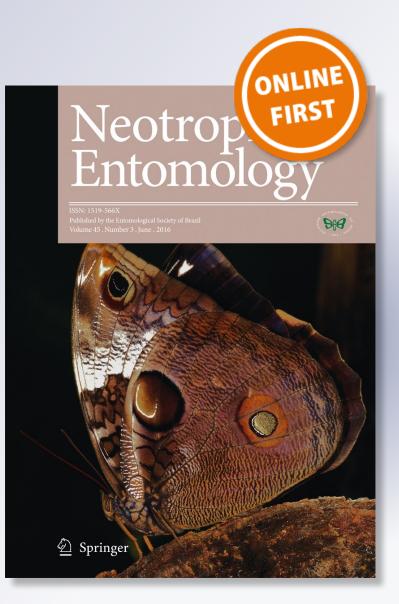
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# Parasitism and Food Web Structure in Defoliating Lepidoptera – Parasitoid Communities on Soybean

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### Keywords

Caterpillars, defoliating, interaction networks

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# Abstract

Food webs are usually regarded as snapshots of community feeding interactions. Here, we describe the yearly and cumulative structure of parasitoid-caterpillar food webs on soybean in central Argentina, analyzing parasitism rates and their variability in relation to parasitoid diversity and food web vulnerability in the system. Lepidoptera larvae were collected along four seasons from soybean crops and reared in laboratory to obtain and identify adults and parasitoids. Eleven species of defoliating Lepidoptera and ten parasitoid species were recorded. Food web statistics showed rather low annual variability, with most variation coefficients in the order of 0.20 and generality showing the most stable values. Parasitism showed the highest variability, which was independent of parasitoid diversity and food web vulnerability, although parasitism rates were negatively related to parasitoid richness. Our study highlights the need to consider food web structure and variability in order to understand the functioning of ecological communities in general and in extensive agricultural ecosystems in particular.

# Introduction

Soybean (*Glycine max*) is an important global crop, providing animal protein feed and vegetable oil, and currently representing a major export commodity for many countries (Gudynas 2008). Argentina is one of the top world producers accounting, together with Brazil, for nearly half of global soybean production (Aramburu Merlos *et al* 2015). Land dedicated to soybean cultivation in Argentina, increased from less than a million ha in 1970 to over 19.5 million ha in 2012–2013 (WWF 2014). Soybean crops sustain a number of defoliating caterpillar (Lepidoptera) species, many of them reaching pest status (Luna & Sánchez 1999, Marayuma *et al* 2001, Colomo *et al* 2009) and, in turn, sustaining diverse parasitoid assemblages (Luna & Sánchez 1999, Sánchez & Luna 2004, Avalos 2007, Colomo *et al* 2009). Economic thresholds, within Integrated Pest Management strategies prioritizing biological control, have been established for some of these defoliating species in the region (Bueno *et al* 2013).

Parasitoids are key players in biological pest control (Waage & Hassell 1982, Bompard *et al* 2013), an essential ecosystem service for sustainable crop production (Power 2010). Parasitism rates could be affected by the number of parasitoid species, as expected from a diversity–function relationship (Balvanera *et al* 2006) but also by the structure of the food webs in which they are embedded (Montoya *et al* 2003, Gagic *et al* 2012). Food webs define feeding interactions among species occupying different trophic levels and may help exploring and understanding ecological community organization and persistence (Lewis *et al* 2002). Quantitative descriptors of food web complexity provide tools to explore the structure of ecological communities (Bersier *et al* 2002, Banasĕk-Richter *et al* 2009), an approach that has begun to be explored in agricultural systems by using parasitoid food

webs (e.g., Valladares & Salvo 1999, Tylianakis *et al* 2007, Jonsson *et al* 2009, Macfadyen *et al* 2009, Gagic *et al* 2011, Lohaus *et al* 2013).

Food webs are limited in their capacity to capture the natural temporal and spatial variations in trophic relationships (Winemiller & Rose 1992). In this regard, "cumulative" webs developed over many sampling seasons may offer different information compared to "snapshot" webs based on a narrower set of observations (Dunne 2006). Scale dependence of food web statistics has been widely debated (Rieder et al 2010); however, their variability along time has received little attention (e.g., Müller et al 1999, Gagic et al 2012, Kaartinen & Roslin 2012). Food web temporal variability and its interaction with ecosystem function remain poorly understood (Thompson et al 2012). In the particular case of parasitoid food webs, temporal variability in parasitism rates indicates the stability of pest control and can be linked to parasitoid diversity (Veddeler et al 2010, Macfadyen et al 2011).

