.2	1.6	
	Forest cover	1540.3	25.7	
	Null	1540.8	26.3	

 Table S5 – Scale effects of forest cover on arthropod communities, soybean herbivory, and soybean yield in central Argentina. For each response variable, the AICc values for each landscape scale are shown and the scale with the lowest AICc value is highlighted in bold.

Response variable	0.5 km	1 km	1.5 km
Predator richness	132.19	131.87	131.76
Predator abundance	273.19	273.16	273.10
Parasitoid richness	86.76	86.84	86.74
Stink bug parasitoid abundance	213.43	211.56	210.47
Caterpillar parasitoid abundance	242.14	244.91	245.66
Herbivore richness	4082.18	4081.80	4081.54
Stink bug abundance	2611.69	2608.73	2609.33
Caterpillar abundance	4302.70	4302.43	4304.08
Soybean herbivory	-51.42	-52.48	-52.65
Total number of pods per plant	2287.67	2286.40	2285.63
Number of full pods per plant	1766.42	1761.86	1761.52
Soybean yield (g per plant)	1542.27	1540.68	1540.25

Table S6 – Table of path coefficients from the best piecewise SEM models explaining the effects of forest cover and proximity, predators, natural enemies, herbivores on soybean, and herbivory on soybean yield (g / plant). Models considering (a) species richness and (b) abundance of arthropod groups. On (a), herbivore richness was not included in the best model as either a predictor or a response variable. We used the BIC,

Fisher s	Cand	p values for model selection	Dn.	C E		<u>n</u> 2
Response variable	Pree	dictor variable	Estimate	5.E.	р	R²
(a) Model with richness						
Predator richness (R^2_m =0.27; R^2_c =0.93)	÷	Forest cover (Ø 1.5 km)	7.93	5.13	0.16	0.40
	÷	Forest proximity	3.09	0.16	< 0.0001	0.38
Predator richness ↔ Parasitoid	l richne	SS	0.30	NA	< 0.0001	0.31
Parasitoid richness ($R^2_m=0.10$; $R^2_c=0.78$)	÷	Forest proximity	0.72	0.07	< 0.0001	0.33
Herbivore richness ($R^2_m=0.19$; $R^2_c=0.97$)	÷	Forest proximity	0.41	0.05	< 0.0001	0.27
	÷	Predator richness	-0.16	0.01	< 0.0001	-0.87
	←	Parasitoid richness	0.19	0.03	< 0.0001	0.28
Herbivory	÷	Forest cover (Ø 1.5 km)	-0.12	0.05	0.04	-0.33
$(R^2_{\rm m}=0.46; R^2_{\rm c}=0.62)$	÷	Forest proximity	-0.10	0.01	< 0.0001	-0.66
	÷	Predator richness	0.004	0.002	0.05	0.25
	÷	Parasitoid richness	-0.01	0.006	0.04	-0.19
Soybean yield ($R^2_m=0.24; R^2_c=0.67$)	÷	Predator richness	0.95	0.28	0.0009	0.42
	←	Parasitoid richness	1.92	0.87	0.03	0.23
(b) Model with abundance						
Predator abundance ($R^2_m=0.32$; $R^2_c=0.86$)	÷	Forest proximity	115.81	5.23	< 0.0001	0.58
Predator abundance ↔ Caterpillar	parasit	oid abundance	0.39	NA	< 0.0001	0.39
Stink bug parasitoid abundance \leftrightarrow Caterpillar	parasito	oid abundance	0.45	NA	< 0.0001	0.45
Stink bug parasitoid abundance ($R^2_m=0.29$; $R^2_c=0.74$)	÷	Forest cover (Ø 1.5 km)	80.93	31.36	0.02	0.56
Caterpillar parasitoid abundance ($R^2_m=0.26$; $R^2_c=0.81$)	÷	Forest cover (Ø 0.5 km)	531.99	254.27	0.07	0.50
	←	Forest proximity	-91.36	13.74	< 0.0001	-0.21
Stink bug abundance ($R^2_m=0.04$; $R^2_c=0.35$)	÷	Stink bug parasitoid abundance	-0.02	0.008	0.03	-0.22
Caterpillar abundance ($R^2_m=0.12$; $R^2_c=0.80$)	÷	Forest proximity	-24.25	8.18	0.003	-0.20
	÷	Predator abundance	-0.10	0.05	0.07	-0.16
	 C 	abundance	0.04	0.02	0.07	0.14
Herbivory ($R^2_m=0.54$; $R^2_c=0.63$)	←	Forest cover (Ø 1.5 km)	-0.14	0.04	0.005	-0.39
	←	Forest proximity	-0.08	0.007	< 0.0001	-0.56
	÷	Caterpillar parasitoid	0.0001	0.0000	< 0.0001	0.33
Southean yield $(P^2 - 0.21, P^2 - 0.62)$	4	abundance Predator abundance	0.03	0.007	0.0005	0.27
Solution for $(\pi_m - 0.21, \pi_c - 0.02)$	`~	Stink bug parasitoid	0.03	0.007	0.005	0.27
		abundance	0.00	0.05	0.000	5.25
	÷	Caterpillar abundance	-0.05	0.01	0.0004	-0.32

