Synergistic effects of ground cover and adjacent vegetation on natural enemies of olive insect pests

Daniel Paredes, Luis Cayuela, Mercedes Campos

A B S T R A C T

The use of pesticides in conventional agriculture poses several risks to humans and to the environment, and may turn out to be inefficient in the long-term as pests can develop resistance to pesticides. Non-chemical control methods can be preferable to prevent pest damage. One way to achieve this involves the establishment of ground cover or the restoration of vegetation adjacent to the crop. Either of these methods can effectively increase the abundance of natural enemies, particularly in perennial crops, but their interaction has been typically neglected. In this study we used maximum likelihood methods to analyse the synergistic effects of ground cover and different types of adjacent vegetation (herbaceous, woody) on the abundance of the main natural enemy groups of insect pests in olive groves. A Gaussian function was used to predict their abundance as a response of time, ground cover, different types of adjacent vegetation and year (2010, 2011). We examined 40 different alternative models for each group of natural enemies: spiders, ants, predatory Heteroptera, and parasitoids. Spiders, parasitoids, and one species of predatory Heteroptera (Deraeocoris punctum) showed a greater abundance in ground cover plots. Overall, herbaceous and large woody vegetation adjacent to the crop influenced the abundance of natural enemies more than small woody vegetation. However, this effect was modulated by ground cover. When both structures were present in the crop, the abundance of some groups of natural enemies (spider and parasitoids) was positively influenced by adjacent vegetation, whereas this effect was lower or even reversed in bare soil crops. We thus encourage olive farmers to use both habitat management approaches simultaneously, since the interaction of these ecological infrastructures produces an effect that maximises the abundance of natural enemies.

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1. Introduction

Olive culture is of great importance in the circum-Mediterranean region. Olive crops occupy ca. 7.6 million hectares, of which 2.5 million hectares are in Spain, the main olive oil producer and exporter. In 2012 alone, this crop yielded approximately 1.5 million tonnes of olive oil in Spain. Conventional production practices are based on the use of fertilizers, herbicides and pesticides. This has led to important environmental problems, such as the loss of natural vegetation and bare soil due to herbicide use, which can cause erosion and loss of natural soil fertility (Metzidakis et al., 2008). To avoid some of these problems, new policies are currently being implemented in the European Union, aiming at the restoration of adjacent natural vegetation and the establishment and maintenance of ground cover (IOBC, 2012).

Vegetation adjacent to the crop (henceforth natural vegetation) has been shown to be an efficient tool to enhance the abundance and diversity of natural enemies (Altieri and Letourneau, 1982; Bianchi et al., 2006; Griffiths et al., 2008; Thomson and Hoffmann, 2009). This in turn can translate into decreased crop damage in adjacent crops and could provide direct benefits by reducing the use of costly pesticides (Tscharntke et al., 2002; Tsitsilas et al., 2006) and associated environmental and human health concerns (Meehan et al., 2011). Herbaceous and woody vegetation patches interspersed within the crop, or located at the crop margins mainly form this natural vegetation (Bianchi et al., 2006). Overall, these structures are very important for the establishment and survival of arthropods (Thies and Tscharntke, 1999), since they can provide food resources such as nectar, pollen or alternative prey, and shelter when the crop is disturbed (Landis et al., 2000). Therefore, they have been used to increase natural enemy efficiency in order to reduce the incidence of crop pests (Scheid et al., 2011; Simpson et al., 2011).

In perennial crops, the use of natural or planted ground cover vegetation can also contribute to an increase in the abundance of
natural enemies, in addition to reduced soil erosion. Ground cover has been reported to increase the abundance of different groups of natural enemies (Smith et al., 1996; Rieux et al., 1999; Danne et al., 2010; Silva et al., 2010) but in some studies this increase has not been reported (Costello and Daane, 1998; Bone et al., 2009). Most of these studies, however, have systematically neglected the role of natural vegetation interspersed within or near the crop, thus ignoring the possibility of synergistic effects between ground cover and natural vegetation (but see Woltz et al., 2012 for a case study in soybean fields).

