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Single best species or natural enemy assemblages? a correlational approach to investigating ecosystem function

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Abstract Though biodiversity can have an effect on biological control of pests, there is debate about whether a single species or a more complex assemblage of natural enemies will exert better control of the pest population. We explore the relationship between numbers of different taxa of natural enemies in an olive grove to identify cases of significant positive and negative correlations between enemy taxa. Integrating herbivore data we identified enemy taxa and assemblages that were associated with low numbers of olive pests. Overall, single species such as *Anthocoris nemoralis*, or relatively simple predator assemblages, such as that formed by the spider families Araneidae and Liniphiidae, and the green lacewing *Chrysoperla carnea*, were associated with better biological control

than complex assemblages, where intraguild predation and other trophic interactions might hamper the effectiveness of enemies. For a Lepidopteran pest with a complex life cycle, the single best predator taxon was markedly poorer at suppression than the most effective assemblage. In contrast, a Hemipteran pest with a simple life cycle was controlled nearly as well by the single best predator taxon as by the most effective assemblage. Statistical approaches offer good scope to identify optimal aspects of biodiversity to maximise ecosystem services such as biological control.

Keywords *Anthocoris nemoralis* · Conservation biological control · *Euphyllura olivina* · Intraguild predation · *Prays oleae*

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Introduction

In agricultural systems, biodiversity can have a profound effect on ecosystem function and offers potential benefits in the form of ecosystem services such as biological control of pests (Letourneau et al. 1999; Gurr et al. 2012). Nevertheless, knowledge about the nature of the interactions between natural enemies is needed to optimally manipulate components of biodiversity and, thereby, maximise the delivery of ecosystem services (Cardinale et al. 2003; Wilby et al. 2005). From a “biodiversity-ecosystem function” assemblages of multiple natural

enemies can reduce the density of agricultural pests (Symondson et al. 2002; Cardinale et al. 2003, 2006), but there is debate about whether a single species or a simple natural enemy assemblage will exert better control of a pest population than will more complex assemblages (Hassell and May 1986; Denoth et al. 2002). Predators can interact antagonistically and disrupt biological control or positively with the opposite outcome for this ecosystem service (Rosenheim et al. 1995; Hodge 1999; Finke and Denno 2004; Batchelor et al. 2005).

Straub et al. (2008) proposed three potential effects by which increased species richness might impact pest control: a reduction of pest density, a neutral effect, or a disruption of biological control. The first is an outcome of a niche complementarity whereby a single pest species can provide multiple types of prey resource that are fully exploited only by more than one enemy species. Two mechanisms can lead to this process, resource partitioning and facilitation (Hooper et al. 2005). Alternatively, a neutral effect on pest density may arise if multiple enemy species are functionally redundant so all exploit the same prey resource in the same microhabitat at the same time. Increasing the number of species with the same function leads to interspecific competition (Ives et al. 2006). Finally, intraguild predation occurs when a top predator (intraguild predator) consumes an intermediate predator (intraguild prey), with which it competes for a common prey resource (the pest) (Polis et al. 1989; Polis and Holt 1992; Pérez-Lachaud et al. 2004). So, for conservation biological control practitioners, determining when multiple predator species provide better pest suppression than single species is a key step towards developing ecologically-informed pest management (Ehler 1990; Batchelor et al. 2006; Straub et al. 2008).

