Ant versus bird exclusion effects on the arthropod assemblage of an organic citrus grove

JOSEP PIÑOL,1,2 XAVIER ESPADALER,1,2 NÚRIA CAÑELLAS,3 JORDI MARTÍNEZ-VILALTA,1,2 JOSÉ A. BARRIENTOS1 and DANIEL SOL2 1Department of Animal Biology, Plant Biology and Ecology, Universitat Autònoma de Barcelona, Spain, 2Centre for Ecological Research and Forestry Applications (CREAF), Universitat Autònoma de Barcelona, Barcelona, Spain and 3I. Rubiò i Tudurí, Marquès de Comillas, 36, 08038 Barcelona, Spain

Abstract. 1. Predation-exclusion experiments have highlighted that top-down control is pervasive in terrestrial communities, but most of these experiments are simplistic in that they only excluded a single group of predators and the effect of removal was evaluated on a few species from the community. The main goal of our study was to experimentally establish the relative effects of ants and birds on the same arthropod assemblage of canopy trees.

2. We conducted 1-year long manipulative experiments in an organic citrus grove intended to quantify the independent effects of bird and ant predators on the abundance of arthropods. Birds were excluded with plastic nets whereas ants were excluded with sticky barriers on the trunks. The sticky barrier also excluded other ground dwelling insects, like the European earwig Forficula auricularia L.

3. Both the exclusion of ants and birds affected the arthropod community of the citrus canopies, but the exclusion of ants was far more important than the exclusion of birds. Indeed, almost all groups of arthropods had higher abundance in ant-excluded than in control trees, whereas only dermapterans were more abundant in bird-excluded than in control trees. A more detailed analysis conducted on spiders also showed that the effect of ant exclusion was limited to a few families rather than being widespread over the entire diverse spectrum of spiders.

4. Our results suggest that the relative importance of vertebrate and invertebrate predators in regulating arthropod populations largely depends on the nature of the predator–prey system.

Key words. Forficula auricularia, Mediterranean, spiders, Theridiidae, Thomisidae, Xysticus.

Introduction

Since the pioneering work of Paine (1966), the experimental exclusion of predators has been regarded as a major tool for uncovering interactions among species in ecological communities. Such exclusions have revealed that predators often exert top-down control on herbivores and that the effect sometimes cascades down to primary producers in terrestrial ecosystems (Marquis & Whelan, 1994; Pace et al., 1999; Schmitz et al., 2000; Halaj & Wise, 2001). Whereas most predator exclusions do exclude multiple predators, studies excluding more than one predator group factorially on a shared prey assemblage to allow measuring the individual effects of each group are rather scarce (Pacala & Roughgarden, 1984; Spiller & Schoener, 1994; Halaj et al., 1997; Hooks et al., 2003; Philpott et al., 2004; Mooney, 2007; Kalka et al., 2008; Williams-Guillén et al., 2008). Following Philpott et al. (2004) and Mooney (2007), we argue that the simultaneous exclusion of several predators might provide a more realistic view on the top-down processes that regulate communities, providing in addition important clues about the appropriateness of aggregating species into trophic groups to describe food webs (Philpott et al., 2004) and, in a more applied setting, informing us about which predators are worth
manipulating to improve the control of agricultural and forest insect pests.

Two of the most important predator groups of terrestrial arthropod-dominated communities are ants and birds. Ant and bird exclusion from communities has frequently been shown to increase herbivore abundance (Schmitz et al., 2000; Halaj & Wise, 2001; and references therein). The meta-analytical studies of Schmitz et al. (2000) and Halaj and Wise (2001) also showed that predatory effects were of similar magnitude for vertebrate and invertebrate predators. However, a more controversial picture emerges when one focuses on the few studies that excluded ants and birds from the same community and that studied their effect on the entire arthropod assemblage rather than on one or a few species (Philpott et al., 2004; Mooney, 2007). While Philpott et al. (2004) found that birds had stronger negative effects on arthropods than ants in a coffee farm in Chiapas (Mexico), Mooney (2007) reported that the effects of birds were consistently weaker than those of ants in a ponderosa pine stand in Colorado (U.S.A.). It is important to remember that ants have a dual role in ecological communities, as they are not only arthropod predators, but also hemipteran mutualists (Styrsky & Eubanks, 2007).

