## Journal of Insect Conservation

# Herbivores, saprovores and natural enemies respond differently to within-field plant characteristics of wheat fields --Manuscript Draft--

Manuscript Number:	JICO-D-15-00153R1				
Full Title:	Herbivores, saprovores and natural enemies respond differently to within-field plant characteristics of wheat fields				
Article Type:	Original Article				
Keywords:	functional approach; plant-arthropod interaction; biological control; legumes; ecosystem services; insect functional traits				
Corresponding Author:	Berta Caballero López, Ph.D University of Barcelona Barcelona, Catalonia SPAIN				
Corresponding Author Secondary Information:					
Corresponding Author's Institution:	University of Barcelona				
Corresponding Author's Secondary Institution:					
First Author:	Berta Caballero López, Ph.D				
First Author Secondary Information:					
Order of Authors:	Berta Caballero López, Ph.D				
	José Manuel Blanco-Moreno, Professor				
	Juli Pujade-Villar, Professor				
	Daniel Ventura, PhD-student				
	Josep Anton Sánchez-Espigares, Professor				
	Francesc Xavier Sans, Professsor				
Order of Authors Secondary Information:					
Funding Information:	Becas Predoctorales para Personal Investigador (2005 FI)	Mrs Berta Caballero López			
	Ministerio de Ciencia y Tecnología (CGL2006-c03-01/BOS)	Dr. Francesc Xavier Sans			
	Ministerio de Ciencia y Tecnología (CGL2009-13497-c02-01)	Dr. Francesc Xavier Sans			
	Ministerio de Ciencia e Innovación (CGL2012-39442)	Dr. Francesc Xavier Sans			
Abstract:	Understanding ecosystem functioning in a farmland context by considering the variety of ecological strategies employed by arthropods is a core challenge in ecology and conservation science. We adopted a functional approach in an assessment of the relationship between the three functional plant groups (grasses, broad-leaved and legumes) and the arthropod community in winter wheat fields in a Mediterranean dryland context. We sampled the arthropod community as thoroughly as possible with a combination of suction catching and flight-interception trapping. All specimens were identified to the appropriate taxonomic level (family, genus or species) and classified according to their form of feeding: chewing-herbivores, sucking-herbivores, flower-consumers, omnivores, saprovores, parasitoids or predators. A richer plant community favours a greater diversity of herbivores and, in turn, a richness of herbivores and saprovores enhances the communities of their natural enemies, which supports the classical trophic structure hypothesis. The positive effect of grass cover on sucking-herbivores, saprovores and their natural enemies is due to				

#### Click here to view linked References

±

Herbivores, saprovores and natural enemies respond differently to within-field plant characteristics of wheat fields

Berta Caballero-López<sup>1,4\*</sup>, José M. Blanco-Moreno<sup>2,4</sup>, Juli Pujade-Villar<sup>3</sup>, Daniel Ventura<sup>5,6</sup>, Josep A. Sánchez-Espigares <sup>7</sup> & F. Xavier Sans<sup>2,4</sup>

 <sup>1</sup> Dept. of Arthropods, Natural Sciences Museum of Barcelona, Barcelona, Spain; <sup>2</sup> Dept. of Plant Biology, Faculty of Biology, University of Barcelona, Barcelona, Spain; <sup>3</sup> Dept. of Animal Biology, Faculty of Biology, University of Barcelona, Barcelona, Spain; <sup>4</sup> IRBio, University of Barcelona, Spain; <sup>5</sup> Dept. of Food Industries and Environmental Sciences, Polytechnic School, University of Vic, Vic, Spain; <sup>6</sup> Functional Ecology and Climate Change Group (GAMES - ECOFUN), Forest Sciences Center of Catalonia (CTFC), Solsona, Spain;
 <sup>7</sup> Dept. of Statistics and Operations Research (UPC), Barcelona, Spain.

\*Corresponding author's address: Dept. of Arthropods, Lab. of Nature, Museu de Ciències Naturals de Barcelona, Picasso Av., E-08003 Barcelona (Catalonia/Spain). E-mail address: <u>bcaballerolo@bcn.cat</u>, Phone: (+34) 93 256 22 11.

### 18 Acknowledgements

We are indebted to Lluís Tarés and Joan Ramon Salla for their willingness to participate in this project and for generously allowing us to work in their fields. We are grateful to Amador Viñolas (Coleoptera), Miguel Carles-Tolrà (Diptera) and Marcos Roca-Cusachs (Hemiptera) for the huge task of identifying specimens and for offering information about arthropod feeding habits, which was of great help when deciding upon the most appropriate feeding categories. We would also like to thank Albert Ferré and Arnau Mercadé (Cartography group, Plant Biology Department, University of Barcelona) for their technical assistance with the GIS analyses in the margin assessment. The authors would like to thank the two anonymous referees whose suggestions significantly contributed to improve our manuscript. This research represents part of the PhD project by the leading author and was funded by the FI Fellowship (Agència de Gestió d'Ajuts Universitaris i de Recerca, Generalitat de Catalunya) and the Spanish Ministry of Economy and Competitiveness (CGL2006-c03-01/BOS; CGL2009-13497-c02-01; CGL2012-39442).

## 30 Abstract

Understanding ecosystem functioning in a farmland context by considering the variety of ecological strategies employed by arthropods is a core challenge in ecology and conservation science. We adopted a functional approach in an assessment of the relationship between the three functional plant groups (grasses, broad-leaved and legumes) and the arthropod community in winter wheat fields in a Mediterranean dryland context. We sampled the arthropod community as thoroughly as possible with a combination of suction catching and flight-interception trapping. All specimens were identified to the appropriate taxonomic level (family, genus or species) and classified according to their form of feeding: chewing-herbivores, sucking-herbivores, flower-consumers, omnivores, saprovores, parasitoids or predators.

A richer plant community favours a greater diversity of herbivores and, in turn, a richness of herbivores and saprovores enhances the communities of their natural enemies, which supports the classical trophic structure hypothesis. The positive effect of grass cover on sucking-herbivores, saprovores and their natural enemies is due to grasses' ability to provide – either directly or indirectly alternative resources or simply by offering better conditions of environmental parameters. By the inclusion of legumes in agroecosystems we can improve the conservation of beneficial arthropods like predators or parasitoids, and enhance the provision of ecosystem services like the natural pest control.

Keywords: functional approach, plant-arthropod interaction, biological control, legumes, ecosystem services,
insect functional traits.