This study investigated the relationships amongst predator natural enemies and two pest species in olive groves. The study is built on research on the effects of habitat management (ground cover and different types of vegetation adjacent to the crop) on the abundance of different groups of natural enemies (Paredes et al. 2013a) and two important pests in olive groves: the olive moth (*Prays oleae*) and the olive psyllid (*Euphyllura olivina*) (Paredes et al. 2013b). The results of those studies revealed that: (1) patches of adjacent natural vegetation increased the abundance of some groups of natural enemies

(Paredes et al. 2013a) and decreased the abundance of pests (Paredes et al. 2013b); and (2) ground cover increased the abundance of most natural enemies (Paredes et al. 2013a), but had no effect on pests (Paredes et al. 2013b). There are two potential explanations for the latter result. First, those natural enemies promoted by ground cover are not the ones that can reduce pest abundance. And second, potential interactions amongst natural enemies might obscure the response of pest abundance to different habitat management strategies. This study aimed to explore these issues by analysing correlations between natural enemy assemblages and pest abundances in order to test for the action of the mechanisms described by Straub et al. (2008), and thereby identify the natural enemy taxa or assemblages most strongly associated with reduced pest densities in olive groves.

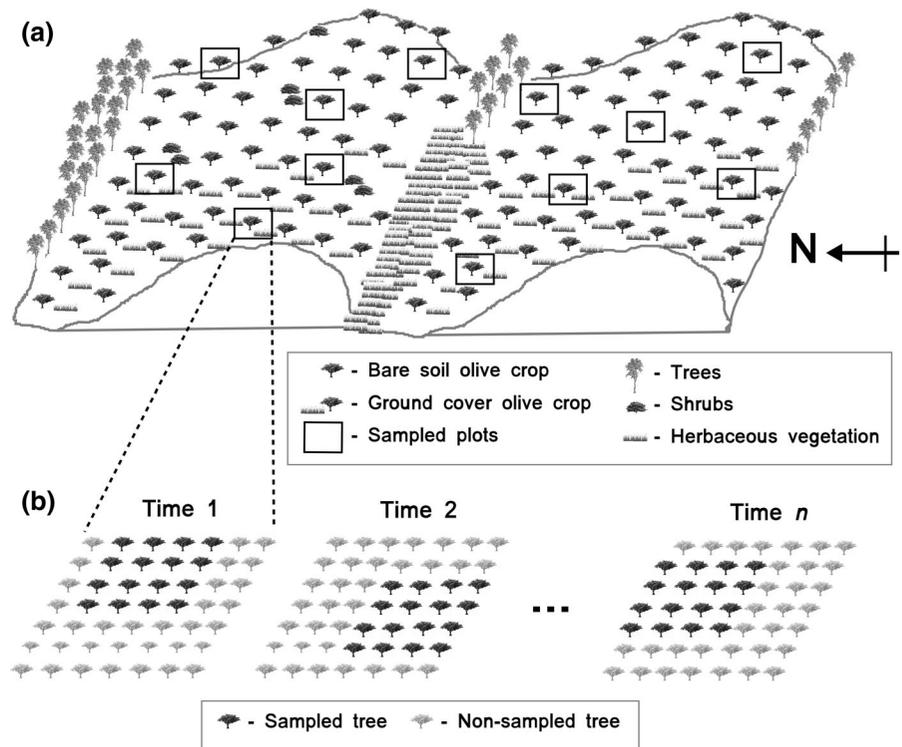
Specific goals of the research were: 1) to explore correlations between the abundance of different groups of natural enemies, 2) to investigate the relationship between assemblages of natural enemies and key pest species using unconstrained ordination, and 3) to identify particular assemblages of natural enemies that best correlate with low pest abundance. Following Wilby et al. (2005), we hypothesised that prey with a more complex life cycle, such as the holometabolous *P. oleae*, would be better suppressed by a more diverse natural enemy assemblage than would herbivores with a simpler life cycle, such as the hemimetabolous *E. olivina*. Because our analyses are based on correlations between variables, causality cannot be inferred. Yet our study provides a novel statistical approach for exploring the relationship between biodiversity and ecosystem function. In the particular case of biological pest suppression, this work provides empirical evidence to untangle the ecological processes underlying positive and negative interactions between natural enemies and their prey and, thereby, constitutes a framework for guiding conservation biological control.