Here we present a comparative study of the relative effects of the exclusion of the ant and bird communities on a terrestrial arthropod assemblage. The ecological setting of this study, a Mediterranean organic citrus grove, is more similar to the coffee plantation of Philpott et al. (2004) than to the natural forest of Mooney (2007). Like Philpott et al. (2004), we expected that studying a system (an organic farm) that is less diverse than a natural forest would facilitate the identification of functional relationships that are difficult to detect in natural ecosystems. We studied all canopy arthropods present in the trees, but we paid particular attention to the effect of ant and bird exclusion on spiders. We selected spiders as a test group because of their abundance in the community, and because they often increase their abundance following the removal of both ants (Mody & Linsenmair, 2004; Mooney, 2007) and birds (Gruner, 2004; Gunnarsson, 2008). As spiders are intermediate predators, their consumption by ants and birds has to be considered in the context of intra-guild predation; in particular, if spider abundance was affected by ant or bird exclusion, the effect could cascade down to other arthropod groups in their diet. In addition, given the variety in size and behaviour of spiders, the effect of ant and bird predation on them could be family-specific. We asked three main questions: (i) Do birds and/or ants affect arthropod assemblages in canopy trees? (ii) Do birds and ants differ in their relative effects on arthropods? (iii) Is the effect of birds and ants different for different families and species of spiders?

**Material and methods**

**Study site**

The study site was a plantation of citrus trees located at La Selva del Camp (Tarragona, northeast Spain; 41°13′5′′N, 1°9′7′′E). Climate is Mediterranean, with a rainy spring and autumn and a dry winter and summer. The grove consisted of ca 300 Clementine trees grafted on the hybrid rootstock Carrizo citrange (Poncirus trifoliata (L.) Raf. × Citrus sinensis (L.) Osb.). The grove complies with all organic agriculture standards, i.e., no pesticides, fungicides or herbicides were applied and only organic manure was used as fertiliser. Trees were regularly watered during dry periods.

**Bird- and ant-exclusion experiments**

Twenty-four trees from three rows of 23 trees each planted in 1999 were randomly chosen. Each of these trees was randomly assigned to one of three groups: control trees ($n = 8$), to which birds and crawling insects had free access; bird-excluded trees ($n = 8$) that were covered with a net to prevent bird access to their canopies (exclosures); and banded trees ($n = 8$) in which a sticky barrier was applied to the trunk to prevent the access of crawling insects to the canopies. As we were interested in the main effects of ants and birds, we did not perform a fourth treatment with both predators excluded; consequently possible additive, competitive, and synergistic effects of ants and birds were not explored (Haemig, 1994). The trunk-barrier consisted of a polibutene-based sticky barrier (Rata Stop®) applied on an alimentary plastic film tightly attached over a padding cylinder in contact with the trunk (Samways & Tate, 1985). The trunk barrier was highly effective in keeping ants away from the canopies but, occasionally, some were still found in the experimental trees. Ants normally found their way into the canopy via tall weeds or, more often, by crossing the glue barrier using dead insects as stepping stones. Trees were inspected on a weekly basis and, when a problem was detected it was immediately solved by cutting the tall weeds or by adding more glue to the trunk barrier. Trees had a trunk diameter of $8.4 \pm 1.2$ cm (mean $\pm$ SD) and a crown diameter of ca 2.5 m. The net for bird exclusion (mesh $20 \times 20$ mm) was supported by a parallelepipedic metallic structure with a base of $3 \times 3$ m and 2 m height that covered the whole tree. Mesh size allowed vespid wasps inside the exclosures, but probably prevented the access of larger arthropods like butterflies. Treatments were established in January 2006 and thereafter, trees were sampled on a monthly basis. The exclosures were dismantled after the November 2006 sampling. Thus, there is one pre-experiment sample (January), and 10 monthly samples from control and experimental trees (February to November).