We hypothesised that populations of natural enemies within the olive grove may be affected by adjacent natural vegetation, and their response might differ depending on the presence of ground cover within the crop. We therefore aimed to: (i) establish the effect that ground cover, as compared to bare soil areas, has on the abundance of natural enemies in olive groves; (ii) determine the influence of different types of adjacent natural vegetation on their abundance; and (iii) identify potential synergistic effects between ground cover and different types of adjacent natural vegetation.

The results of this study will contribute to a deeper understanding of the interactions between arthropods, ground cover and adjacent vegetation, and will provide mechanisms to improve the biological control of pest outbreaks in so widespread and socially important crop such as olive orchards, while reducing environmental and production costs by avoiding (or minimising) the use of chemical products.

2. Material and methods

2.1. Study area

The study was conducted in an experimental olive grove (235 ha) located in southern Spain, near the city of Granada (37°17’N and 3°46’W). It comprised two adjacent zones separated from each other by a creek occupied by natural vegetation (Fig. 1). The topographical conditions were typical of the olive groves in the region. Climatic conditions were different in both years. Average annual precipitation was higher in 2010 (565.12 mm) than in 2011 (368.82 mm). In 2010 mean average temperature was lower (22.1 °C) than in 2011 (24.5 °C). Average maximum monthly temperature from April to June was 24.7 °C in 2010 and 27.8 °C in 2011. The main insect pests in this area were the olive moth Prays oleae Bern. (Lepidoptera: Plutellidae), and the olive psyllid Euphyllura olivina Costa (Hemiptera: Psyllidae). Both are widely distributed in the circum-Mediterranean region and often cause costly damage to crops by reducing the number and/or size of the fruits, with a subsequent reduction in the yield and quality of the resulting fruit or oil (Tzanakakis, 2006). Four main natural enemies groups were considered: spiders (Araneae), ants (Hymenoptera: Formicidae), predatory Heteroptera (Hemiptera: Heteroptera) and parasitoids (Hymenoptera: Parasitica). Most of these groups have been reported as natural enemies of P. oleae (Morris et al., 1999).

Three different types of adjacent natural vegetation patches were found in and near the crop, namely herbaceous, large and small woody vegetation patches. Herbaceous vegetation was dominated by Anchusa sp., Anacyclus clavatus Desf. and Echium plantagineum L. Woody vegetation patches were divided into two groups namely large woody patches, dominated by trees which occupied the ravines surrounding the grove, and small woody patches, formed by shrubs occupying no more than a few square metres and located inside the grove, usually at hilltops, in areas inaccessible to machinery (Fig. 1). Large woody patches were dominated by Phyllirea angustifolia L. and Quercus rotundifolia Lam., whereas small woody patches were mainly composed by Genista

![Fig. 1. Location, elevation profile and arrangement of the experimental olive grove. (a) Location of the study area in southern Spain; and (b) distribution of the adjacent natural vegetation and ground cover and bare soil plots within the experimental grove.

hirsuta M. Vahl, Cistus albidus L., Cistus clusii Dunal, and Rosmarinus officinalis L.]

2.2. Experimental design and sampling

Each zone within the grove was divided into two subzones, each one occupied by either bare soil or ground cover, respectively. Two broad spectrum herbicides (glyphosate and oxyfluorfen) were sprayed in the bare soil subzones in early spring 2010 and 2011 to remove weeds. In subzones with ground cover, spontaneous herbaceous vegetation was allowed to grow in a 2.5 m wide strip between tree lines. The remaining area between trees was treated with the same herbicides as for bare soil. No insecticides were used in the grove for two years throughout the experiment. Ground cover was composed of herbaceous plants dominated by Medicago minima L., A. clavatus Desf., Hordeum leporinum L., Lolium rigidum Gaudich., and Bromus madritensis L.