#### Introduction

Although traditionally considered as mere competitors of crop plants (Albajes et al. 2011), weeds do in fact play a key role in the aboveground food chain in agro-ecosystems (Clough et al. 2007) by providing resources for pollinators and herbivorous insects, and by supporting prey species for natural enemies (Norris and Kogan 2000; Hyvönen and Huusela-Veistola 2008). Nonetheless, how herbivores and natural enemies respond to the within-field plant community is still a matter of debate and the information in the literature is rather contradictory. Birkhofer et al. (2008) and Harwood et al. (2001) reported more predators in weedy fields -probably as a response to increased prey availability – but other authors have found that the abundance of predatory invertebrates seldom responds significantly to the weed community (Fuller et al. 2005). Some authors state that weedy plots do not necessarily have higher predator densities as other authors have claimed (Altieri and Nicholls 1999; Amaral et al. 2013)

These discrepancies arise because most predictions are limited to particular species groups that are unable to provide accurate generalizations of observed patterns that are applicable to the entire arthropod community (Perner and Voigt 2007). Indeed, arthropods account for over 80% of all known living animal species and play a wide range of functional roles in ecosystems (Maleque et al. 2006). On the other hand, complete community-level assessments are rarely conducted given the huge amount of time, money and human resources (i.e. taxonomists) that are required (Cardoso et al. 2004). Nevertheless, several authors have adopted a community approach using higher taxonomic levels such as families as surrogates for inventories at species level (Balmford et al. 1996a; Balmford et al. 1996b; Wickramasinghe et al. 2004; Biaggini et al. 2007), which is a way of circumventing the enormous amount of resources required for close-to-complete inventories (Cardoso et al. 2004). The use of families as a taxonomic level not only allows parataxonomists to complete the required classification tasks - which permits groups that had not previously been considered to be bioindicators (due to taxonomic difficulties) to be included – but can also save time and money (Balmford et al. 1996a; Balmford et al. 1996b).

Here we adopt a community approach and work at family level. We use a functional approach based on species' way-of-feeding strategies and, rather than relying on traditional taxonomic analyses, we amalgamate different groups according to their trophic behaviour. This combination of a community approach at family level and a functional approach is novel, and provides a link between taxonomic diversity and ecosystem functioning (Grimm 1995; McCann 2000; Hawes et al. 2009).

Assessing how within-field plant communities affect whole arthropod assemblages is therefore essential for understanding local processes related to agro-ecosystem functioning, and to accomplish this task it is crucial to

gain a broader picture of the different players on the scene.

Floristic richness as well as vegetation structure has been widely recognised as key factors influencing insect assemblage (Schaffers et al. 2008). As plant species richness and vegetation complexity tend to cascade up to higher trophic levels leading to high invertebrate diversity (Landis et al. 2000). Therefore we would expect that with a richer assemblage in the within-plant community is likely to improve the conservation of multiple arthropod groups. In this study we were interested in assessing the effect of richer within-field plant communities as a component of habitat restoration strategies to improve and sustain biological control in an arable cropping system. The research reported here aimed to examine how contrasting within-field plant communities in wheat fields affect the whole community of insects associated to this crop. We hypothesised that plant-feeders and saprovores would respond to the within-field plant assemblage according to the classical diversity-trophic structure hypothesis, and that the abundance and richness of potential prey items would enhance the parasitoid and predator assemblages.

#### **Material and Methods**

#### Study area

The study was carried out about 150 km south of Barcelona (41°29'0.9"N, 1°7'16.4"E; 627 m a.s.l.). The arable fields – mainly cereal crops – represented only 40% of the agricultural landscape and formed a mosaic with patches of natural vegetation. Field boundaries consisted of perennial grasslands dominated by Brachypodium phoenicoides (L.) Roemer & Schultes, as well as a mix of Prunus spinosa L., and Rubus ulmifolius L. thickets, and Rosmarinus officinalis L. scrub.

Four organically and four conventionally managed winter wheat fields (Triticum aestivum L.) were selected in an area of  $2 \times 2$  km. First, the organic fields were randomly selected from the 12 such fields in the area and, then, the conventional fields were selected, none of which were further than 1 km from or adjoining the organic fields. All selected fields were flat in order to avoid any differences due to slope or aspect. The selected organic fields had been managed for over a decade along Catalan organic guidelines (Consell Català de la Producció Agrària Ecològica 2013) and were certified by the Catalan Council for Organic Farming following the European guidelines (EEC 2007). The management of organic fields relies on mechanical weed control and organic fertilisation using green manure and occasionally chicken manure. Conventional fields were regularly sprayed with herbicides – but not insecticides or fungicides – and fertilised with a combination of pig slurry and mineral fertilisers. Although we tried to select fields of similar size and shape, we considered the homogeneity of the boundary vegetation to be more important than the homogeneity of the fields' dimensions, above all because the

fields were all relatively small. Even so, conventional fields were significantly larger (mean  $\pm$  SE; 4.08  $\pm$  0.8 ha) than organic fields (2.19  $\pm$  0.3 ha,  $\chi_{1\,df}^2 = 5.78$ , *P* value = 0.016). By contrast, the perimeter-to-area ratio was significantly greater in organic (mean  $\pm$  SE; 0.09  $\pm$  0.01) than in conventional fields (0.06  $\pm$  0.01,  $\chi_{1\,df}^2 = 4.85$ , *P* value = 0.028). All selected fields were sown with winter wheat between the 27 October and 7 November 2003 (for further agronomic details, see Caballero-López et al. 2010).

The contrast in a common area between organic and conventional cereal fields whose boundaries share the same vegetation but differ in terms of the non-crop plants they host appears to be a suitable model for exploring the relationship between plant and arthropod communities. In addition, the comparison of fields under organic and under conventional insecticide-free management in a Mediterranean context also avoids the confounding indirect effects of insecticide application on the plant-arthropod interactions (Hole et al., 2005).

In each field we established an 80m transect diagonally across the centre of the field, starting at 55m from the edge. Within each transect, five 1m×1m plots at 20m intervals were surveyed. Arthropod suction-sampling and plant surveys were carried out successively in each plot. In addition, three flight-interception traps (FIT) were positioned along each transect at 40m intervals.

#### ) <u>Sampling</u>

Arthropod communities were sampled using (i) flight interception traps (hereafter FIT) to assess aerial communities and (ii) a petrol-driven Blow&Vac (McCullogh BVM250, Italy; sampling cylinder 60cm high and 12 cm in diameter) converted to suction sampler following Stewart and Wright (1995) to survey terrestrial communities.

Each FIT consisted of an outer white plastic cup (150 mm in height, 200 mm internal diameter) mounted on a 1-m-high wooden pole and an inner plastic cup (140×180 mm) with two 30×30 cm Plexiglas pieces fixed along their midline in a cross-shape. The inner plastic cup contained approximately 1 litre of a NaCl-solution as a preservative, with a drop of detergent added to decrease the surface tension. FIT are useful for catching many of the small flying insects that tend to fly downwards when they hit a wall (Koricheva et al. 2000).

The petrol-driven suction sampler was operated on full power to produce an estimated constant airflow of 0.142 m<sup>3</sup>/s (according to manufacturer's operating instructions). The pipe was held vertically and slowly passed over the wheat plants in the 1-m<sup>2</sup> quadrat and suction was performed for 60 seconds. After each plot sampling, the bag was removed from the machine, placed in a labelled plastic bag and stored in a portable refrigerator to prevent predatory activity in the bag. The sampling campaign lasted for two days and the eight fields were

sampled in a random order to avoid any systematic bias due to daytime sampling. All samples were taken by the 1 146 same two people to reduce sampling variability. This method has been shown to provide a good representation of 3 147 all trophic levels interacting with vegetation (Letourneau and Goldstein 2001), and is used extensively to study arthropods in crops (Stewart and Wright 1995; Elliott et al. 2006).