**Arthropod sampling and classification**

Arthropods on the tree canopy were sampled once a month, using beating trays, captured with entomological pooters and immediately preserved in 70% alcohol. The collection tray was a white square of 0.5 m$^2$, normally positioned ca 50 cm below the foliage. Arthropods were dislodged with three vigorous hits in the tree crown; this was repeated twice at opposite sides of the tree on each sampling date. In the laboratory, all spiders (Araneae), beetles (Coleoptera), bugs (Hemiptera: Heteroptera), earwigs (Dermaptera), and ants (Hymenoptera: Formicidae) were identified to species. Insects of other groups were also counted and identified to family or order.
As coleopterans and heteropterans were determined to species level, it was possible to calculate the total number of predatory and herbivorous species in each sample. Predators were calculated as the sum of all Araneae, all Neuroptera, predatory Coleoptera (mainly Coccinellidae, but also a few Staphylinidae, Cantharidae, Malachidae, and Carabidae), and predatory Heteroptera (Anthocoridae, Reduviidae, and some Miridae and Pentatomidae). Herbivores were calculated as the sum of Hemiptera: Sternorrhyncha, herbivorous Coleoptera (Apionidae, Elateridae, Curculionidae, and Chrysomelidae), herbivorous Hemiptera: Heteroptera (some Miridae, most Pentatomidae and Lygaeidae, Tingidae, Phyrrocoridae, and Alydidae), Thysanoptera, Lepidoptera, Orthoptera, and the fly Ceratitis capitata (Wiedemann) (Diptera: Tephritidae).

Bird censuses

Monthly censuses were conducted during the 2006 breeding season (April to July) to roughly estimate the abundance of insectivorous bird species at the studied grove and variation over time. Each census consisted of two 10-min point counts (Bibby et al., 2000) conducted on two consecutive days. The first count was performed approximately 1 h before sunset, and the second count was conducted 1 h after sunrise. Upon arrival we waited 10 min, and then all birds seen or heard from the centre of the grove were recorded, indicating whether they had been detected inside or outside the grove. For the purpose of this study, birds were classified as insectivores if their diet consisted at least partially of insects during the nesting season (according to Cramp, 1988–1994).

Spider diversity

The diversity of spiders was estimated in each sample (24 trees × 11 months = 264 samples) with the number of species \( S \) and as the Shannon diversity index \( H \):

\[
H = - \sum_{i=1}^{i=S} p_i \cdot \log_2 p_i
\]

where \( p_i \) is the proportion of individuals of each species (up to a total of \( S \) species) in a sample.

In some samples, not all specimens could be identified to species, thus we proceeded conservatively when counting the number of species. By doing so, the reported values of \( S \) and \( H \) must be considered as a minimum value of spider diversity.

Analyses

The first step in the analysis was a MANOVA of all arthropod groups abundance with ‘treatment’ as between-subjects factor. The response variables were the cumulative abundance of each group in each tree from February to November. Two different MANOVAs were conducted, one to compare ant-excluded versus control trees, and a second one to compare bird-excluded versus control trees.

When the MANOVAs showed a significant treatment effect, we proceeded with the analysis of the effect on the abundance of each individual arthropod group, spider family, and on the diversity of spider species using a repeated-measures ANOVA design, with ‘month’ as a within-subjects factor and ‘treatment’ as between-subjects factor. Finally, we conducted an additional set of repeated measures ANOVAs comparing ant-excluded versus bird-excluded trees. Only 10 months were considered (February to November), as the January sampling was conducted before the establishment of the treatments. When the interaction between treatment and time was statistically significant, we conducted Tukey HSD post hoc analyses to highlight periods where the difference between treatments was statistically significant. Abundance were square-root transformed to achieve normality. Analyses were conducted with Statistica v.6 (StatSoft Inc., 2001).

Results

Bird and ant communities

The abundance of insectivorous and omnivorous passerines in the study area remained relatively high over the study period, although was lower during the last census, conducted in July (Table S1). In summary, a total of 13 insectivorous or omnivorous species were detected, five of them being known foliage gleaners. The most abundant species were the Spotless Starling (Sturnus unicolor Temminck), Sturnidae and two sparrows (Passer domesticus L. and Passer montanus L.; Passeridae) which, together, included 74% of all detected individuals. These three species had important nesting populations in several large, farm-like buildings nearby the study grove; one of them being within less than 50 m. Other abundant bird species included Serinus serinus L., Carduelis carduelis L. (Fringillidae), Parus ater L. (Paridae) and Sylvia melanocephala Gmelin (Sylviidae).