Table S7 – Table of path coefficients from the best alternative piecewise SEM models explaining the effects of forest cover and proximity, predators, natural enemies, herbivores on soybean, and herbivory on soybean yield (g / plant). Models considering (a) species richness of arthropods and forest cover at diameter 0.5 km (b) abundance of arthropods and forest cover at diameter 0.5 km, (c) species richness and forest cover at diameter 1 km, (d) abundance and forest cover at diameter 1, (e) species richness and forest cover at diameter 1.5 km, and (e) abundance and forest cover at diameter 1.5 km.

We used the BIC, Fisher's C and p values for model selection.						
Response variable		Predictor variable	Estimate	S.E.	р	R^2
(a) Model with richness – Forest cover at \emptyset 0.5						
km						
(Fisher's $C = 10.39$; $P = 0.73$)						
Predator richness ($R^2_m=0.13$; $R^2_c=0.92$)	÷	Forest proximity	3.09	0.16	< 0.0001	0.38
Predator richness \leftrightarrow P	arasit	oid richness	0.30	NA	< 0.0001	0.31
Parasitoid richness ($R^2_m=0.10$; $R^2_c=0.78$)	÷	Forest proximity	0.72	0.07	< 0.0001	0.33
Herbivore richness ($R^2_m=0.19$; $R^2_c=0.97$)	←	Forest proximity	0.41	0.05	< 0.0001	0.27
	←	Predator richness	-0.16	0.01	< 0.0001	-0.87
	←	Parasitoid richness	0.19	0.03	< 0.0001	0.28
Herbivory	÷	Forest cover	-0.06	0.06	0.16	-0.24
$(R^2_{\rm m}=0.42; R^2_c=0.63)$	←	Forest proximity	-0.10	0.01	< 0.0001	-0.64
	←	Predator richness	0.004	0.002	0.09	0.22
	←	Parasitoid richness	-0.01	0.006	0.03	-0.20
Soybean yield ($R^2_m=0.19$; $R^2_c=0.60$)	÷	Forest proximity	1.86	1.37	0.18	0.10
	←	Predator richness	0.63	0.35	0.08	0.27
	←	Parasitoid richness	1.74	0.88	0.05	0.21
(b) <i>Model with abundance – Forest cover at ø</i>						
0.5 km (Fisher's C = 17.60; P = 0.99)						
Predator abundance ($R^2_m=0.32$; $R^2_c=0.86$)	←	Forest proximity	115.81	5.23	< 0.0001	0.58
Predator abundance ↔ Caterpil	lar pa	rasitoid abundance	0.39	NA	< 0.0001	0.39
Stink bug parasitoid abundance \leftrightarrow Ca	terpil	lar parasitoid abundance	0.45	NA	<0.0001	0.45
Cotomillon nonocitoid obundance $(D^2 = 0.26)$		Equat cover	521.00	254.27	0.07	0.15
Caterphiar parasitoid abundance ($R^{-}m^{-}0.20$; $R^{2} = 0.81$)	~	Forest provimity	01.36	13 74	0.07 <0.0001	0.30
$\frac{R^2}{c^{-0.81}} = \frac{1}{c^{-0.81}} + \frac{1}{c^{$			-91.50	15.74	<0.0001	-0.21
Stink bug abundance $(R^2_m=0.04; R^2_c=0.35)$	~	Stink bug parasitoid abundance	-0.02	0.008	0.03	-0.22
Caterpillar abundance ($R^2_m=0.12$; $R^2_c=0.80$)	$\overline{\mathbf{x}}$	Porest proximity	-24.25	8.18	0.003	-0.20
	Σ ∠	Cotomillon nonce	-0.10	0.05	0.07	-0.10
$(D^2 + 0.52, D^2 + 0.64)$	~		0.04	0.02	0.07	0.14
Herbivory (R^2 m=0.52; R^2 c=0.64)	Σ ∠	Forest cover	-0.15	0.04	0.008	-0.41
	Ž	Productor abundance	-0.08	0.007	< 0.0001	-0.46
			-0.0001	0.0001	0.12	-0.14
(1, 1)	~	Caterpillar parasitoid abundance	0.0001	0.0000	<0.0001	0.39
Soyuean yield ($K^{-}m=0.21; K^{-}c=0.62$)	~	r redator abundance	0.03	0.007	0.0005	0.27
		Stink bug parasitoid abundance	0.08	0.03	0.005	0.25
		Caterpillar abundance	-0.05	0.01	0.0004	-0.32
(c) Model with richness – Forest cover at \emptyset 1						
(Fisher's C = 14.66; $P = 0.55$)	,		2.00	0.16	-0.0001	0.20
Predator richness ($R^2_m=0.13$; $R^2_c=0.92$)	+	Forest proximity	3.09	0.16	<0.0001	0.38
$Predator richness \leftrightarrow P$	arasit	oid richness	0.30	NA	< 0.0001	0.31
Parasitoid richness ($R^2_m=0.10; R^2_c=0.78$)	←	Forest proximity	0.72	0.07	< 0.0001	0.33
Herbivore richness ($R^2_m = 0.19; R^2_c = 0.97$)	\leftarrow	Forest proximity	0.41	0.05	< 0.0001	0.27
	←	Predator richness	-0.16	0.01	< 0.0001	-0.87
	←	Parasitoid richness	0.19	0.03	< 0.0001	0.28
Herbivory	\leftarrow	Forest cover	-0.10	0.04	0.05	-0.32
$(R^2_{\rm m}=0.46; R^2_{\rm c}=0.62)$	←	Forest proximity	-0.10	0.01	< 0.0001	-0.66
	←	Predator richness	0.004	0.002	0.05	0.25