Materials and methods

Study area and experimental design

The study was conducted in an olive grove of 235 ha located in southern Spain, near the city of

Fig. 1 **a** Schematic representation of the experimental olive grove with different vegetation structures (ground cover, woody and herbaceous adjacent vegetation). **b** Random arrangement of sampled trees within plots



Granada (37°17'N and 3°46'W), during 2010 and 2011. The grove comprised two adjacent zones separated from each other by a creek occupied by natural vegetation (Fig. 1). A further description of the study area can be found in Paredes et al. (2013a).

The basic experimental unit in our study was the plot. There were a total of twelve equidistant plots separated by at least 150 m from each other (Fig. 1a). Each plot had a square shape comprising 7 × 7 olive trees and an area of 4,900 m², as olive trees were 10 m from all other adjacent olive trees (Fig. 1b). Within each plot, a square of 4 × 4 olive trees was randomly selected at each date, corresponding to an area of 1,600 m² (Fig. 1b). Samples were collected every ten days, weather allowing, from early April to early July in 2010 and in 2011, which is the period when the two main pests analysed in this study were found in the orchard. Overall there were ten sampling dates in 2010 and nine sampling dates in 2011. A modified vacuum device CDC Backpack Aspirator G855 (John W. Hock Company, Gainesville, Florida, USA) was used to trap the arthropods in the canopy of each of the 16 olive trees (2 mins per tree).

Arthropod taxa

The most common predators known to eat the two studied pest species were considered in our study. Of them five were spider families: Thomisidae, Philodromidae, Araneidae, Linyphiidae, Salticidae; three were ant genera: *Camponotus*, *Tapinoma* and *Plagiolopis*; four were predatory Heteropteran species: *Deraeocoris punctum*, *Anthocoris nemoralis*, *Brachynotocoris ferreri* and *Pseudoloxops coccineus*; and one was a green lacewing species: *Chrysoperla carnea*.

Two pest species typically of olives were considered in this study: the flower generation of the olive moth (*P. oleae*) and the olive psyllid (*E. olivina*). The flower generation of *P. oleae* is the most abundant of the three generations, and lays the eggs of the fruit generation. There is a strong correlation between the numbers of adults of the flower generation and the degree of olive fruit infestation (Ramos et al. 1989), and therefore it is assumed that controlling the adult population of the flower generation of *P. oleae* might ultimately reduce fruit infestation. Eggs and larvae of the flower generation of *P. oleae* appear at the same time as that of *E. olivina* nymphs (Paredes et al.

2013b), but are not efficiently sampled by the vacuum method used in the present study.

Data analysis

To analyse the data and avoid temporal autocorrelation of samples, we pooled together all samples taken each year. Thus for each plot we obtained a representative measure of the overall abundance of each natural enemy and pest species for 2010 and 2011. Samples from different years collected within the same plots were treated in further analyses as independent.

The analytical procedure used in this study can be summarized as follows: (1) Pearson's correlations were initially obtained to look at the relationships between the abundance of pairs of natural enemies; (2) Non-metric multidimensional scaling (NMDS) was then used to investigate the overall pattern of species composition in the predator assemblages, and group species that could respond similarly to environmental conditions, habitat structures and resource availability; and (3) Mantel test of matrix correspondence was performed to determine whether similarities in the whole natural enemy community were correlated with similarities in pest abundance.

To minimize the risk of a Type I error (i.e. to reduce the risk of erroneous conclusion of the presence of a significant correlation) as a result of calculating numerous correlations, we applied Bonferroni correction. Although correlations between natural enemies could be also due to environmental factors not explicitly accounted for in this study, the small extent of the orchard and its relatively homogeneity would support the interpretation of correlations in terms of potential interactions between groups of natural enemies. Following this logic, negative correlations would indicate intraguild predation or resource competition, whereas positive correlations would indicate niche complementarity or facilitation.