Ten species of ants were found in the canopies of the trees sampled by beating trays. Of these, Lasius grandis Forel (43% of the individuals), Plagiolepis pygmaea (Latreille) (31%), Formica rufibarbis Fabricius (16%), Tapinoma nigerimur (Nylander) (5%), and Formica subrufa Roger (4%) were the most abundant. All these species, except P. pygmaea, which is nectarivorous, are known aphid tenders. The remaining less abundant species were Pheidole pallidula (Nylander), Camponotus cruentatus (Latreille), C. sylvaticus (Olivier), C. aethiops (Latreille), and Tetramorium semilaeve André.

Effect of bird exclusion and ant exclusion on arthropod groups’ abundance

The beating trays produced ca 13 000 arthropod individuals, considering all 24 control and experimental trees and 11 months of sampling. Of these, 30.8% were Psocoptera, 16.1% Araneae, 13.0% non-Aphididae Hemiptera: Sternorrhyncha, 10.6% Hymenoptera: Formicidae, 8.8% Coleoptera, 6.2% Diptera, 6.2% Aphididae Hemiptera: Sternorrhyncha, 2.5% non-Formicidae Hymenoptera, 2.4% Dermaptera, 1.9%...
Hemiptera: Heteroptera, 0.9% Neuroptera, and the rest were a few Collembola, Thysanoptera, Lepidoptera, and Orthoptera.

Before the start of the experiment (January), MANOVAS did not show any difference between treatment and control trees in the abundance of arthropods (Ant-excluded vs. control: Wilks $\Lambda = 0.43$, $F_{8,7} = 1.15$, $P = 0.43$; Bird-excluded vs. control: Wilks $\Lambda = 0.55$, $F_{8,7} = 0.69$, $P = 0.69$).

**Effects on ants and other ground-dwelling arthropods.** As planned, there were more ants in control trees than in banded trees (Fig. 1a; Table 1). Only on one occasion was there a noticeable number of ants in the canopies of the banded trees (Fig. 1a); the conspicuous peak of ants of July in banded trees corresponded almost entirely to 75 individuals of the tiny *P. pygmaea* sampled from a single tree. As the exclusion of this single sample from the statistical analyses did not change appreciably any result, we kept the data from this tree in the database. There were no differences in ant abundance between bird-excluded and control trees ($F_{1,14} = 0.73$, $P = 0.41$; Fig. 1a).

The sticky barrier was also effective against other crawling insects, such as the earwig *Forficula auricularia* L., the only dermapteran in the community (Fig. 1b). Consequently, this ant-exclusion experiment has to be interpreted as the exclusion of ants and other ground-dwelling arthropods. However, to keep it short, we will use the term ant-exclusion throughout the paper. On the other hand, bird-excluded trees had a significantly higher abundance of earwigs than control trees ($F_{1,14} = 5.78$, $P = 0.03$; Fig. 1b).

**Effects on other arthropod groups.** MANOVA showed a significant overall effect of ant-exclusion on the abundance of other arthropod groups (Wilks $\Lambda = 0.13$, $F_{9,6} = 4.14$, $P = 0.049$; ant and earwig abundance were not included as response variables as they were purposely excluded by the experimental treatment). On the contrary, the MANOVA comparing bird-excluded versus control trees revealed no significant overall effect of birds on the abundance of all other arthropod groups (Wilks $\Lambda = 0.13$, $F_{11,4} = 2.53$, $P = 0.19$).

The difference between ant-excluded and control trees was statistically significant for all individual groups except Heteroptera and non Aphididae Hemiptera: Sternorrhyncha (mainly scale insects, especially *Ceroplastes sinensis* Del Guercio) (Fig. 1c–k; Table 1). There were also more carnivores in ant-excluded than in the control ones ($P < 0.001$; Fig. 2; Table 1). Herbivores were also more abundant in ant-excluded trees, but the difference was only marginally significant ($P = 0.08$; Fig. 2; Table 1).

All arthropod groups, except ants and earwigs, had a significant interaction ant-exclusion × time (Table 1). Post hoc analyses of the interaction revealed that ant exclusion did not have a significant effect on any group until May. Later on there were significant effects on some groups every month except in August (Fig. 1).

A second set of repeated measures ANOVA comparing the treatments of ant exclusion versus bird exclusion showed that the abundance of all arthropod groups (except Heteroptera and non Aphididae Hemiptera: Sternorrhyncha) differed between treatments (Table S2). This result reinforces the main outcome of the experiment, i.e. that in this particular grove and year, the effect of ants was larger than the effect of birds on the abundance of canopy arthropods.