Here, we describe the yearly and cumulative structure of parasitoid–caterpillar food webs on soybean crops in central Argentina, in what constitutes, to our knowledge, the first parasitoid–caterpillar food web study in an extensive crop. We also address a possible structure–function relationship by analyzing parasitism rates and their variability in relation to parasitoid diversity and food web vulnerability (an indicator of consumer diversity per prey) in the system. Based on the generally acknowledged diversity–function relationship, we expected higher parasitism rates in food webs with richer parasitoid assemblages and higher vulnerability.

# **Material and Methods**

The study was conducted at the Manfredi INTA (Instituto Nacional de Tecnología Agropecuaria) Experimental Station (31°49'12" S and 63°46'00" W) located 75 km southeast of Córdoba city, in Central Argentina. Weekly samples were collected in a 1-ha plot demarcated within 20-40-ha soybean fields, from November to December (depending on sowing date) until late April or early May, between 1997 and 2001. Herbicide tolerant genetically modified soybean varieties (ASGROW and FA INTA Conesa) under no-till farming were used in the study, following the common practices in the region. No insecticide treatments were applied during the study. On each sampling date, 18 linear meters of soybean crop were sampled, by collecting lepidopterous larvae with a modified white drop-cloth method (Kogan & Herzog 1980). A one linear meter PVC tube, open lengthwise and holding a vertical white plastic sheet on one edge, collected the insects fallen after beating the soybean plants against the plastic sheet. This procedure was carried out on two sampling points (covering a linear meter each time) within each of nine crop rows.

In the laboratory, collected larvae were counted, identified (Igarzábal *et al* 1994), and reared under controlled conditions ( $T=25\pm2^{\circ}$ C; 60–70% RH and 14:10 h light:dark photoperiod) in individual plastic boxes, fed with artificial diet (Poitout & Bues 1970) and monitored every 48 h until adult emergence (lepidopterous or parasitoid). Parasitoids were kept in Khan tubes, identified, and counted. Gregarious parasitoids emerging from a single host were counted as one interaction in the food webs.

# Food web construction

Data were organized in a matrix (one for each sampling season and one for cumulative data) in which host (Lepidoptera) species were represented as rows and parasitoid species as columns, with the values within each cell indicating the frequency of each host-parasitoid interaction in our observations. With these data, we constructed quantitative food webs and estimated the following metrics for yearly and cumulative data (see full formulae and software details in Bersier et al 2002 and Dormann et al 2009): number of higher trophic species (parasitoids); number of lower trophic species (caterpillars); linkage density: mean number of links per species; connectance: the realized proportion of possible links; vulnerability: mean number of consumers per prey; generality: mean number of prey per consumer; and interactions evenness: a measure of the uniformity of energy flows along different pathways. Quantitative food web statistics were calculated and graphic representation was drawn using the Bipartite package (Dormann et al 2009) that runs in the R environment for statistical computing (R Development Core Team 2012).

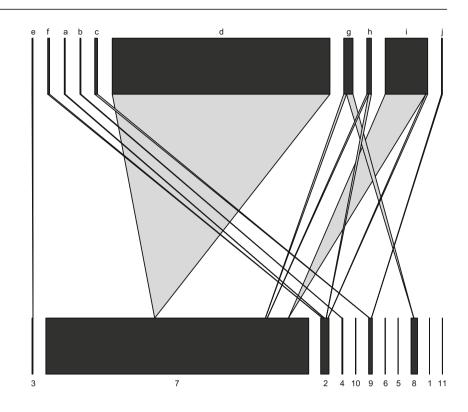
## Data analysis

Parasitism rates were estimated as the percentage mortality caused by parasitoids on their hosts (number of adult parasitoids/number of hosts reared). Overall coefficients of variation (standard deviation/mean) were calculated for parasitism rates and for each food web metrics using annual data, in order to assess their temporal variability. The relationship between yearly percentage parasitism rates or their variation coefficients and parasitoid species richness or food web vulnerability was explored through correlation analysis.