Data used for the NMDS were square-root transformed and then subjected to Wisconsin double standardization (Legendre and Gallagher 2001). We used the Bray-Curtis dissimilarity distance to compute the resemblance matrix among plots. Based on the NMDS, we generated smooth surfaces to explore associations between particular predator species or assemblages and pest species for the two pest abundances. Smooth surfaces are the result of fitting thin

plate splines in two dimensions using generalized additive models. This function automatically selects the degree of smoothing by generalized cross-validation and interpolates the fitted values on the NMDS plot (Oksanen et al. 2012).

Finally, the standardised form of the Mantel test was used, which computes the Spearman's correlation coefficient, to correlate different assemblages of natural enemies with pest abundance for the two pest species and for the combined abundance of both pests together. The statistical significance of each correlation was determined by a Monte Carlo test with 999 permutations. Mantel tests for the best possible subsets of predator abundances (Clarke and Ainsworth 1993) were also run on distances matrices to select the combination of predatory species that most correlate with pest abundance. All the analyses were performed with the R software (R Development Core Team 2012), including the 'vegan' package (Oksanen et al. 2012).

Results

We collected a total of 26,490 arthropods: 14,484 in 2010, and 12,006 in 2011 (Table 1). Only four correlations between predator taxa were statistically significant after applying Bonferroni correction (Table 2): the spider family Araneidae with *C. carnea* ($r = 0.722$; $p < 0.01$), *C. carnea* with *D. punctum* ($r = 0.677$; $p < 0.001$), *D. punctum* with Linyphiidae ($r = 0.706$; $p < 0.001$), and Linyphiidae with Araneidae ($r = 0.722$; $p < 0.001$). Both spider families (Araneidae, Linyphiidae) and the green lacewing *C. carnea* were associated with low abundance of *P. oleae* (Fig. 2). So they were the predatory Heteroptera *A. nemoralis* and *Tapinoma* ants (Fig. 2).

There was a significant correlation between the whole natural enemy community and *P. oleae* ($r = 0.239$; $p = 0.004$), *E. olivina* ($r = 0.379$; $p = 0.002$), and the combined abundance of both pests together ($r = 0.377$; $p = 0.003$), as revealed by Mantel tests. The selection of subsets of predator species that had the best correlations with the two pest species indicated that the highest correlation with their abundance could be explained by three and five taxa, respectively (Table 3). The correlation between the subset of predators formed by *B. ferreri*, *P. coccineus* and *A. nemoralis*, and the pest *P. oleae* was $r = 0.490$,

Table 1 Mean (\pm SD) total abundance per plot per year of the different arthropods involved in the study

Type of organism	Taxon	2010	2011
Spiders	Thomisidae	13.50 \pm 6.93	9.92 \pm 6.27
	Philodromidae	7.92 \pm 3.28	8.50 \pm 3.55
	Araneidae	10.08 \pm 6.20	14.00 \pm 5.62
	Linyphiidae	31.25 \pm 16.11	45.75 \pm 33.44
	Salticidae	11.17 \pm 2.48	10.67 \pm 4.16
Ants	<i>Plagiolepis</i>	28.08 \pm 14.63	13.92 \pm 12.34
	<i>Camponotus</i>	52.00 \pm 23.22	35.08 \pm 11.00
	<i>Tapinoma</i>	93.33 \pm 204.03	110.83 \pm 97.76
Predatory Heteroptera	<i>B. ferreri</i>	367.42 \pm 104.12	192.92 \pm 67.82
	<i>P. coccineus</i>	87.08 \pm 18.39	61.92 \pm 19.01
	<i>D. punctum</i>	89.33 \pm 35.08	81.92 \pm 48.34
	<i>A. nemoralis</i>	13.17 \pm 10.41	48.25 \pm 21.55
Lacewings	<i>C. carnea</i>	14.25 \pm 5.86	19.75 \pm 8.07
Pests	<i>E. olivina</i>	80.83 \pm 37.94	134.75 \pm 91.69
	<i>P. oleae</i>	295.00 \pm 55.92	116.67 \pm 17.92