**Spider community**

Spiders belonged to 15 families. The most abundant ones were Theridiidae (31.4% of the captured individuals), Philodromidae (16.6%), Araneidae (15.7%), Salticidae (8.5%), Thomisidae (8.0%), and Linyphiidae (6.9%). In the statistical analyses of the next section, these six most abundant families were considered separately, whereas the remaining nine less abundant families were pooled together. A complete list of the spiders of the community and their abundance is given as supplementary material (Table S3).

Before the start of the experiment (January), there were no differences between treatment and control trees in the abundance of any of the families of spiders (Ant-excluded vs. control: Wilks $\Lambda = 0.52$, $F_{7,8} = 1.04$, $P = 0.47$; Bird-excluded vs. control: Wilks $\Lambda = 0.70$, $F_{7,8} = 0.49$, $P = 0.81$).

**Effect of bird exclusion and ant exclusion on spiders**

Abundance of spiders was higher on ant-excluded compared to control trees mainly due to increases of Theridiidae and Thomisidae (Table 2; Table S4). The increase in Theridiidae abundance in ant-excluded compared to control trees started in late summer and remained high during autumn (Fig. 3a). In contrast, the higher abundance of Thomisidae in ant-excluded trees occurred only in June (Fig. 3e), and it was due to a single genus, *Xysticus*. As the *Xysticus* peak of June followed the aphid peak of May, we calculated the correlation (log–log) between the abundance of *Xysticus* sp. in June and the abundance of aphids in May on a tree basis, and found it to be statistically significant ($r = 0.53$; $n = 24$; $P = 0.008$). The pool of the nine less abundant families was also slightly more abundant in ant-excluded than in control trees in the second half of the year (Fig. 3g; Table 2). It was mainly due, at its peak of August to September, to Miturgidae (*Cheiracanthium* sp.) and Clubionidae (*Clubiona genevensis* L. Koch). One more spider family, Philodromidae, had a significant treatment × time interaction (Table 2). The post hoc analysis showed that the abundance of Philodromidae was higher in ant-excluded trees only in July (Fig. 3b).

Ant exclusion significantly increased the diversity of the spider assemblage, measured both as the number of species $S$ ($P < 0.001$ Fig. 4a; Table 2) or as the Shannon diversity index $H$ ($P = 0.007$ Fig. 4b; Table 2). On the contrary, neither $S$ nor $H$ was affected by the exclusion of birds (Fig. 4; $F_{1,14} = 0.48$, $P = 0.50$ for $S$ and $F_{1,14} = 0.13$, $P = 0.72$ for $H$).
Fig. 1. Temporal variation of arthropod abundance in ant-excluded (banded), bird-excluded (exclosures) and in control trees from January to November 2006. Each value corresponds to the mean (±SE) value of individuals per beat tray sample in each of the eight trees of each treatment. When the interaction treatment × time of an arthropod group was significant (Table 1) it is also shown in which months the abundance was significantly different between control and ant-excluded trees according to a Tukey HSD post hoc comparison. Significance: ***P < 0.001; **P < 0.01; *P < 0.05. Codes: For, Hymenoptera: Formicidae; Der, Dermaptera; Pso, Psocoptera; Ste, non-Aphididae Stenorrhyncha; Ara, Araneae; Col, Coleoptera; Dip, Diptera; Aph, Hemiptera: Stenorrhyncha: Aphididae; Hym, non-Formicidae Hymenoptera; Neu, Neuroptera; Het, Hemiptera: Heteroptera.
Table 1. Summary of a repeated measures ANOVA of arthropod abundance between control and ant-excluded trees from February to November.