# Results

From a total of 1520 caterpillars, 216 were parasitized. Thirteen host-parasitoid interactions were recorded (Fig 1), involving 11 Lepidoptera host species in five families and 10

Fig 1 Caterpillar-parasitoid food webs on soybean crops in Central Argentina, cumulative data from 4-year samples. Each rectangle represents a species, with caterpillars in the lower row and parasitoids in the upper row. The size of each rectangle is proportional to the abundance of the corresponding species. Triangles represent hostparasitoid interactions, their width indicate the strength of the interaction (proportional to the number of specimens involved). Species identity (numbers for caterpillar hosts and letters for parasitoids) is indicated in Table 1.



parasitoid species, belonging to four families in Hymenoptera and Diptera (Table 1).

The food web showed a strongly dominant interaction (Fig 1) between *Rachiplusia nu* (Guenée) (Noctuidae) (47%

of all Lepidoptera larvae collected) and *Copidosoma floridanum* (Ashmead) (Hymenoptera, Encyrtidae) (76.85% of all parasitic links recorded). Nearly half of the defoliating Lepidoptera species on soybean were not parasitized in this

Table 1 Species involved in the caterpillar–parasitoid food webs on soybean crops in Central Argentina.

Caterpillars		Parasitoids	
Species	Order and family	Species	Order and family
	Lepidoptera		Hymenoptera
1—Achyra bifidalis (Fabricius)	Crambidae	a. Aleiodes sp.1	Braconidae
2—Anticarsia gemmatalis Hubner	Eribidae	b. <i>Aleiodes</i> sp.2	Braconidae
3 <i>—Colias lesbia</i> (Fabricius)	Pieridae	c. <i>Colpotrochia</i> sp.	Ichneumonidae
4—Heliothis gelotopoeon (Dyar)	Noctuidae	d. <i>Copidosoma floridanum</i> (Ashmead)	Encyrtidae
5 <i>—Peridroma saucia</i> (Hubner)	Noctuidae	e. Cotesia ayerza (Brèthes)	Braconidae
6— <i>Pseudaletia unipuncta</i> (Haworth)	Noctuidae	f. <i>Cotesia</i> sp.	Braconidae
7—Rachiplusia nu (Guenée)	Noctuidae		Diptera
8— <i>Spilosoma virginica</i> (Fabricius)	Arctiidae	g. <i>Lespesia</i> sp.	Tachinidae
9— <i>Spodoptera cosmioides</i> (Walker)	Noctuidae	h. <i>Patelloa</i> sp.	Tachinidae
10— <i>Spodoptera frugiperda</i> (Smith)	Noctuidae	i. <i>Voria ruralis</i> (Fallén)	Tachinidae
11—Geometridae sp.	Geometridae	j. <i>Winthemia</i> sp.	Tachinidae

Numbers preceding caterpillar species and letters preceding parasitoid species indicate position in graphic food web (Fig 1).

study, whereas the remaining hosts supported up to four parasitoid species (Fig 1).

**Food web statistics** Annual and cumulative food web statistics are presented in Table 2. Between 6 and 10 of the total 11 host species were recorded each year, with parasitoids ranging from 3 to 5 species. Vulnerability values (average 1.72) indicated that each host species supported nearly two parasitoid species, with each parasitoid in turn exploiting just one host species according to the estimated generality values (average 1.06).

**Temporal variability of food web statistics** The variation coefficients of annual food web statistics showed the smallest values for generality (near 8%) and the largest—four times higher—for interaction evenness (Table 2).

Parasitism rates were extremely variable (Table 2), being disproportionally high on the second year (over 25%) but keeping much lower values along the remaining sampling seasons (Table 2). Parasitism was negatively correlated with the number of parasitoid species involved (r=-0.95, p=0.05, n=4) and independent of vulnerability values (r=0.05, p=0.95, n=4). The yearly variation coefficients of parasitism rates were unrelated to either the number of parasitoid species (r=-0.15, p=0.85, n=4) or vulnerability (r=0.27, p=0.73, n=4).

# Discussion

The food webs involving parasitoids and externally feeding Lepidoptera larvae on soybean crops in central Argentina were distinctly dominated by one species at each trophic level and their mutual interaction. Strong dominance is a common feature in food webs from agricultural systems (Valladares & Salvo 1999, Tylianakis *et al* 2007, Albrecht *et al* 2007), in comparison with those from less disturbed environments where species and interactions tend to be more evenly distributed.