Fit trapping took place on 20 May 2004 and 26 June 2004 to coincide with the wheat's anthesis stage and the mid-milk-ripe cereal development stage (Zadoks et al. 1974), respectively. In total, 24 traps were active during two periods of eight days. Suction sampling was also performed twice to coincide with the two chosen growth stages, the first campaign taking place on 25–27 May and the second on 24–26 June 2004, both at 10:00– 19:00 and under sunny weather conditions (temperature  $> 20^{\circ}$ C). Thus, in all, 40 m<sup>2</sup> of plots were assessed twice during the study period.

Vegetation was surveyed twice and concomitant with the suction-sampling. The cover of crop species and each weed species was recorded in each plot by means of a ground cover scale. Weed species were identified according to Bolòs et al. (2005). Plant species were classified into three functional groups (grasses, forbs and legumes) following Koricheva et al. (2000). Legumes have been separated from the other forbs due to the generally higher nitrogen content of their tissues, which would make them a higher-quality resource for herbivores, whereas grasses have tough tissues with low nitrogen content and structural characteristics that deter plant-feeders (Koricheva et al. 2000).

#### Arthropod processing

Arthropods captured by suction sampling were frozen for subsequent sorting and identification, whilst FIT trap catches were preserved in 70% alcohol. All samples were hand-sorted using a dissecting microscope to separate animals from debris. Catches were quantified as the total numbers of individuals (adults and immature stages) and with a few exceptions most arthropods were identified to family level; due to taxonomic difficulties, some taxa were only identified to superfamily level (e.g. Apoidea, Curculionoidea and Staphylinoidea) or to order level (e.g. Acari and Thysanoptera). Lepidoptera were only identified to order level because specimens were too badly damaged by the sampling process to be properly identified.

The use of higher taxonomic levels is particularly useful when a functional-group perspective is required as the majority of family members belong to the same feeding group (see the considerations below). Nevertheless, the process of amalgamating taxa into functional groups requires the acceptance of assumptions regarding the importance of certain common features (Hawes et al. 2009).

When taxa of the same family had different feeding preferences (e.g. Drosophilidae, Opomyzidae), specimens were determined to genus or species level, and the predominant feeding habit of the most abundant genus or species was used to classify the entire family and its feeding group. We initially considered splitting families possessing several species into similar proportions and different feeding strategies; although in the end no family fulfilled this condition.

All identified taxa were classified into one of the seven feeding groups: chewing-herbivores, flowerconsumers, omnivores, parasitoids, predators, saprovores and sucking-herbivores. The definition of each feeding group was based on field observations, a literature review and specialist advice (see Acknowledgements), and contained different ways-of-feeding strategies. Granivores, plant-chewers and miners were included in the chewing-herbivore category, while plant sapsuckers were added to the suction-herbivore category. Flower consumers consisted of flower predators, pollen consumers and nectarivores. Saprovores included mycetophages, plant saprovores, animal saprovores and scavengers.

Arthropods with different feeding preferences in larval and adult stages were counted in both feeding groups in order to consider the impact of their whole life cycles. A small number of difficult-to-classify larvae were taken into account only for total abundance but were excluded from the feeding group analyses. Other groups were also excluded from the analyses due to their scarcity (families with less than three individuals were excluded from the data) or a lack of available information about their biology. In addition, other groups such as most parasitoids, which do not feed in the adult stage or whose effect is so small as to be insignificant, were categorised as not having any trophic interaction (for further details, see Supplementary material). All the specimens are now deposited in the Arthropod collection of the Natural Sciences Museum of Barcelona.

#### 196 <u>Data analysis</u>

In order to simplify the statistical analyses and results section, the results are grouped into two categories: primary and secondary consumers. Chewing-herbivores, sucking-herbivores and flower-consumers were considered primary consumers and so are mainly herbivores, while parasitoids and predators were categorised as secondary consumers given that they are entomophagous. Saprovores chew dead organic matter, bacteria and fungi, and occasionally soil arthropods, and thus theoretically occupy an intermediate position between primary and secondary consumers. However, they were included arbitrarily as primary consumers owing to the lack of reliable information about their consumption rate of potential prey items.

The models for primary consumers and secondary consumers were analysed according to sampling method (FIT vs. suction) and sampling period (first vs. second), with a common set of covariates (cover of broad-leaved

herbs, legumes and grasses, and total plant-species richness) as explanatory variables. Additionally, due to their different ecological requirements, the models of secondary consumers also included certain additional variables depending on the focus. For instance, when we modelled the family richness of secondary consumers we included the family richness of the main primary consumer groups, which could act as potential prey items or hosts, and when the focus was on the abundance of secondary consumers, we included the abundance of the different primary consumer groups.

The analyses were performed using linear mixed models with normal error distribution. 'Field' was included as a random effect factor to account for the fact that the samples from a field were not independent (Pinheiro and Bates 2000). All the models reported are full models; no model simplification was used to avoid the inherent bias of stepwise regression in a measuring experiment. Prior to the analysis, the collinearity of the independent variables included in the models was evaluated with the variance inflation factor (VIF =  $(1-R^2)^{-1}$ ) to check the robustness of the model (Kutner et al. 2004). In the models for primary consumers, no variable present a high VIF (between 1.17 and 3.7) and had to be excluded from the analyses. For parasitoids and predators, the abundance/richness of flower consumers showed correlation with other predictors but it was not significant and the conclusions were the same when dropping the variable from the model. Assumptions of the linearity, normality and homogeneity of the variances were evaluated by examining the residuals; data were log-transformed when necessary. Analyses were performed using R (R Development Core Team 2013); package lme4 (Bates et al. 2008) was used for the model fitting and package languageR (Baayen 2008) was used to determine the significance of the predictors using Markov Chain Monte Carlo methods.

#### Results

#### <u>Arthropods</u>

During the sampling period, 25,518 arthropods were caught and identified. They were found to belong to three classes (Insecta, Entognatha, Arachnida), 14 orders and 133 families, although only 113 families were abundant enough to be included in the feeding group analyses.

The number of families and abundance of individuals were greater using the FIT than the suction-sampler and, overall, the FIT catches were more abundant and diverse (16,587 specimens and 110 families) than the suction catches (8,931 individuals and 82 families). Although the majority of the families were captured by both sampling methods, a considerable proportion (32%) including many dipteran, hemipteran and hymenopteran families was only recorded in the FIT. The most abundant feeding groups from the FIT samples were flowerconsumers and suction-herbivores, which were more abundant than saprovores and omnivores. In the suction catches, the suction-herbivores group was dominant, followed at a distance by saprovores and predators, andother groups such as parasitoids or chewing-herbivores were far less abundant (see Appendix for further details).

Most of the feeding groups also displayed significant differences between sampling periods. The catches of chewing-herbivores, flower-consumers, saprovores (Fig. 1) and parasitoids and predators (Fig. 2) were greater in the first sampling period during wheat anthesis; by contrast, only suction-herbivores showed the opposite pattern, with larger captures in the second period coinciding with the milk-ripening stage. Conversely, the pattern for richness was slightly more diverse due to the fact that the chewing-herbivore, flower-consumer and saprovore families were better represented in the first than in the second sampling period (Fig. 3); the opposite trend was observed for sucking-herbivores, parasitoids and predators (Fig. 4).