The basic experimental unit in our study was the plot. There were a total of 12 plots, three in each subzone, which were sampled in different dates (Fig. 1). Plots were located equidistant from
each other in the two zones and subzones. Each plot had a square shape comprising 7 × 7 olive trees and an area of 4900 m²; as olive trees are 10 m apart from all other adjacent olive trees. Within each plot, a square of 4 × 4 olive trees was randomly selected at each date, corresponding to an area of 1600 m². Samples were collected every ten days, weather allowing, from late March to early October in 2010 and from early April to early July in 2011. Overall, there were 20 sampling dates in 2010 and nine sampling dates in 2011. A modified vacuum device CDC Backpack Aspirator G855 (John W. Hock Company, Gainsville, FL, USA) was used for 2 min to trap the arthropods in the canopy of each of the 16 olive trees. Once the arthropods were collected; they were stored in ice for transportation to the laboratory where they were classified. Parasitoids and spiders were determined to family level, ants were determined to genus level, and predatory Heteroptera to species level. Other groups of natural enemies, such as criocerids and coccinellids, were also collected but in low abundance, so they were not considered in this study. Phytophagous insects were determined to species level but analysed separately in a different study (D. Paredes, unpublished results). Samples from all 16 trees in each plot and date were pooled together to obtain a measure of abundance for each group of natural enemies.

2.3. Other explanatory variables

We digitalised all patches of natural vegetation using aerial photographs, and a 1 m × 1 m resolution grid was superimposed upon the resulting vector maps. A bivariate Gaussian kernel density function (Diggle, 1985) was computed from the 1 m × 1 m grid and its value was calculated for each plot in order to obtain a distance weighted measure of the influence of each natural vegetation type on that plot. A standard deviation of 120 m was chosen for the Gaussian kernel density function, as Milczyszy and Horton (2005) reported this as the maximum distance of dispersal of some groups of natural enemies in orchards. Other studies have reported even minimum distances of dispersal: 100 m for parasitoids and 50 m for spiders in vineyards (Thomson and Hoffmann, 2009); 60 m for arthropods in winter wheat crop (Holland et al., 2004); and 58 m for generalist predators of beetles in cereal crops (Collins et al., 2002). This measure also allowed incorporating the influence of vegetation at distances further than 120 m by assigning progressively lower weights, by means of the Gaussian density function, as we moved away from the plot. These analyses were performed with the R package ‘spatstat’ (Baddeley and Turner, 2005).

\[
\text{Abundance} = (a + \gamma) \exp \left( - \frac{(X - b)^2}{2c^2} \right)
\]

(3)

\[
\text{Abundance} = (a_j + \gamma) \exp \left( - \frac{(X - b)^2}{2c^2} \right)
\]

(4)

Because we conducted our study throughout two consecutive years, we also included year, a factor with two levels (2010, 2011), as an explanatory variable in the models. Differences between years are assumed to occur as a direct response of arthropod abundance to changes in climatic conditions and other non-measured variables that display inter-annual variability.

2.4. Data analysis

We used a Gaussian function to describe the predicted abundance of the main groups of natural enemies in response to time, since these groups typically show an increase in abundance during spring, reaching a maximum and declining afterwards. The Gaussian curve is a characteristic symmetric “bell curve” shape defined by three parameters: \( a \), \( b \) and \( c \). Parameter \( a \) is the height of the curve’s peak; in our case, the maximum abundance that a certain group could reach. The point in time when the highest abundance is reached is represented by parameter \( b \), which is days since the first of January, and represents the mean of the Gaussian curve. Parameter \( c \) represents the standard deviation and controls the width of the “bell”. Our basic model is represented by the equation below:

\[
\text{Abundance} = a \exp \left( - \frac{(X - b)^2}{2c^2} \right)
\]

(1)

where \( X \) is time, measured in Julian days since the first of January. Note that the account of days restarts every year.

The basic Gaussian function was modified to account for differences in the estimated parameters across treatments (ground cover and bare soil; parameter \( a \)) and years (2010, 2011; parameters \( a, b, c \)), as well as to incorporate the effect of different types of natural vegetation on the estimated curve’s peak (parameter \( a \)). We used likelihood methods and model selection as an alternative to traditional hypothesis testing (Johnson and Omland, 2004; Canham and Uriarte, 2006), for data analysis. Following the principles of likelihood estimation, we estimated model parameters that maximised the likelihood of observing the abundance measured in the field, given a suite of alternative models. Overall, we examined 40 different alternative models for each group of natural enemies and for their most representative lower taxonomic division.