The lower level was relatively well represented in each annual food web (with up to 90% of defoliating species), whereas parasitoid species showed a greater turnover, with less than half of them being present each year. Our parasitoid assemblage was poorer in comparison with older records from conventional soybean crops in the region (23 species, Luna & Sánchez 1999) but closer to those from other no-till soybean fields (14 species, Colomo et al 2009). Parasitoid reduction could be linked to landscape simplification due to the remarkable increase in soybean cultivation area (Aizen et al 2009) and to reduced tillage techniques, applied to most soybean crops in the region (Gudynas 2008). On the other hand, our parasitoid identification did not always reach species level, a most common limitation in parasitoid food webs (e.g., Murakami et al 2008, Gagic et al 2011, Fabian et al 2013) which may bias some results. Given the limited knowledge on neotropical parasitoids, and the specialist collaboration we received (see acknowledgements), species identified to genus level likely represent undescribed species.

Food webs are usually defined as snapshots of community interactions, but approaches including food web temporal variations (Hirao & Murakami 2008, Gagic *et al* 2012, Macfadyen *et al* 2011) have begun to reveal their importance. Nonetheless, variation coefficients of network metrics have not been considered in this context. In our food webs, most variation coefficients showed values around 0.2. Variation coefficients of the number of higher trophic species in farm host–parasitoid food webs (Macfadyen *et al* 2011), being generally above 0.6, provide the only available comparison and suggest low annual variability in the soybean Lepidoptera– parasitoid food webs. Generality showed the most stable values and pointed to a predominantly narrow host range in the parasitic assemblage, thus suggesting specialization as

Annual Cumulative Variation Coefficient 1997-98 1998-99 1999-2000-01 2000 N<sup>o</sup> higher trophic 4 5 5 10 0.22 3 species  $\ensuremath{\mathsf{N}^{\mathsf{o}}}$  lower trophic 6 7 10 8 11 0. 22 species Connectance 0.17 0.19 0.12 0.12 0.11 0.23 Generality 1.00 1.06 0.07 1.00 1.03 1.17 Vulnerability 2.42 1.59 1.33 1.56 1.72 0.27 Link density 1.25 1.28 0.15 1.71 1.31 1.38 Interaction evenness 0.82 0.36 0.77 0.73 0.34 0.31 0.88 Percentage of 4.85 ± 0.27 7.20 ± 7.51  $25.43 \pm 18.74$  $6.37 \pm 8.07$ 10.96 parasitism

Table 2 Statistics for annual and cumulative caterpillar–parasitoid food webs on soybean crops. Parasitism rates (means  $\pm$  SD) are also provided.

a pervading trait in the system. This could result from the dominance of koinobionts, which tend to be specialists (Askew & Shaw 1986, Althoff 2003).

On the other extreme, variation coefficients of parasitism rates were at least three times higher than those observed in any of the food web statistics, suggesting a stronger functional than structural instability in these food webs. Annual parasitism rates and their variations were similar to those observed in a comparable system in northern Argentina (Colomo *et al* 2009). Despite their temporal fluctuations, parasitism rates remained below the minimum level (36%) proposed by Hawkins & Cornell (1994) as the lower threshold for parasitoids to regulate their host populations, thus suggesting a limited performance in terms of the ecosystem service of pest control.

Diversity may stabilize ecosystem functioning in multitrophic systems (Srivastava & Vellend 2005, Long et al 2007) by reducing variability in function over time. However, variability in parasitism (as indicated by variation coefficients) was not related either to the number of parasitoid species or to vulnerability in the soybean parasitoid-caterpillar food webs. Nonetheless, parasitism rates were negatively related to parasitoid richness, suggesting that parasitoids may function better in simplified food webs (Montoya et al 2003, Gagic et al 2012). These results, contrary to the generalized expectations of biodiversity-ecosystem functioning relationships (Cardinale et al 2012), suggest that ecosystem functioning might not be easy to predict from changes in food web structure. A negative relationship between parasitoid richness and parasitism rates could be linked to the presence of a very efficient species defining parasitism rates on the soybean caterpillar-parasitoid food webs (Winfree et al 2015), although the diversity-function in host-parasitoid systems may involve multiple factors at resource and consumer levels (Fenoglio et al 2012).

Summarizing, our results have shown caterpillarparasitoid food webs on soybean being strongly dominated by a pair of interacting host-parasitoid species, with small or moderate annual variations in most metrics and low but highly variable parasitism rates. We hope these results will encourage the use of the food web approach to understand the functioning of ecological communities in extensive agricultural ecosystems.

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