Plants

The total plant cover was significantly higher in conventional than in organic fields due to a higher percentage of crops: wheat cover represented 97.2% of grass cover in conventional fields and 91.4% in organic fields. The mean total plant species richness was more than twice as high in organic than in conventional fields; legumes thrived exclusively in organic fields, either as weeds or volunteer crops (see Caballero-López et al. 2010 for further details).

#### Arthropod-plant links

The abundances of flower-consumers, saprovores, parasitoids and predators captured reveal a significant and positive correlation with grass cover. Greater cover of legumes also enhanced the abundance of parasitoids and predators but only marginally benefited the populations of flower-consumers (Tables 1 and 2). By contrast, there were no differences between the abundances of chewing-herbivores and sucking-herbivores according to plant community (Table 1). Greater abundances of parasitoids and predators occurred in plots with greater abundances of sucking-herbivores (Table 2).

The number of families of flower-consumers, sucking-herbivores, saprovores, parasitoids and predators were significantly and positively correlated to greater grass cover (Tables 3 and 4). Additionally, the family richness of sucking-herbivores was favoured in plots with greater plant species richness (Table 3). The family richness of parasitoids was closely and positively associated to the cover of grasses and legumes but in the case of predators was only significantly associated with grass cover (Table 4). Furthermore, sucking-herbivore and saprovore richness showed a significant and positive effect on the family richness of both parasitoids and predators, suggesting that a relationship exists between these groups. The family richness of predators was also enhanced by the chewing-herbivores richness (Table 4).

5 271

**272** 

#### 59 Discussion

The arthropod community found in wheat fields was dependent above all on the sampling method used, the sampling period considered and the interaction between these variables, although clear patterns relating to local factors such as intra-field plant community variables and the primary-secondary consumer interactions were also present. The functional approach presented here shows that there are consistent responses in plant and arthropod trophic groups to differences in habitat conditions.

#### Primary consumers

The numbers of sucking-herbivores across fields were similar regardless of vegetation parameters, although the family richness of sucking-herbivores was positively associated to the plant species richness. These findings were in accordance with previous studies showing that the diversity of plant-feeders was related to the diversity of their resources (Murdoch et al. 1972; Siemann 1998; Knops et al. 1999). In addition, the sucking-herbivore community – with aphids (Homoptera) as the most abundant representatives – was also richer where the grass cover was greater, which usually occurred in the conventional fields, where wheat crop represents the 97% of the grass cover. This can be explained by the fact that conventional farmers apply more fertilisers, and to the higher mean yields in conventional (4,000- 4,100 kg ha<sup>-1</sup>), than in organic (2,000–2,200 kg ha<sup>-1</sup>) fields (farmers *pers. com.*). Given that many components of the Homoptera groups benefit when the nitrogen fertiliser supply increases (Hasken and Poehling 1995; Duffield et al. 1997; Ghorbani et al. 2010; Rostami et al. 2012), the enrichment of grass aphids community in conventional fields is not surprising. However, our study did not enable us to identify whether grass cover or nitrogen supply was the most relevant factor for explaining the sucking-herbivores pattern.

The saprovore community was found to be richer and more abundant where the grass cover was greater, as in the studied conventional fields. This reinforces the findings of previous authors (Moreby et al. 1994; Mäder et al. 2002), who suggest that taxa involved in decomposition are likely to benefit from organic fertilisation, which in the studied systems only occurred on organic fields. However, pig slurry is an abundant and cheap organic fertiliser in Catalonia and is commonly used in conventionally managed fields. Our results also support the findings of Clough et al. (2007), who showed that a higher activity-density and diversity of saprovores in conventional fields indicates good soil health and high potential productivity, as shown above by the mean yield values.

Flower-consumer abundance is expected to be positively related to legume cover since this group benefits 1 299 from floral food resources such as nectar and pollen (Bianchi and Wäckers 2008). Nonetheless, our data provides only limited support for this relationship. However, both the abundance and richness of the flower-consumer community are enhanced with increasing grass cover. Given that flower-consumers do not feed on grasses, this effect is most probably due to the greater plant cover offered by wheat, which generates a more complex plant community with more and better places to shelter. This phenomenon may reflect that plant architecture is likely to be an important component of the predation risk, and that plant-feeders have a better chance of escaping from predators in complex plant architectures (Moreby et al. 1994; Norris and Kogan 2000; Casas and Djemai 2002). In addition, it is also known that plant structure determines microclimatic conditions, which may also affect the movement patterns of both herbivores and predators (Willmer et al. 1996; Souza and Martins 2004) and also lead to considerable variation in microhabitat temperatures that can regulate the larval development (Wilson et al. 2014).

#### Secondary consumers

Predators and parasitoids probably benefited from the abundance of their potential prey items (see Table 2). Consequently, a greater abundance of sucking-herbivores probably led to higher predator and parasitoid abundances, which may indicate an aggregation response to prey distribution (Müller and Godfray 1998; Evans 2008; Vucic-Pestic et al. 2010). This scenario agrees with the patterns of correlation among herbivores, predators and parasitoids found by previous studies (Koricheva et al. 2000; Haddad et al. 2001).

Parasitoid richness appears to be closely associated with the sucking-herbivore and saprovore richness, whereas predators were only significantly correlated to the family richness of chewing-herbivores, sucking-herbivores and saprovores. These findings reflect those of Haddad et al. (2001) and Wardle et al. (1999). Our findings support the results of Wardle et al. (1999), i.e. secondary consumers could switch between prey items found in decomposition soil food-webs and those in leaf-based food-webs. Nonetheless, the relationship between herbivores and natural enemies has created much more controversy and attention than the interaction between natural enemies and saprovore assemblages due to the implications for pest management (Wardle et al. 1999).

The presence of legumes in organic cereal fields seems to play a key role in enhancing both the abundance and richness of parasitoid communities, a fact that could be explained by the direct enrichment of alternative food supplies such as nectar, pollen and sap (Norris and Kogan 2000; Banks et al. 2008; Bianchi and Wäckers 2008). We also observed a positive correlation between the number of predators and legume cover. This supports existing evidence that consuming flowers and extrafloral nectaries improves the survival and nutrient reserves of
 predators during periods of prey scarcity, and that the availability of nectar during these periods improves the
 long-term reproductive capacity of predators (Hodek and Honek 1996; Norris and Kogan 2000; Isaacs et al.
 2009; Lundgren and Seagraves 2011; Amaral et al. 2013).

The positive effect of grass cover on predator and parasitoid communities may be due to plants' role as indirect providers of non-host resources to natural enemies (e.g. by supporting alternative hosts) or simply as structures for oviposition and/or protection (Moreby et al. 1994; Norris and Kogan 2000; Souza and Martins 2004; Nicholls and Altieri 2012; Amaral et al. 2013). On the other hand, the response to grass cover might also been justified with better conditions of environmental parameters because as Antvogel and Bonn (2001) suggested the composition of the ground beetle assemblage was strongly influenced by microclimatic parameters and vegetation structure. In addition to this, as not all relationships are trophic ones, maybe some of the patterns described in our study may also being associated with a resource-based habitat approach hypothesis (Shreeve et al. 2001). However, our approach did not allow us to distinguish among these different responses.