whereas the correlation between the subset formed by Thomisidae, Salticidae, *Tapinoma*, *P. coccineus* and *A. nemoralis*, and the pest *E. olivina* was $r = 0.530$ (Table 3). For *P. oleae*, the single best taxon (*A. nemoralis*) provided a markedly weaker correlation ($r = 0.373$; Table 3) than did the best-performing assemblage. In contrast, the single best taxon that correlated with *E. olivina* (*Tapinoma*) provided a correlation coefficient that was only marginally lower than the more complex and best-performing assemblage ($r = 0.508$; Table 3).

Discussion

Untangling the relationships amongst predator species in the arthropod assemblages is not straightforward as there are many paths, direct or indirect, that may be involved. Our analysis revealed that assemblages of some groups of natural enemies are significantly correlated with the two pest species, but there are potential interactions in the natural enemies assemblages that might be interfering with the response of predators to pests. We found that the prey species with the more complex life cycle, *P. oleae*, was best correlated with a richer assemblage of three enemy taxa whereas the prey with a simpler life cycle, *E. olivina*, was best correlated with a richer assemblage of five enemies. Whilst this finding contrasts with that

of Wilby et al. (2005), the trend within each species differs and is consistent with complex life cycle pests requiring multiple enemies in order to be maximally exploited by consumers. In our study system, the eggs, larvae and adults of *P. oleae* are found in different microhabitats. Thus, a single enemy taxon has a weaker influence on this pest than a more complex assemblage of natural enemies, similarly to the results reported by Wilby et al. (2005) for lepidopteran. In contrast, *E. olivina* nymphs aggregate in the olive flowers, and thus are more vulnerable to be predated by a single taxon. This is supported by similar correlations for best subsets between one single taxon (in our case *Tapinoma* ants) and more complex assemblages. This corresponds with the hemipteran prey type in the study by Wilby et al. (2005).

An assemblage formed by the spider families Araneidae and Linyphiidae, and the green lacewing *C. carnea* was associated with low abundances of *P. oleae*. These groups might fulfil complementary functional roles determined by the way they catch prey (Straub et al. 2008; Uetz et al. 1999). The Araneidae family are orb-weaving spiders that make orbicular webs placed vertically, whereas Linyphiidae, sheet weaver spiders, make tangled web placed horizontally. Both families can potentially predate on the adults of *P. oleae* when they fly within the olive canopy. *C. carnea*, on the other hand, is a branch dweller that predate on the eggs and larvae of

Table 2 Pearson's correlation matrix between predator taxa. Significant correlations (p value ≤ 0.05) after Bonferroni correction are indicated in bold

	Thomisidae	Philodromidae	Araneidae	Linyphiidae	Salticidae	Plagiolepis	Camponotus	Tapinoma	B. ferreri	P. coccineus	D. punctum	A. nemoralis	C. carnea
Thomisidae	1.000												
Philodromidae	0.028	1.000											
Araneae	0.254	0.411	1.000										
Linyphiidae	0.198	0.483	0.722	1.000									
Salticidae	0.070	0.290	0.034	0.059	1.000								
Plagiolepis	0.118	-0.027	-0.215	-0.042	0.039	1.000							
Camponotus	0.551	0.206	0.142	0.030	0.107	0.283	1.000						
Tapinoma	-0.252	-0.098	-0.160	-0.114	0.290	-0.220	-0.353	1.000					
B. ferreri	0.395	-0.082	-0.185	-0.138	-0.011	0.029	0.443	-0.152	1.000				
P. coccineus	0.357	0.141	0.110	0.017	-0.174	0.494	0.288	-0.373	0.357	1.000			
D. punctum	0.589	0.263	0.623	0.706	-0.008	0.223	0.433	-0.426	0.204	0.460	1.000		
A. nemoralis	-0.200	0.105	0.156	0.054	0.205	-0.489	-0.584	0.438	-0.622	-0.404	-0.258	1.000	
C. carnea	0.514	0.260	0.722	0.589	-0.139	-0.211	0.234	-0.278	-0.059	0.077	0.677	0.191	1.000

P. oleae. Overall, the presence of these predators in the orchard can also be a promising option to reduce *P. oleae* populations.