	←	Parasitoid richness	-0.01	0.006	0.03	-0.19
Soybean yield ($R^2_m=0.24$; $R^2_c=0.67$)	÷	Predator richness	0.95	0.28	0.0009	0.42
	←	Parasitoid richness	1.92	0.87	0.03	0.23
(d) Model with abundance – Forest cover at ø						
1 km (Fisher's C = 20.76; P = 0.98)						
Predator abundance ($R^2_m=0.32$; $R^2_c=0.86$)	←	Forest proximity	115.81	5.23	< 0.0001	0.58
Predator abundance ↔ Caterpil	lar pa	rasitoid abundance	0.39	NA	< 0.0001	0.39
Stink bug parasitoid abundance \leftrightarrow Ca	aterpil	lar parasitoid abundance	0.45	NA	< 0.0001	0.45
Stink bug parasitoid abundance (R^2_m =0.21; R^2_c =0.75)	÷	Forest cover	59.07	29.27	0.07	0.48
Caterpillar parasitoid abundance ($R^2_m=0.18$;	÷	Forest cover	365.48	231.77	0.15	0.41
$R^2 = 0.81$)	←	Forest proximity	-91.36	13.74	< 0.0001	-0.21
Stink bug abundance ($R^2_m=0.04$; $R^2_c=0.35$)	←	Stink bug parasitoid abundance	-0.02	0.008	0.03	-0.22
Caterpillar abundance ($R^2_m=0.12$; $R^2_c=0.80$)	÷	Forest proximity	-24.25	8.18	0.003	-0.20
	←	Predator abundance	-0.10	0.05	0.07	-0.16
	←	Caterpillar parasitoid abundance	0.04	0.02	0.07	0.14
Herbivory ($R^2_m = 0.55; R^2_c = 0.64$)	←	Forest cover	-0.13	0.03	0.004	-0.42
	←	Forest proximity	-0.07	0.01	< 0.0001	-0.47
	←	Predator abundance	-0.0001	0.0001	0.16	-0.13
	←	Caterpillar parasitoid abundance	0.0001	0.0000	< 0.0001	0.37
Soybean yield ($R^2_m=0.21; R^2_c=0.62$)	←	Predator abundance	0.03	0.007	0.0005	0.27
		Stink bug parasitoid abundance	0.08	0.03	0.005	0.25
		Caterpillar abundance	-0.05	0.01	0.0004	-0.32
(e) Model with richness – Forest cover at \emptyset 1.5						
km						
(Fisher's C = 11.71; P = 0.63)						
Predator richness ($R^2_m=0.27$; $R^2_c=0.93$)	←	Forest cover	7.93	5.13	0.16	0.40
	←	Forest proximity	3.09	0.16	< 0.0001	0.38
Predator richness \leftrightarrow P	arasito	pid richness	0.30	NA	< 0.0001	0.31
Parasitoid richness ($R^2_m=0.10$; $R^2_c=0.78$)	←	Forest proximity	0.72	0.07	< 0.0001	0.33
Herbivore richness ($R^2_m=0.19$; $R^2_c=0.97$)	←	Forest proximity	0.41	0.05	< 0.0001	0.27
	←	Predator richness	-0.16	0.01	< 0.0001	-0.87
	←	Parasitoid richness	0.19	0.03	< 0.0001	0.28
Herbivory	÷	Forest cover	-0.12	0.05	0.04	-0.33
$(R^2_{\rm m}=0.46; R^2_c=0.62)$	←	Forest proximity	-0.10	0.01	< 0.0001	-0.66
	←	Predator richness	0.004	0.002	0.05	0.25
	←	Parasitoid richness	-0.01	0.006	0.04	-0.19
Soybean yield ($R^2_m=0.24$; $R^2_c=0.67$)	÷	Predator richness	0.95	0.28	0.0009	0.42
	←	Parasitoid richness	1.92	0.87	0.03	0.23
(f) Model with abundance – Forest cover at \emptyset						
1.5 km (Fisher's C = 26.00; P = 0.96)						
Predator abundance ($R^2_m=0.32$; $R^2_c=0.86$)	←	Forest proximity	115.81	5.23	< 0.0001	0.58
Predator abundance ↔ Caterpil	lar pa	rasitoid abundance	0.39	NA	< 0.0001	0.39
Stink bug parasitoid abundance ↔ Ca	aterpil	lar parasitoid abundance	0.45	NA	< 0.0001	0.45
Stink bug parasitoid abundance (R^2_m =0.29; R^2_c =0.74)	÷	Forest cover	80.93	31.36	0.03	0.56
Caterpillar parasitoid abundance (R^2_m =0.04; R^2_c =0.80)	÷	Forest proximity	-91.36	13.74	< 0.0001	-0.21
Stink bug abundance (R^2_m =0.04; R^2_c =0.35)	←	Stink bug parasitoid abundance	-0.02	0.008	0.03	-0.22
Caterpillar abundance ($R^2_m=0.12$; $R^2_c=0.80$)	←	Forest proximity	-24.25	8.18	0.003	-0.20
_ ` ` ` /	←	Predator abundance	-0.10	0.05	0.07	-0.16
	←	Caterpillar parasitoid abundance	0.04	0.02	0.07	0.14