<table>
<thead>
<tr>
<th>Group</th>
<th>Treatment</th>
<th>Time</th>
<th>Treatment × time</th>
</tr>
</thead>
<tbody>
<tr>
<td>For</td>
<td>74.13</td>
<td>4.08</td>
<td>1.92</td>
</tr>
<tr>
<td>Der</td>
<td>85.58</td>
<td>2.59</td>
<td>1.94</td>
</tr>
<tr>
<td>Pso</td>
<td>25.49</td>
<td>13.91</td>
<td>4.33</td>
</tr>
<tr>
<td>Ste</td>
<td>0.32</td>
<td>12.45</td>
<td>3.87</td>
</tr>
<tr>
<td>Ara</td>
<td>30.15</td>
<td>17.81</td>
<td>3.70</td>
</tr>
<tr>
<td>Col</td>
<td>17.12</td>
<td>15.68</td>
<td>7.33</td>
</tr>
<tr>
<td>Dip</td>
<td>14.04</td>
<td>19.27</td>
<td>2.35</td>
</tr>
<tr>
<td>Aph</td>
<td>6.11</td>
<td>29.43</td>
<td>3.73</td>
</tr>
<tr>
<td>Hym</td>
<td>13.71</td>
<td>6.09</td>
<td>5.11</td>
</tr>
<tr>
<td>Neu</td>
<td>15.35</td>
<td>2.91</td>
<td>2.54</td>
</tr>
<tr>
<td>Het</td>
<td>2.22</td>
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<td>2.13</td>
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<tr>
<td>Car</td>
<td>21.85</td>
<td>28.20</td>
<td>7.65</td>
</tr>
<tr>
<td>Her</td>
<td>3.47</td>
<td>14.07</td>
<td>2.31</td>
</tr>
</tbody>
</table>

Codes for arthropod groups: For, Hymenoptera: Formicidae; Der, Dermaptera; Pso, Psocoptera; Ste, non Aphididae Stenorrhyncha; Ara, Araneae; Col, Coleoptera; Dip, Diptera; Aph, Stenorrhyncha: Aphididae; Hym, non-Formicidae Hymenoptera; Neu, Neuroptera; Het, Heteroptera; Car, all carnivores; Her, all herbivores.

Discussion

The reported experiments showed that both the exclusion of ants and birds affected the arthropod community of the studied citrus canopies and that the exclusion of ants was far more important than the exclusion of birds. Indeed, almost all groups of arthropods had higher abundance in ant-excluded than in control trees, whereas only dermapterans were significantly more abundant in bird-excluded than in control trees. Our results are thus similar to those of Mooney (2007) who also reported that the effects of birds were consistently weaker than those of ants on the arthropod community of _Pinus ponderosa_ trees of the Rocky Mountains and contrast with those of Philpott et al. (2004) who found a stronger effect of birds than ants in the canopies of a coffee plantation. Tamhuanpaee et al. (2001) also reported a more important effect of birds than ants, but in their study the focus was on the abundance of a single caterpillar species rather than on the entire arthropod assemblage.

The reasons why ants and birds vary in the top-down control they exert on arthropod communities remain obscure, but they may be related to the species richness of insectivorous birds in a given community. A recent meta-analysis of bird predation on arthropods in tropical agroecosystems (Philpott et al., 2009) showed that no functional attribute of the bird community predicted arthropod removal better than species richness. They provide an empirical equation relating arthropod reduction and number of species of insectivorous birds (Fig. 2 of Philpott et al., 2009). Using the insectivorous species richness of our community (13; Table S1) in the equation predicts a 0.6% of arthropod reduction by birds. Such a small value would not be detectable experimentally, which is in agreement with our results.

![Fig. 2. Temporal variation of carnivore (a) and herbivore (b) abundance in ant-excluded (banded), bird-excluded (exclusion) and control trees from January to November 2006. Each value corresponds to the mean (±SE) value of individuals per beat tray sample in each of the eight trees of each treatment. When the interaction treatment × time was significant (Table 1) it is also shown in which months the abundance was significantly different between control and ant-excluded trees according to a Tukey HSD post hoc comparison. Significance: ***P < 0.001; **P < 0.01; *P < 0.05.](image-url)

Table 2. Summary of a repeated measures ANOVA of the abundance of spider families and of spiders’ diversity (both measured as the number of species _S_ and as the Shannon diversity index _H_).