The basic model was modified in order to allow the maximum abundance \( (a) \) to vary between treatments (bare soil, ground cover). Such models will be referred to henceforth as ground cover models (Eq. (2)).

\[
\text{Abundance} = a_j \exp \left( - \frac{(X - b_j)^2}{2c^2} \right)
\]

(2)

where \( a_j \) represents the maximum abundance of natural enemy groups in each treatment \( j \).

Eqs. (1) and (2) were further modified to include the effect of natural vegetation density. The effect of each type of natural vegetation (herbaceous, large woody and small woody patches) on parameter \( a \) was modelled separately by adding a set of new parameters \( (d_{\text{herb}}, d_{\text{lwp}}, d_{\text{swp}}) \). This is reflected by:

\[
\gamma = (d_{\text{herb}} \cdot X_{\text{herb}} + d_{\text{lwp}} \cdot X_{\text{lwp}} + d_{\text{swp}} \cdot X_{\text{swp}})
\]

(5)

where \( \gamma \) represents the effect of natural vegetation patches on the maximum abundance of natural enemy groups, as expressed by parameters \( d_{\text{herb}}, d_{\text{lwp}}, \) and \( d_{\text{swp}} \), which can be positive or negative. \( X_{\text{herb}}, X_{\text{lwp}}, \) and \( X_{\text{swp}} \) are the values of the kernel density function at each plot for herbaceous, large, and small woody vegetation patches respectively. A positive or negative effect of the natural vegetation represents contribution to (source vegetation patches) or removal from (sink vegetation patches) the grove, respectively (Duelli et al., 1990).

A variation of Eq. (4) would be that in which the effect of different types of natural vegetation patches on the abundance of natural enemy groups is allowed to vary between bare soil and ground cover plots. Such effects can be regarded as an interaction between
natural vegetation density and treatment. This model is described by equation:

\[
\text{Abundance} = (a_1 + \gamma_j) \exp \left( - \frac{(X - b_1)^2}{2c_1^2} \right) \tag{6}
\]

where \( \gamma_j \) represents the effect of natural vegetation patches on the maximum abundance of natural enemy groups in each treatment \( j \), which results from multiplying parameters \( a_1 \), \( b_1 \), and \( c_1 \). These parameters were estimated separately for bare soil and ground cover, by the observed values of herbaceous (Xherb), large (Xlwp) and small woody patch (Xswp) densities, respectively.

Inter-annual climatic variability could also influence the shape of the abundance response curve. Such an effect was included in former models (Eqs. (1)–(4) and (6)) by allowing all possible combinations of parameters \( a \), \( b \), and \( c \) to vary between years. The basic model allowing all three parameters to vary between years is expressed as:

\[
\text{Abundance} = a_1 \exp \left( - \frac{(X - b_1)^2}{2c_1^2} \right) \tag{7}
\]

We used simulated annealing, a global optimisation procedure, to determine the most likely parameters (i.e. the parameters that maximise the log-likelihood) given our observed data (Goffe et al., 1994). We used a Poisson error structure for all response variables. Alternative models were compared using the Akaike Information Criterion (AICc) corrected for small sample size (Burnham and Anderson, 2002). Models with a difference in AICc > 2 indicate that the worse model has virtually no support and can be omitted from further consideration. We used asymptotic two-unit support intervals to test the strength of evidence for individual maximum likelihood parameter estimates (Edwards, 1992). The R² of the model fit (1 – SSE/SST, sum of squares error (SSE) sum of squares total (SST)) of observed versus predicted was used as a measure of goodness-of-fit. All analyses were performed using the ‘likelihood’ package (Murphy, 2008) written for the R environment (R Development Core Team, 2010).