Herbivory ($R^2_m=0.54$; $R^2_c=0.63$)	÷	Forest cover	-0.14	0.04	0.005	-0.39
	←	Forest proximity	-0.08	0.007	< 0.0001	-0.56
	÷	Caterpillar parasitoid abundance	0.0001	0.0000	< 0.0001	0.33
Soybean yield ($R^2_m=0.21; R^2_c=0.62$)	←	Predator abundance	0.03	0.007	0.0005	0.27
	←	Stink bug parasitoid abundance	0.08	0.03	0.005	0.25
	÷	Caterpillar abundance	-0.05	0.01	0.0004	-0.32

Figure S1 – Temporal distribution of samplings methods for arthropods on soybean plants, flying insects, soybean herbivory and soybean yield throughout the soybean cycle. Colored arrows indicate sampling occasions with different sampling methods (white = beating-sheet; yellow = pan trap; green = soybean leaf collection; brown = soybean plant harvest). The different phases of soybean crops are illustrated and the stages according to Fehr et al. (1971) and equivalent dates during the study year are shown.





Figure S2 – Alternative best piecewise SEMs for the effects of natural enemies, herbivores, and herbivory on soybean yield tested. Best models for: (a) species richness of arthropods and forest cover at diameter 0.5 km (b) abundance of arthropods and forest cover at diameter 0.5 km, (c) species richness and forest cover at diameter 1 km, (d) abundance and forest cover at diameter 1 km, and (e) abundance and forest cover at diameter 1.5 km. Dashed lines indicate non-significant and solid lines significant relationships (thin lines: p<0.05; thick lines: p<0.01). Black and red lines indicate positive and negative relationships respectively. Grey, double-headed arrows are used for correlated errors. Conditional R2 values (including random effects) are shown for response variables. See table S7 for detailed statistics of each model.



Fisher's C = 20.76 (P = 0.98)

Fisher's C = 14.66 (P = 0.55)