The ant genus *Tapinoma* has previously been reported to have a detrimental effect on other natural enemies in olive groves (Morris et al. 1999; Pereira et al. 2004). High abundances of *Tapinoma* were associated in the present study with low abundances of all other natural enemies and with high abundances of the pest *E. olivina*. This fact could disrupt the biological control that natural enemies exert on *E. olivina*.

Euphyllura olivina was also positively associated to another natural enemy, *A. nemoralis*, in accordance with the results found by other authors in pear orchards (Scutareanu et al. 1999; Shaltiel and Coll 2004). This predator overwinters in adult stage (Sigsgaard et al. 2006), particularly in natural vegetation adjacent to the orchard (Horton and Lewis 2000; Paredes et al. 2013a). Its presence in the orchard is probably mediated by herbivore induced plant volatiles (HIPVs) produced by attacked trees (Drukker et al. 1995). Thus, when *E. olivina* reaches high abundance, HIPVs are likely to induce an increase of *A. nemoralis*. This is a key finding because *A. nemoralis* was also related with low abundance of *P. oleae*. When adults of *A. nemoralis* arrive to the tree, they lay the eggs of the next generation. Due to their small size, the offspring do not have any other available prey but the eggs of *P. oleae*, thus reducing the abundance of this pest. As a result of this process, *A. nemoralis* might be highlighted as one of the most effective biological control agents against *P. oleae*.

The predators *B. ferreri*, *P. coccineus* and *D. punctum*, all of them predatory Heteroptera, the ant genera *Camponotus* and *Plagiolepis*, and the spider family Thomisidae, were associated with high abundance of *P. oleae*. In the case of *B. ferreri* and *P. coccineus*, these species coexist with *A. nemoralis* at nymphal stages, which are susceptible to predation. Thus they are likely to act as alternative prey that disrupt the biological control that *A. nemoralis* exerts on *P. oleae* (Koss and Snyder 2005). In addition, spider species from the Thomisidae family, as well as *Camponotus* and *Plagiol-*
epis, can prey on *A. nemoralis* as reported in other studies (Fataye and Taffin 1989; Khoo and Chung 1989), and would therefore be involved in an intraguild predation process which would ultimately

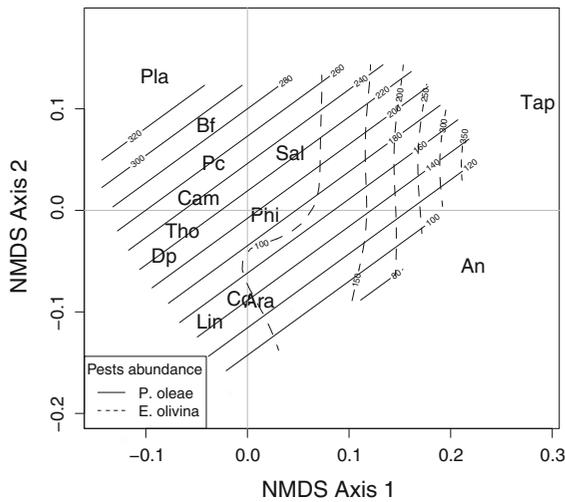


Fig. 2 Non metric multidimensional scaling (NMDS) of total predator abundance. Species scores, representing the different natural enemies taxa, have been added to the final NMDS plot as weighted averages, based on their relative abundance. Proximity of groups of natural enemies within the ordination plot indicates that their abundances are positively related. The ordination axes have been related to the two main pest species abundance by means of generalized additive models, and are represented by lines in the plot with different levels of abundance of pests (*Prays olivina*, *Euphyllura olivina*) ranking in a gradient. This allows to indirectly relating the abundance of pests with the abundance of different groups of natural enemies. Tho Thomisidae, Phi Philodromidae Ara Araneae, Lin Linyphiidae, Sal Salticidae, Cam *Camponotus*, Tap *Tapinoma*, Pla *Plagiolepis*, Dp *D. punctum* An *A. nemoralis*, Bf *B. ferreri*, Pc *P. coccineus*, Cc *C. carnea*