3. Results

A total of 47,938 arthropods were trapped during the two years of the study. Of these, 5,842 were spiders, 5,025 were ants, 14,651 were predatory Heteroptera, and 22,402 were parasitoids. Comparison of alternative models revealed that best fit the different response variables (Table 1). The resulting estimated parameters are shown in Table 2. A detailed account of the results for each group of natural enemies follows.

3.1. Spiders

The best fit model for spiders was found in the ground cover model, with differential effects of adjacent natural vegetation on bare soil and ground cover plots, and an effect of inter-annual variability on parameters \( b \) and \( c \) (AICc = 111636.0, R² = 0.59; Table 1). The peak of abundance was notably higher in ground cover (45 spiders/plot) than in bare soil plots (35 spiders/plot) (parameter \( a \); Table 2). The timing of the highest abundance and the width of the bell differed between years (parameters \( b \) and \( c \); respectively; Table 2).

Fig. 2a summarises the effects of different types of natural vegetation on spider abundance. A negative effect of herbaceous vegetation was found in both bare soil and ground cover plots (parameter \( d \); Table 2). Large woody vegetation patches had a positive effect on spider abundance in ground cover plots and a negative effect in bare soil plots (parameter \( d \); Table 2). Small woody vegetation patches always had a positive effect on spider abundance, but this effect was almost threefold in ground cover plots than in bare soil plots (parameter \( d \); Table 2). Patches that displayed a positive effect (mostly large woody vegetation, Fig. 2) remarkably increased spider abundance in ground cover plots, whereas this increase was less marked in bare soil plots (Fig. 3).

The models did not explain differences in abundance for the most representative spider families in the study area (Linphidae, \( R^2 = 0.42 \); Thomsidae, \( R^2 = 0.40 \); Salticidae, \( R^2 = 0.32 \); Table 3; Appendix 1) to the extent it did for all spider families together (\( R^2 = 0.72 \); Table 1).

3.2. Ants

The best model for ants resembled that of spiders, but with a poorer fit (AICc = 6560.82, \( R^2 = 0.14 \); Table 1). Therefore, we did not show the resulting estimated parameters for this group nor figures summarising the effects of different types of natural vegetation on its abundance.

3.3. Preyatory Heteroptera

The best-fit model for predatory Heteroptera only included the effect of natural vegetation and inter-annual variability on the abundance of this group (AICc = 6341.28, \( R^2 = 0.63 \); Table 2). The peak of abundance was higher in 2010 (114 predatory Heteroptera/plot) than in 2011 (80 predatory Heteroptera/plot) (parameter \( a \); Table 2). The point when the maximum abundance was reached and the width of the bell also differed between years (parameters \( b \) and \( c \); respectively; Table 2).

Fig. 2b summarises the effects of different types of natural vegetation on the abundance of predatory Heteroptera. Herbaceous vegetation and small woody vegetation patches displayed a positive effect on Heteropteran abundance (parameters \( d \) and \( d \); Table 2) whereas the effect of large woody vegetation patches was negative (parameter \( d \); Table 2). Overall, patches that displayed a negative effect (i.e. large woody vegetation, Fig. 2) exerted a more marked influence on the abundance of this group than patches that displayed a positive effect (small woody and herbaceous, Fig. 3).

At species level (Table 3), the best-fit models for three of the most abundant Heteropteran species were similar to that found for the main group (Appendix 1), with differences in the effects of different types of natural vegetation (Appendix 2). Two of these three species, Pseudolopha coccineus (Meyer Dur 1843) and Brachymecotoma ferruginata, sp. Bauna [in the same family Brachymecotomidae], did show a very good-fit (\( R^2 = 0.84 \) and \( R^2 = 0.73 \); Appendix 1), whereas Anthocoris nemoralis (Fabricius 1794) did not show such a good-fit as the other species (\( R^2 = 0.38 \); Appendix 1). The same poor-fit (\( R^2 = 0.38 \); Appendix 1) was found for Deraeocoris punctum (Rambur 1839), but in this particular case the best fit model included a positive effect of ground cover, differential effects of adjacent natural vegetation between bare soil and ground cover plots, and differences between years (Appendix 2).