<table>
<thead>
<tr>
<th>Group</th>
<th>Treatment</th>
<th>Time</th>
<th>Treatment × time</th>
</tr>
</thead>
<tbody>
<tr>
<td>The</td>
<td>23.67</td>
<td>13.14</td>
<td>3.27</td>
</tr>
<tr>
<td>Phi</td>
<td>3.86</td>
<td>3.74</td>
<td>2.02</td>
</tr>
<tr>
<td>Ara</td>
<td>2.75</td>
<td>6.37</td>
<td>1.22</td>
</tr>
<tr>
<td>Sal</td>
<td>1.57</td>
<td>8.89</td>
<td>0.96</td>
</tr>
<tr>
<td>Tho</td>
<td>18.15</td>
<td>6.80</td>
<td>3.40</td>
</tr>
<tr>
<td>Lin</td>
<td>0.31</td>
<td>6.10</td>
<td>0.74</td>
</tr>
<tr>
<td>Oth</td>
<td>8.65</td>
<td>3.73</td>
<td>0.99</td>
</tr>
<tr>
<td>S</td>
<td>19.12</td>
<td>15.02</td>
<td>2.98</td>
</tr>
<tr>
<td>H</td>
<td>9.90</td>
<td>9.71</td>
<td>0.96</td>
</tr>
</tbody>
</table>

Between groups factor: treatment (control vs. ant-excluded); within groups: time (February to November). Codes for spider families: The, Theridiidae; Phi, Philodromidae; Ara, Araneidae; Sal, Salticidae; Tho, Thomisidae; Lin, Linyphiidae; Oth, all other minor families added up.

In the studied community ants play a dual role, as they act as hemipteran mutualists and as generalist predators. The increased abundance of Coleoptera (mostly the predaceous
Fig. 3. Temporal variation of the spider’s abundance in ant-excluded (banded trees), bird-excluded (exclosures), and in control trees from January to November 2006. The six most abundant families are considered individually (a–f) and the remaining nine families are pooled together (g). Each value corresponds to the mean (±SE) value of spiders per beat tray sample in each of the eight trees of each treatment. When the interaction treatment × time of a spider family was significant (Table 2) it is also shown in which months the abundance was significantly different between control and ant-excluded trees according to a Tukey HSD post hoc comparison. Significance: ***P < 0.001; **P < 0.01; *P < 0.05.
Earwigs were the only group of arthropods that changed their abundance following bird exclusion. Gunnarsson et al. (2009) also reported a very important increase of earwig abundance in a bird-exclusion experiment in Sweden. This would suggest that earwigs are an important prey of insectivorous birds in the study site, consistent with what is known about the diet of these bird species (Table S1). This result was not surprising also, because the earwig Forficula auricularia is the largest common arthropod species in the canopies of the grove, making them a valuable prey item for insectivorous birds. Maybe one important reason for not detecting significant effects of birds on the abundance of more arthropod groups in this study is that most of them are in general rather small and, probably, not really attractive prey for gleaning birds.

The effect of bird predation on earwigs, combined with their possible role in aphid control, points to earwigs as an important species in the studied grove community. Earwigs have also proved to be able to control populations of aphids in apple orchards of temperate areas in Europe (Solomon et al., 2000), the U.S.A. (Carroll & Hoyt, 1984), Australia (Nicholas et al., 2005), and New Zealand (Suckling et al., 2006). Since less environmentally aggressive agricultural practices that favour earwig lifestyle, such as integrated pest management and organic agriculture, are currently expanding, their role as generalist predators in the control of agricultural pests could become more important in the near future (Piñol et al., 2009b).

The negative effect of ants on spiders has already been documented in previous studies (Buckley, 1990; Heikkinen, 1999; James et al., 1999; Sanders & Plattner, 2007; but see Vogt et al., 2002). Nevertheless, the possibility that this effect varies according to spider identity has been more rarely reported (but see Halaj et al., 1997). Our results showed that the negative effect of ants on spiders was not present in all spider groups, but it manifested only in a subset of families, especially in Thomisidae and Theridiidae. It is worth noticing that Thomisidae are cursory and Theridiidae are web-spinning spiders, so the effect of ants is not limited to a single functional group of spiders. The case of Thomisidae is especially striking because ants affected one single species, Xysticus sp. Recently, Birkofer et al. (2008) clearly showed using molecular markers that Xysticus cristatus (Clerck) feed on aphids and this could explain the peak of Thomisidae in June (Fig. 3) following the peak of aphids in May (Fig. 1). The negative effect of ants on spider diversity complies with the classical view that predator exclusion reduces prey diversity (Paine, 1966). Unexpectedly, and in contrast with many results reporting a marked negative effect of birds on spiders (Greenberg et al., 2000; Philpott et al., 2004; Recher & Majer, 2006; Gunnarsson, 2008), we could not detect any significant effect of bird exclusion on spider abundance or assemblages through the year.