#### **Conclusions and implications**

The clear response by the different feeding groups to local factors such as grass and legume cover indicates that the weed-herbivore-natural enemy system must be taken into account if we are to improve our understanding of the interactions between organisms at different trophic levels. Our results show that the conservation of farmland insect biodiversity is possible through the maintenance of within-field plant diversity in agroecosystems. Our findings also provide evidence that inclusion of legumes in agroecosystems can improve the conservation of beneficial arthropods like predators or parasitoids, which are the key players in order to support the correct ecosystem functioning. This type of studies should encourage policies with a more weed tolerant perspective, because by the inclusion of additional flower traits within the crop fields, we are enhancing arthropod conservation and guaranteeing the provision of ecosystem services, like natural pest control.

The functional approach tested is a robust tool with two major advantages and one disadvantage. Firstly, it can be adopted relatively easily for use by parataxonomists, thereby saving time and money over multi-taxa approaches. Secondly, the adoption of a feeding-group approach gives a broader picture of the different players operating in functional agro-ecosystems. Nonetheless, working with the whole arthropod community means to sort out, identify, and count a considerable volume of groups, and it's not feasible to work at landscape scale approach, in the general context of a resource limited project. Therefore, the next step could be the selection of a wide variety of groups that represents different feeding groups. Having a wider perspective could improve our

360 understanding of agro-ecosystem functioning, and thus enable the design of crop management strategies that

ensure conservation of the different arthropods' trophic groups and their functional role.

3 362 363 References 364 8 365 Albajes R, Lumbierres B, Pons X (2011) Two heteropteran predators in relation to weed management in 10 366 herbicide-tolerant corn. Biol Control 59:30-36. doi: 10.1016/j.biocontrol.2011.03.008 12 367 Altieri MA, Nicholls CI (1999) Biodiversity, ecosystems function and pest management agricultural systems. In: 14 368 Collins WW, Qualset CO (eds) Biodiversity in Ecosystems. CRC Press, Boca Raton, FL, pp 69-84 16 369 Amaral DSSL, Venzon M, Duarte MVA, Sousa FF, Pallini A, Harwood JD (2013) Non-crop vegetation 18 370 associated with chili pepper agroecosystems promote the abundance and survival of aphid predators. Biol 20 371 Control 64:338-346. doi: 10.1016/j.biocontrol.2012.12.006 22 372 Antvogel H, Bonn A (2001) Environmental parameters and microspatial distribution of insects: a case study of 24 373 carabids in an alluvial forest. Ecography 24:470-482. 26 374 Baayen RH (2008) languageR: Data sets and functions with "Analyzing Linguistic Data: A practical introduction <sup>28</sup> 375 to statistics". R package version 0.953. 376 Balmford A, Green MJB, Murray MG (1996a) Using higher-taxon richness as a surrogate for species richness: I. <sup>32</sup> 377 Regional tests. Proc R Soc London- Biol Sci Ser B 263:1267-1274. doi: doi: 10.1098/rspb.1996.0186 <sup>34</sup>/<sub>57</sub> 378 Balmford A, Jayasuriya AHM, Green MJB (1996b) Using higher-taxon richness as a surrogate for species 379 richness: II. Local Applications. Proc R Soc London- Biol Sci Ser B 263:1571-1575. doi: doi: 380 10.1098/rspb.1996.0230 381 Banks JE, Bommarco R, Ekbom B (2008) Population response to resource separation in conservation biological 382 control. Biol Control 47:141-146. 383 Bates D, Maechler M, Dai B (2008) lme4: Linear mixed-effects models using S4 classes. R package version 384 0.999375-28. http://CRAN.R-project.org/package=lme4. 385 Biaggini M, Consorti R, Dapporto L, Dellacasa M, Paggetti E, Corti C (2007) The taxonomic level order as a 386 possible tool for rapid assessment of Arthropod diversity in agricultural landscapes. Agric Ecosyst Environ 387 122:183-191. 388 Bianchi FJJA, Wäckers FL (2008) Effects of flower attractiveness and nectar availability in field margins on 57 **389** biological control by parasitoids. Biol Control 46:400-408. 59 **390** Birkhofer K, Fliessbach A, Wise DH, Scheu S (2008) Generalist predators in organically and conventionally

- managed grass-clover fields: implications for conservation biological control. Ann Appl Biol 153:271-1 392 280. 3 393 Caballero-López B, Blanco-Moreno JM, Pérez N, Pujade-Villar J, Ventura D, Oliva F, Sans FX (2010) A functional approach to assessing plant-arthropod interaction in winter wheat. Agric Ecosyst Environ 137:288-293. 11 397 13 398 15 399  $^{17} 400$ 19 401 <sup>23</sup> 403  $_{54}$  418 56 419 58 420 60 421
  - Cardoso P, Silva I, de Oliveira NG, Serrano ARM (2004) Higher taxa surrogates of spider (Araneae) diversity and their efficiency in conservation. Biol Conserv 117:453-459. Casas J, Djemai I (2002) Canopy architecture and multitrophic interactions. In: Tscharntke T, Hawkins BA (eds) Multitrophic level interactions. Cambridge University Press, Cambridge, pp 174–196 Clough Y, Holzschuh A, Gabriel D, Purtauf T, Kleijn D, Kruess A, Steffan-Dewenter I, Tscharntke T (2007) Alpha and beta diversity of arthropods and plants in organically and conventionally managed wheat fields. J Appl Ecol 44:804-812. doi: doi: 10.1111/j.1365-2664.2007.01294 Consell Català de la Producció Agrària Ecològica (2013) Guia per a la certificació ecològica i informació pública. Generlaitat de Catalunva. Barcelona Duffield SJ, Bryson RJ, Young JEB, Sylvester-Bradley R, Scott RK (1997) The influence of nitrogen fertiliser on the population development of the cereal aphids Sitobion avenae (F) and Metopolophium dirhodum (Wlk) on field grown winter wheat. Ann Appl Biol 130:13–26. doi: doi: 10.1111/j.1744-7348.1997.tb05779 EEC (2007) Council Regulation (EC) No 2007, of 28 June 2092/91, on organic production and labelling of organic products and repealing Regulation (EEC). Elliott NC, Tao FL, Fuentes-Granados R, Giles KL, Elliott DT, Greenstone MH, Shufran KA, Royer TA (2006) D-Vac sampling for predatory arthropods in winter wheat. Biol Control 38:325-330. Evans EW (2008) Multitrophic interactions among plants, aphids, alternate prey and shared natural enemies- a review. Eur J Entomol 105:369-380. Fuller RJ, Norton LR, Feber RE, Johnson PJ, Chamberlain DE, Jovs AC, Mathews F, Stuart RC, Townsend MC, Manley WJ, Wolfe MS, Macdonald DW, Firbank LG (2005) Benefits of organic farming to biodiversity vary among taxa. Biol Lett 1:431-434.
  - Ghorbani R., Mousavi SK, Nazari S, Hatami B (2010) Study of the effect of irrigation and nitrogen fertilizer on sugar beet growth and population dynamism of Empoasca decipiens (Hom.: Cicadellidae) and Thrips tabaci (Thys.: Thripidae). Appl Entomol Phytopathol 78:61-80.
  - Grimm NB (1995) Why link species and ecosystems? A perspective from ecosystem ecology. In: Jones CG,