3.4. Parasitoids

The best-fit model for parasitoids was the same as for spiders, and includes the effects of ground cover and adjacent natural vegetation (AICc = 161563.0, \( R^2 = 0.59 \); Table 1). The peak of abundance was 109 parasitoids/plot in ground cover plots and almost zero in bare soil plots (parameter \( a \); Table 2). The point of highest abundance and the width of the bell differed somewhat between years (parameters \( b \) and \( c \); respectively; Table 2).

Fig. 2c summarises the effects of different types of natural vegetation on parasitoid abundance. The effect of herbaceous vegetation was negative for parasitoid abundance in bare soil plots and positive in ground cover plots (parameter \( d \); Table 2). Woody vegetation had an overall positive effect on abundance. There were almost no differences in the effects of woody vegetation patches on parasitoid abundance between bare soil or ground cover plots (parameter \( d \); Table 2). However, the influence of small woody vegetation patches on abundance of ground cover plots was approximately one and a half times larger than that on bare soil plots (parameter \( d \); Table 2). Model predictions showed a remarkable effect of patches that displayed a positive effect (all vegetation types except for herbaceous vegetation in bare soil plots, Fig. 2) on the abundance of parasitoids (Fig. 3). This effect was greater in bare soil plots.

At lower taxonomic levels, best-fit models for families Scelionidae, Elasmidae and Braconidae (Table 3), were similar to the one reported for the main group (\( R^2 = 0.58 \), \( R^2 = 0.67 \), \( R^2 = 0.41 \) respectively; Appendix 1). All effects were similar for Scelionidae and Elasmidae families, whereas for Braconidae, there was a negative effect of herbaceous vegetation and small woody patches on ground cover plots (Appendix 2). No effects of ground cover or natural vegetation were found for Encyrtidae (\( R^2 = 0.47 \); Appendix 1).

4. Discussion

Two approaches have been traditionally adopted as an alternative to the use of insecticides in order to control insect pests in...
Table 1
Comparison of alternative models (using AICc) for the main arthropod natural enemy groups of insect pests in olive groves. The best model (lowest AICc) is indicated in boldface type. The number of parameters and $R^2$ refer to the best model. For brevity, we have presented in Table 1 only the most parsimonious (i.e. lowest AICc) of all possible models that include inter-annual variability with one, two or three parameters varying between years.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Spiders</th>
<th>Ants</th>
<th>Predatory Heteroptera</th>
<th>Parasitoids</th>
</tr>
</thead>
<tbody>
<tr>
<td>Basic model</td>
<td>No vegetation effect</td>
<td>General response</td>
<td>3093.54</td>
<td>7630.75</td>
</tr>
<tr>
<td></td>
<td>Inter-annual variability</td>
<td>2999.24</td>
<td>7481.92</td>
<td>6491.16</td>
</tr>
<tr>
<td></td>
<td>Natural vegetation effect</td>
<td>General response</td>
<td>2943.26</td>
<td>7175.32</td>
</tr>
<tr>
<td></td>
<td>Inter-annual variability</td>
<td>2849.77</td>
<td>7050.85</td>
<td>6341.28</td>
</tr>
<tr>
<td>Ground cover model</td>
<td>No vegetation effect</td>
<td>General response</td>
<td>2838.93</td>
<td>7534.68</td>
</tr>
<tr>
<td></td>
<td>Inter-annual variability</td>
<td>2750.40</td>
<td>7429.08</td>
<td>6786.72</td>
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<tr>
<td></td>
<td>Natural vegetation effect</td>
<td>General response</td>
<td>2740.33</td>
<td>7169.50</td>
</tr>
<tr>
<td></td>
<td>Inter-annual variability</td>
<td>2651.92</td>
<td>7064.01</td>
<td>6545.10</td>
</tr>
<tr>
<td></td>
<td>Natural vegetation effect x ground cover</td>
<td>General response</td>
<td>2737.32</td>
<td>6666.36</td>
</tr>
<tr>
<td></td>
<td>Inter-annual variability</td>
<td>2648.93</td>
<td>6560.82</td>
<td>6734.16</td>
</tr>
</tbody>
</table>

| Number of Parameters | 12 | 12 | 9 | 12 |

orchards: (1) implementation and maintenance of ground cover within the field; and (2) management of the adjacent natural vegetation. This study reveals that none of these approaches provide a unique response for all groups of arthropod natural enemies, and the combination of both can result in synergistic effects that are difficult to tell apart if analysed separately.