dampen the pressure that *A. nemoralis* exerts on *P. oleae* (Finke and Denno 2004).

Overall, large assemblages of natural enemies appear to be less correlated with pest abundance than are single-best taxa or simple assemblages of up to five spider and insect predators. For a lepidopteran pest that has a complex life-cycle, the single-best predator taxon was less correlated than was evident for a hemipteran with a simple life-cycle. The statistical approach used in the present study offers scope to explore the relationship between biodiversity and ecosystem function and merits testing in a wider range of agricultural systems. By correlating the abundance of different groups of natural enemies, we can determine trends about the process that are carrying on within the agroecosystem, and point to those natural enemies that might disrupt or enhance biological control. In addition, the association of different groups of natural enemies with pest abundance allow

Table 3 Correlations for best possible predator subsets that maximize correlation with pest species, namely *Prays oleae* (a), and *Euphyllura olivina* (b)

(a) <i>Prays oleae</i>	
An	0.373
Bf An	0.457
Bf Pc An	0.490
Ara Bf Pc An	0.459
Cam Tap Bf Pc An	0.430
Ara Cam Tap Bf Pc An	0.418
Ara Pla Cam Tap Bf Pc An	0.398
Tho Ara Pla Cam Tap Bf Pc An	0.366
Tho Phi Ara Pla Cam Tap Bf Pc An	0.337
Tho Phi Ara Pla Cam Tap Bf Pc An Cc	0.312
Tho Phi Ara Sal Pla Cam Tap Bf Pc An Cc	0.287
Tho Phi Ara Sal Pla Cam Tap Bf Pc Dp An Cc	0.265
Tho Phi Ara Lin Sal Pla Cam Tap Bf Pc Dp An Cc	0.239
(b) <i>Euphyllura olivina</i>	
Tap	0.508
Tap Pc	0.450
Tap Pc An	0.478
Tho Tap Pc An	0.508
Tho Sal Tap Pc An	0.530
Tho Sal Tap Pc Dp An	0.510
Tho Sal Tap Bf Pc Dp An	0.495
Tho Sal Pla Tap Bf Pc Dp An	0.482
Tho Lin Sal Pla Cam Tap Pc Dp An	0.470
Tho Lin Sal Pla Cam Tap Bf Pc Dp An	0.455
Tho Lin Sal Pla Cam Tap Bf Pc Dp An Cc	0.440
Tho Phi Lin Sal Pla Cam Tap Bf Pc Dp An Cc	0.415
Tho Phi Ara Lin Sal Pla Cam Tap Bf Pc Dp An Cc	0.379

The number of variables that are selected to maximize correlations with pests has been highlighted in bold

Tho Thomisidae, Phi Philodromidae, Ara Araneae, Lin Linyphiidae, Sal Salticidae, Cam *Camponotus*, Tap *Tapinoma*, Pla *Plagiolepis*, Dp *D. punctum* An *A. nemoralis*, Bf *B. ferreri*, Pc *P. coccineus*, Cc *C. carnea*

us to determinate which are the natural enemies that contribute the most to biological control in olive orchards. Ultimately, such approaches could be a useful guide to optimising ecosystem services such as biological control by allowing identification of the key aspects of diversity to promote strategies such as habitat manipulation.

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- D. Paredes** recently successfully presented his dissertation entitled: “Ecological infrastructures and conservation biological control in olive groves”. This manuscript is a substantial part of this work.
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