- 9 427 11 428 13 429  $^{15}\ 430$ 17 431 <sup>23</sup> 434 <sub>54</sub> 449  $_{56}$  45058 451 60 452
- 422 Lawton JH (eds) Linking Species and Ecosystems. Chapman & Hall, New York, pp 5–15
  - Haddad NM, Tilman D, Haarstad J, Ritchie M, Knops MH (2001) Contrasting effects of plant richness and
     composition on insects communities: a field experiment. Am Nat 158:17–35.
    - Harwood JD, Sunderland KD, Symondson WOC (2001) Living where the food is: web location by linyphiid
      Wheat, in relation to prey availability in winter. J Appl Ecol 38:88–99.
      - Hasken KH, Poehling HM (1995) Effects of different intensities of fertilisers and pesticides on aphids and
        aphids predators in winter wheat. Agric Ecosyst Environ 52:45–50.
      - Hawes C, Haughton AJ, Bohanb DA, Squire GR (2009) Functional approaches for assessing plant and
         invertebrate abundance patterns in arable systems. Basic Appl Ecol 10:34–42. doi:

doi:10.1016/j.baae.2007.11.007

432 Hodek I, Honek A (1996) Ecology of Coccinellidae. Kluwer Academic Publishers, Dordrecht, The Netherlands

433 Hyvönen T, Huusela-Veistola E (2008) Arable weeds as indicators of agricultural intensity. A case study from
434 Finland. Biol Conserv 141:2857–2864.

- Isaacs R, Tuell J, Fiedler A, Gardiner M, Landis D (2009) Maximizing arthropod-mediated ecosystem services
  in agricultural landscapes: the role of native plants. Front Ecol Environ 7:196–203.
- Knops JMH, Tilman D, Haddad NM, Naeem S, Mitchell CE, Haarstad J, Ritchie ME, Howe KM, Reich PB,
  Siemann E, Groth J (1999) Effects of plant species richness on invasion dynamics, disease outbreaks,

insect abundances and diversity. Ecol Lett 2:286-293.

- Koricheva J, Mulder CPH, Schmid B, Joshi J, Huss-Danell K (2000) Numerical responses of different trophic
  groups of invertebrates to manipulation of plant diversity in grasslands. Oecologia 125:271–282. doi: doi:
  10.1007/s004420000450
- 443 Kutner MH, Nachtsheim CJ, Neter J (2004) Applied Linear Regression Models, 4th edn. McGraw-Hill, Irwin
- Landis DA, Wratten SD, Gurr GM (2000) Habitat managment to conserve natural enemies of arthropods pests in
  agriculture.
- Letourneau DK, Goldstein B (2001) Pest damage and arthropod community structure in organic vs. conventional
  tomato production in California. J Appl Ecol 38:557–570.
- Lundgren JG, Seagraves MP (2011) Physiological benefits of nectar feeding by a predatory beetle. Biol J Linn
  Soc 104:661–669. doi: 10.1111/j.1095-8312.2011.01729.x
  - Mäder P, Fließbach A, Dubois D, Gunst L, Fried P, Niggli U, Masters G (2002) Soil fertility and biodiversity in
     organic farming. Science (80- ) 296:1694–97.
  - 2 Maleque MA, Ishii HT, Maeto K (2006) The use of arthropods as indicators of ecosystem integrity in forest

management. J For 104:113-117. 1 454 McCann KS (2000) The diversity-stability debate. Nature 405:228-233. 3 455 Moreby SJ, Aebischer NJ, Southway SE, Sotherton NW (1994) A comparison of the flora and arthropod fauna of organically and conventionally grown winter-wheat in southern England. Ann Appl Biol 125:13-27. Müller C, Godfray H (1998) The response of aphid secondary parasitoids to different patch densities of their 9 458 host. BioControl 43:129–139. Murdoch WW, Evans FC, Peterson CH (1972) Diversity and pattern in plants and insects. Ecology 53:819–829. Nicholls CI, Altieri MA (2012) Plant biodiversity enhances bees and other insect pollinators in agroecosystems. A review. Agron Sustain Dev 33:257-274. doi: 10.1007/s13593-012-0092-y Norris RF, Kogan M (2000) Interactions between weeds, arthropod pests, and their natural enemies in managed ecosystems. Weed Sci 48:94-158. doi: 10.1614/0043-1745(2000)048[0094:IBWAPA]2.0.CO;2 Perner J, Voigt W (2007) Measuring the complexity of interaction webs using vertical links between functional groups. Agric Ecosyst Environ 120:192-200. Pinheiro JB, Bates DM (2000) Mixed-Effects Models in S and S-Plus. Springer, New York, USA R Development Core Team (2013) R: A Language and Environment for Statistical Computing, R Foundation for Statistical Computing. R Dev. Core Team Rostami M, Zamani AA, Goldasteh S, Shoushtari RV, Kheradmand K (2012) Influence of nitrogen fertilization on biology of Aphis gossypii (Hemiptera: Aphididae) reared on Chrysanthemum indicum (Asteraceae). J Plant Prot Res 52:118-121. doi: 10.2478/v10045-012-0019-2 Schaffers AP, Raemakers IP, Sýkora K V, Ter Braak CJF (2008) Arthropods assemblages are best predicted by plant species composition. Ecology 89:782-794. Shreeve TG., Dennis RLH., Roy DB., Mos D (2001) An ecological classification of British butterflies: Ecological attributes and biotope occupancy. J Insect Conserv 5:145-161. Siemann E (1998) Experimental tests of effects of plant productivity and diversity on grassland arthropod diversity. Ecology 79:2057-2070. Souza ALT De, Martins RP (2004) Distribution of plant-dwelling spiders: Inflorescences versus vegetative branches. Austral Ecol 29:342-349. doi: 10.1111/j.1442-9993.2004.01371.x Stewart AJA, Wright AF (1995) A new inexpensive suction apparatus for sampling arthropods in grassland. Ecol Entomol 20:98-102. Vucic-Pestic O, Birkhofer K, Rall BC, Scheu S, Brose U (2010) Habitat structure and prey aggregation determine the functional response in a soil predator-prey interaction. Pedobiologia (Jena) 53:307–312.

Wardle DA, Nicholson KS, Bonner KI, Yeates GW (1999) Effects of agricultural intensification on soil-1 485 associated arthropod population dynamics, community structure, diversity and temporal variability over a 3 486 seven-year period. Soil Biol Biochem 31:1691-1706. doi: doi:10.1016/S0038-0717(99)00089-9 Wickramasinghe LP, Harris S, Jones G (2004) Abundance and species richness of nocturnal insects on organic 7 488 and conventional farms: Effects of agricultural intensification on bat foraging. Conserv Biol 18:1283-9 489 1292. doi: doi: 10.1111/j.1523-1739.2004.00152 11 490 Willmer P, Hughes J, Woodford J, Gordon S (1996) The effects of crop microclimate and associated 13 491 physiological constraints on the seasonal and diurnal distribution patterns of raspberry beetle (Byturus <sup>15</sup> 492 tomentosus ) on the host plant Rubus idaeus. Ecol Entomol 21:87-97. 17 493 Wilson RJ, Bennie J, Lawson CR, Pearson D, Ort??zar-Ugarte G, Guti??rrez D (2014) Population turnover, 19 494 habitat use and microclimate at the contracting range margin of a butterfly. J Insect Conserv 19:205–216. doi: 10.1007/s10841-014-9710-0 <sup>23</sup> 496 Zadoks JC, Chang TT, Konzak CF (1974) A decimal code for the growth stages of cereals. Weed Res 14:415-421. 