Overall, spiders, parasitoids, and the predatory Heteroptera D. punctum showed greater abundance in ground cover plots than in bare soil plots. The effects of the different types of adjacent natural vegetation and its interaction with ground cover were also dependent on the biology of the specific groups.

Spiders showed a strong preference for herbaceous habitats in previous studies (Sunderland and Samu, 2000; Clough et al., 2005; Schmidt and Tschamntke, 2005; Tschamntke et al., 2008; Pluess et al., 2010). When such habitats are found within the crop (i.e. ground cover), spiders can use trees, due to their proximity, as alternative

Table 2
Parameter estimates for the most parsimonious models of abundance of the natural enemy. Parameter a is the maximum abundance of natural enemy groups in each treatment (ground cover, bare soil) and year (2010, 2011); b and c represent the mean and standard deviation of the Gaussian curve in different years. The parameters $d_{\text{herb}}$, $d_{\text{lwp}}$ and $d_{\text{swp}}$ (herbaceous, large and small woody vegetation respectively) represent the effect of adjacent natural vegetation on the maximum abundance of natural enemy groups in bare soil and ground cover plots. Two-unit support intervals in brackets.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Spiders</th>
<th>Predatory Heteroptera</th>
<th>Parasitoids</th>
</tr>
</thead>
<tbody>
<tr>
<td>a</td>
<td>Ground cover</td>
<td>45</td>
<td>[44; 46]</td>
</tr>
<tr>
<td></td>
<td>Bare soil</td>
<td>35</td>
<td>[34; 36]</td>
</tr>
<tr>
<td></td>
<td>2010</td>
<td>114</td>
<td>[111; 116]</td>
</tr>
<tr>
<td></td>
<td>2011</td>
<td>110</td>
<td>[130; 136]</td>
</tr>
<tr>
<td>b</td>
<td>2010</td>
<td>256</td>
<td>183</td>
</tr>
<tr>
<td></td>
<td>2011</td>
<td>303</td>
<td>153</td>
</tr>
<tr>
<td>c</td>
<td>2010</td>
<td>0.0148</td>
<td>0.0311</td>
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<tr>
<td></td>
<td>0.0145; 0.0150</td>
<td>0.0092</td>
<td>0.0334</td>
</tr>
<tr>
<td></td>
<td>0.0091; 0.0094</td>
<td>38.10</td>
<td>[342.04; 446.71]</td>
</tr>
<tr>
<td>d_{\text{herb}}</td>
<td>Ground cover</td>
<td>−1141.07</td>
<td>−1444.25; −829.30</td>
</tr>
<tr>
<td></td>
<td>Bare soil</td>
<td>−1364.83</td>
<td>−1736.01; 987.83</td>
</tr>
<tr>
<td>d_{\text{lwp}}</td>
<td>Ground cover</td>
<td>−8929.13</td>
<td>−10,136.18; −7892.41</td>
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<tr>
<td></td>
<td>Bare soil</td>
<td>2436.06</td>
<td>[1182.47; 3655.55]</td>
</tr>
<tr>
<td>d_{\text{swp}}</td>
<td>Ground cover</td>
<td>5729.09</td>
<td>[2499.92; 8860.34]</td>
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<tr>
<td></td>
<td>Bare soil</td>
<td>3120.14</td>
<td>[232.78; 5957.58]</td>
</tr>
</tbody>
</table>
resources to find food and shelter, particularly after senescence of
the herbaceous vegetation in summer (Landis et al., 2000; Bianchi
et al., 2006). For this reason ground cover increases spider abun-
dance in the tree canopy. Patches of herbaceous vegetation around
the crop will likewise be attractive for spiders, but will have the
opposite effect for spiders found in the tree canopy, potentially
promoting migration outside the grove (Schmidt and Tschamske,
2005). In the absence of ground cover, large woody vegetation
may be more suitable for spiders than olive trees, possibly due to more
prey variety and availability (Harwood et al., 2001), thus decreasing
their abundance within the crop.