In conclusion, in the studied citrus grove, both birds and ants affected the composition and abundance of the arthropod community of the tree canopies. However, the effect of bird exclusion was weaker than that of ant exclusion. The exclusion of ants, and other ground-dwelling arthropods like earwigs, had a widespread effect on most groups of arthropods, whereas the exclusion of birds only increased the abundance of earwigs. Like in previous studies of ant and bird exclusion on the same

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**Fig. 4.** Temporal variation of the diversity of spiders measured as the number of species (a) or Shannon’s diversity index (b) in ant-excluded (banded), bird-excluded (exclosures) and in control trees from January to November 2006. Each value corresponds to the mean (+SE) value of individuals sampled in each of the eight trees of each treatment. When the interaction treatment × time was significant (Table 2) it is also shown in which months the diversity was significantly different between control and ant-excluded trees according to a Tukey HSD post hoc comparison. Significance: ***P < 0.001; **P < 0.01; *P < 0.05.

Coccinellidae), Araneae, Neuroptera, and non-Formicidae Hymenoptera (mostly Chalcidoidea parasitoids) would fit with the notion that ants exert physical interference on aphid and coccid enemies (Bartlett, 1961; Way, 1963; Bishop & Bristow, 2001; Kaneko, 2003). The increased abundance of other herbivores or detritivorous insects like Psocoptera and Diptera and, in general, of all arthropod groups is consistent with the generalist predatory role of ants.

The higher abundance of aphids in ant-excluded than in control trees is more difficult to explain for three reasons: (i) the most abundant ant in the canopies was Lasius gran- dis, an aphid-tending specialist (Paris & Espadaler, 2009); (ii) all aphid species (the most abundant ones were Aphis spiraeola Patch and A. gossypii Glover) found in the grove are ant tended (Suay-Cano et al., 2002); and (iii) carnivores as a whole and several groups of arthropods that contain important aphid predators were also more abundant in ant-excluded trees. The most likely explanation for this phenomenon is the concurrent exclusion of earwigs with ants. Earwigs are known to predate on aphids (Solomon et al., 2000) and in this particular site the negative effect of earwigs on aphid populations seems to be stronger that the positive effect of aphid-tending ants (Piñol et al., 2009a).
prey assemblage (Philpott et al., 2004; Mooney, 2007), ants and birds differed in their effects both qualitatively and quantitatively; thus, aggregating bird and ant species into one trophic group would not be warranted, despite the overlapping of their diets. The more detailed analysis that we conducted on spider families also showed that the effect of ant exclusion was limited to a few families rather than being widespread over the entire diversity spectrum of spiders, hindering again the possibility of including all spiders into one trophic group.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: DOI: 10.1111/j.1365-2311.2010.01190.x

Table S1. Average number of individuals detected in the monthly bird censuses (point counts) inside the grove (or flying over it) and outside the grove. Only species considered as insectivorous are reported (see text). An asterisk (*) indicates that the species feeds on earwigs, and a (#) symbol indicates that the species can feed on canopy insects (in both cases the information is taken from Cramp et al., 1988–1994).

Table S2. Summary of a repeated measures ANOVA of arthropod abundance between ant-excluded and bird-excluded trees from February to November. Codes for arthropod groups as in Table 1.

Table S3. Complete list of all spiders collected using beating trays in 11 samplings dates from January to November 2006 and from 24 citrus trees (8 control, 8 ant-excluded, 8 bird-excluded). A total of 2051 specimens were analysed, of which only 158 (7.7%) were adults (105 females and 53 males). As most of the specimens were juveniles their determination was difficult and, in many cases, it was not possible to go beyond the genera level (Anyphaena, Cyclosa, Lathys, Zelotes, Cheiracanthium, Oxyopes, Philodromus, Salticus, Heliophanus, Anelosimus, Archaearanea, Dipoena, Xysticus, Ozyptila) and in a few cases beyond the family level (10 Araneidae, 1 Gnaphosidae, 81 Linyphiidae, 5 Salticidae, and 6 Theridiidae).

Table S4. Summary of a repeated measures ANOVA of the abundance of spider families and of spiders’ diversity (both measured as the number of species S and as the Shannon diversity index H) Between groups factor: treatment (ant-excluded vs. bird-excluded); within groups: time (February to November). Codes for spider families as in Table 2.

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References


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