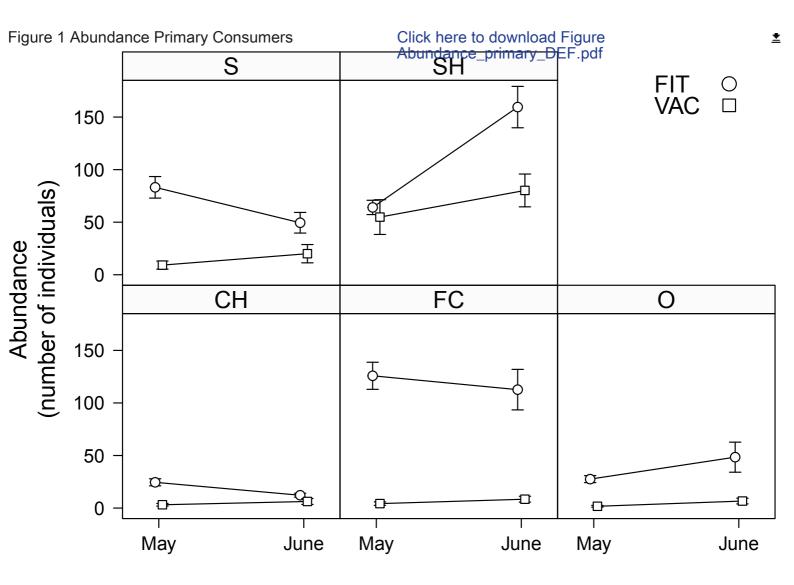
## 500 FIGURE CAPTIONS

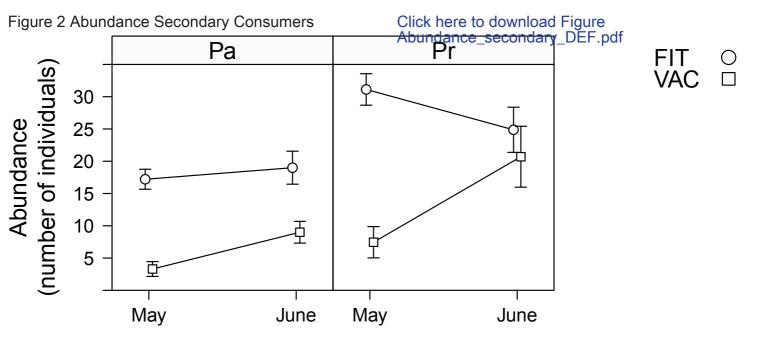
Figure 1. Total number of individuals of primary consumers caught by interception traps (FIT) and suction
 sampling (VAC) in May and June. CH = Chewing-herbivores, FC = Flower-consumers, SH = Sucking herbivores, S = Saprovores and O= Omnivores. Symbols indicate mean values and bars indicate the standard
 error.

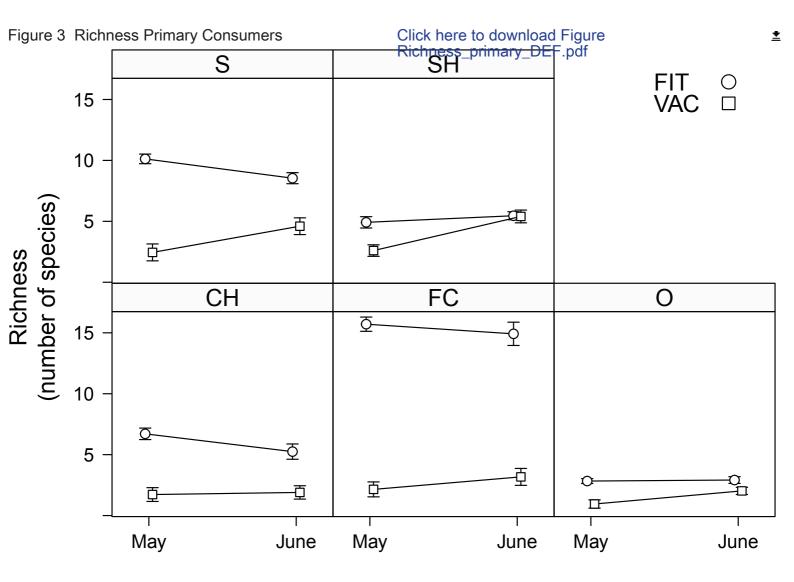
**Figure 2.** Total number of individuals of secondary consumers caught by interception traps (FIT) and suction sampling (VAC) in May and June. Pa = Parasitoids and Pr = Predators. Symbols indicate mean values and bars indicate the standard error.

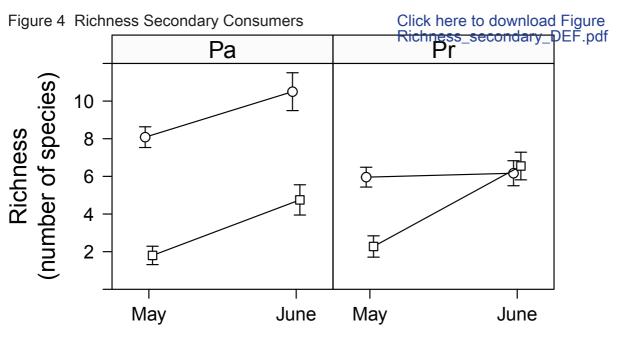
**Figure 3.** Total family richness of primary consumers caught by interception traps (FIT) and suction sampling (VAC) in May and June. CH = Chewing-herbivores, FC = Flower-consumers, SH = Sucking-herbivores, S = Saprovores and O = Omnivores. Symbols indicate mean values and bars indicate the standard error.

**Figure 4.** Total family richness of secondary consumers caught by interception traps (FIT) and suction sampling (VAC) in May and June. Pa = Parasitoids, and Pr = Predators. Symbols indicate mean values and bars indicate the standard error.











**Table 1** Effects of sampling method (SM), sampling period (SP), their interaction (SM\*SP) and plant descriptors such as plant species richness (SR), legume cover (LC), broad-leaved herb cover (BC) and grass cover (GC) on the abundance of primary consumers. The level of significance for the different predictors included in the models was obtained using Markov Chain Monte Carlo methods.