Models for ants were not particularly elucidating, as seen by the
poor fit attained in the best-fit model. A very different behaviour of
the two main genera (Tapinoma sp. and Camponotus spp.) might
be obscuring the general group response. Other factors such as
nest site availability, pressure from competing species and food
resources could explain better their distribution (Buczkowski and
Bennett, 2008).

Predatory Heteroptera were not affected by ground cover, except for D. punctum. Herbaceous vegetation and small woody
patches found nearby and within the olive grove did not exert an
important effect on abundance. Three out of the four species (P. coccineus, B. ferreri and D. punctum) were mirids found at nymphal
stage at the beginning of the season, which implies that they
thrive in the tree canopy without any further interaction with the
herbaceous layer. Large woody patches, on the contrary, had a
negative effect on the abundance of predatory Heteroptera. Such
a response might be related to intra-guild predation, since large
woody patches increase the abundance of spiders and ants within
the crop, which could prey on Heteroptera (Philpott and Armbrecht,
2006; Kobayashi et al., 2011). The absence of wings and the soft
body of the nymphal stage of this group make it vulnerable to the
attack by ants and spiders, supporting this hypothesis. The only
species initially found at the adult stage was A. nemoralis, which
has been reported as a species that overwinters in the surrounding
natural habitat (Horton and Lewis, 2000). For this species, the mod-
els predicted a positive effect, instead of negative effect, of large
woody patches. Aditionally, D. punctum reached higher abundances
in ground cover plots than in bare soil plots. This could be related
to a higher predation by Tapinoma sp. in bare soil plots, which was
observed to appear at the same time in the olive canopy (results
not shown).
Ground cover had a large positive effect on parasitoids. The presence of adjacent natural vegetation also increased their abundance within the olive grove in accordance with the results found by Boccaccio and Petacchi (2009). Their dependence on herbaceous habitats, within or around the crop, as well as on woody vegetation, is much stronger than in other groups. In fact, in the absence of these structures (i.e. in bare soil plots with no adjacent natural vegetation) the predicted abundance for this group is zero.
This could be because parasitoids, as specialist enemies, respond more strongly to landscape complexity at smaller scales (Chaplin-Kramer et al., 2011), highlighting the importance of ground cover to enhance their presence in orchards with a lower density of adjacent natural vegetation, and emphasising the relevance of the analysis of the interaction between ecological infrastructures to understand the distribution of natural enemies within the crop.

4.1. Management implications

Overall, ground cover seems to increase the abundance of most natural enemies and, therefore, this seems a promising option in order to enhance their populations (Danne et al., 2010; Silva et al., 2010). Small patches of woody vegetation interspersed within the crop play a minor role in sustaining populations of natural enemies, but contribute to enhance the overall heterogeneity at the landscape scale (Clough et al., 2005). Large woody patches can help increase the populations of spiders and parasitoids, by creating alternative habitats that might provide a source of migrating individuals into the crop (Thomas et al., 1991; Bianchi et al., 2006). Yet in the absence of ground cover, such habitats can be more attractive for spiders, probably due to the scarcity of resources that ground cover provides, such as alternative preys (Costello and Daane, 1998), which ultimately decrease their abundance within the crop. The presence of ground cover increases the positive effect that patches of herbaceous vegetation have on the abundance of parasitoids and reduces the negative effect on spiders reported for bare soil crops. This is a novel result that will help design habitat management strategies in olive groves, since the use of both complementary approaches produces a total effect that maximises the abundance of natural enemies within the crop.

Since the ultimate goal of habitat management strategies is to prevent insect pests, further research is needed to investigate whether the increase reported in the abundance of natural enemies will have an effect on the abundance of insect pests, as well as to elucidate the potential ecological mechanisms that might be involved (see Chaplin-Kramer et al., 2011).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agee.2013.04.016.

References