	Chewing-herbivore abundance		Flower-consumer abundance		Suction-herbivores abundance		Saprovores abundance	
	$X \pm SE$	P	$X \pm SE$	Р	$X \pm SE$	Р	$X \pm SE$	Р
Intercept	$2.62 \pm 0.52$	0.000	4.09 ± 0.38	0.000	6.12 ± 1.78	0.001	$2.43 \pm 0.42$	0.000
SM	$-2.09 \pm 0.18$	0.000	$-3.27 \pm 0.15$	0.000	$-1.33 \pm 0.65$	0.044	$-2.61 \pm 0.19$	0.000
SP	$-0.66 \pm 0.20$	0.002	$-0.12 \pm 0.17$	0.470	$4.62 \pm 0.73$	0.000	$-0.51 \pm 0.22$	0.020
SM*SP	$1.02~\pm~0.25$	0.000	$0.64~\pm~0.21$	0.002	$-2.46 \pm 0.92$	0.010	$1.53\ \pm\ 0.27$	0.000
SR	$-0.02 \pm 0.04$	0.519	$-0.02 \pm 0.03$	0.490	$0.06 \pm 0.15$	0.827	$0.06\ \pm\ 0.04$	0.154
LC	$0.02~\pm~0.02$	0.320	$0.03~\pm~0.02$	0.052	$0.05 \pm \ 0.07$	0.483	$0.02\ \pm\ 0.02$	0.285
BC	$0.01~\pm~0.01$	0.491	$0.00~\pm~0.01$	0.580	$0.02\pm\ 0.03$	0.530	$0.01\ \pm\ 0.01$	0.435
GC	$0.01~\pm~0.01$	0.058	$0.01~\pm~0.00$	0.003	$0.02 \pm 0.02$	0.468	$0.02\ \pm\ 0.00$	0.000

**Table 2** Effects of sampling method (SM), sampling period (SP), their interaction (SM\*SP) and plant descriptors such as plant species richness (SR), legume cover (LC), broad-leaved herb cover (BC) and grass cover (GC) on the abundance of parasitoids and predators. The abundance of primary consumers was also included in this model. CH = Chewing-herbivores, FC = Flower-consumers, S = Saprovores, SH = Sucking-herbivores (see text for further details). The level of significance for the different predictors included in the models was obtained using Markov Chain Monte Carlo methods.

Parasitoids			Predators	Predators				
	abundance			ab	abundance			
	X ±	SE	Р	X ±	SE	Р		
Intercept	$1.51 \pm$	0.28	0.000	$1.53 \pm$	0.38	0.000		
SM	<b>-</b> 1.13 ±	0.22	0.000	$-1.07 \pm$	0.29	0.000		
SP	-0.03 $\pm$	0.18	0.869	-0.37 $\pm$	0.24	0.107		
SM*SP	0.76 ±	0.22	0.001	$1.33 \pm$	0.29	0.000		
SR	$0.00$ $\pm$	0.02	0.818	0.04 ±	0.03	0.240		
LC	$0.03$ $\pm$	0.01	0.027	0.03 ±	0.01	0.033		
BC	-0.00 $\pm$	0.00	0.886	$0.00$ $\pm$	0.00	0.798		
GC	0.01 ±	0.00	0.001	0.01 ±	0.00	0.002		
Ab.CH	0.01 ±	0.01	0.138	-0.00 $\pm$	0.01	0.971		
Ab.FC	-0.00 $\pm$	0.00	0.898	0.00 ±	0.00	0.561		
Ab.SH	$0.00$ $\pm$	0.00	0.000	0.00 ±	0.00	0.005		
Ab.S	$0.00$ $\pm$	0.00	0.204	0.00 ±	0.00	0.165		

	Chewing-herbivore richness		Flower-consumer richness		Suction-herbivores richness		Saprovores richness	
	$X \pm SE$	Р	$X \pm SE$	Р	$X \pm SE$	Р	$X \pm SE$	Р
Intercept	$1.87~\pm~0.24$	0.000	$2.68 \pm 0.15$	0.000	$2.53 \pm 0.70$	0.001	$2.03 \pm 0.14$	0.000
SM	$-0.92 \pm 0.08$	0.000	$-1.34 \pm 0.07$	0.000	$-2.27 \pm 0.32$	0.000	$-1.00 \pm 0.07$	0.000
SP	$-0.19 \pm 0.09$	0.051	$-0.04 \pm 0.08$	0.653	$0.64\pm0.36$	0.078	$-0.11 \pm 0.07$	0.124
SM*SP	$0.25~\pm~0.12$	0.047	$0.23~\pm~0.10$	0.018	$-2.25 \pm 0.46$	0.000	$0.53\ \pm\ 0.09$	0.000
SR	$0.01~\pm~0.02$	0.715	$-0.01 \pm 0.01$	0.372	$0.19 \pm \ 0.07$	0.005	$0.00\ \pm\ 0.01$	0.720
LC	$0.01~\pm~0.01$	0.158	$0.01 \pm 0.01$	0.158	$0.06 \pm 0.03$	0.074	$0.01\ \pm\ 0.01$	0.153
BC	$0.00~\pm~0.00$	0.968	$0.00~\pm~0.00$	0.419	$-0.01 \pm 0.01$	0.272	$0.00\ \pm\ 0.00$	0.411
GC	$0.00~\pm~0.00$	0.129	$0.00~\pm~0.00$	0.011	$0.02\pm0.00$	0.004	$0.01\ \pm\ 0.00$	0.000

**Table 3** Effects of sampling method (SM), sampling period (SP), their interaction (SM\*SP) and plant descriptors such as plant species richness (SR), legume cover (LC), broad-leaved herb cover (BC) and grass cover (GC) on the richness of primary consumers. The level of significance for the different predictors included in the models was obtained using Markov Chain Monte Carlo methods.

**Table 4** Effects of sampling method (SM), sampling period (SP), their interaction (SM\*SP) and plant descriptors such as plant species richness (SR), legume cover (LC), broad-leaved herb cover (BC) and grass cover (GC) on the richness of parasitoids and predators. The richness of primary consumers was also included in this model. CH = Chewing-herbivores, FC = Flower-consumers, S = Saprovores, SH = Sucking-herbivores (see text for further details). The level of significance for the different predictors included in the models was obtained using Markov Chain Monte Carlo methods

Parasitoids			P	Predators			
	r		richness				
	$X \pm SI$	E P	X ±	SE	Р		
Intercept	$1.51 \pm 0.2$	20 <b>0.000</b>	$0.81 \ \pm$	0.21	0.000		
SM	$-0.46 \pm 0.$	17 <b>0.006</b>	<b>-</b> 0.14 ±	0.17	0.463		
SP	$0.25 \pm 0.0$	07 <b>0.000</b>	0.12 ±	0.07	0.115		
SM*SP	$0.03 \pm 0.$	10 0.785	0.41 ±	0.11	0.000		
SR	$0.00 \pm 0.0$	01 0.970	0.01 ±	0.01	0.519		
LC	$0.01 \pm 0.01$	00 <b>0.026</b>	0.01 ±	0.01	0.093		
BC	$-0.00 \pm 0.00$	00 0.999	0.00 ±	0.00	0.384		
GC	$0.00 \pm 0.0$	00 <b>0.009</b>	0.01 ±	0.00	0.001		
R.CH	$0.02 \pm 0.00$	01 0.318	0.03 ±	0.02	0.039		
R.FC	$-0.00 \pm 0.00$	00 0.815	-0.00 $\pm$	0.01	0.787		
R.SH	$0.04 \pm 0.0$	01 <b>0.012</b>	$0.05$ $\pm$	0.02	0.010		
R.S	$0.03 \pm 0.0$	01 <b>0.026</b>	0.04 ±	0.02	0.012		