Ant exclusion in citrus over an 8-year period reveals a pervasive yet changing effect of ants on a Mediterranean spider assemblage

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Abstract  Ants and spiders are ubiquitous generalist predators that exert top-down control on herbivore populations. Research shows that intraguild interactions between ants and spiders can negatively affect spider populations, but there is a lack of long-term research documenting the strength of such interactions and the potentially different effects of ants on the diverse array of species in a spider assemblage. Similarly, the suitability of family-level surrogates for finding patterns revealed by species-level data (taxonomic sufficiency) has almost never been tested in spider assemblages. We present a long-term study in which we tested the impact of ants on the spider assemblage of a Mediterranean citrus grove by performing sequential 1-year experimental exclusions on tree canopies for 8 years. We found that ants had a widespread influence on the spider assemblage, although the effect was only evident in the last 5 years of the study. During those years, ants negatively affected many spiders, and effects were especially strong for sedentary spiders. Analyses at the family level also detected assemblage differences between treatments, but they concealed the different responses to ant exclusion shown by some related spider species. Our findings show that the effects of experimental manipulations in ecology can vary greatly over time and highlight the need for long-term studies to document species interactions.

Keywords  Agroecosystem · Ant exclusion · Competition · Intraguild interactions · Taxonomic resolution

Introduction

Intraguild interactions among predators are diverse and have a profound impact on the dynamic and structure of food webs and communities (Arim and Marquet 2004; Morin 2011). Field experiments conducted in arthropod communities have shown that these interactions can have non-additive effects on shared prey and can modify trophic cascades (Cardinale et al. 2003, 2006; Vance-Chalcraft et al. 2007). Moreover, effects of ecological manipulations vary over the years, but most research about arthropod assemblages relies on short-term data (Schmitz et al. 2000).

Ants and spiders are ubiquitous generalist predators in terrestrial arthropod communities, they exert top-down control on herbivore populations (Buddle et al. 2000; Schmidt et al. 2003; Sanders et al. 2008) that can potentially cascade down to plants (Snyder and Wise 2001; Sanders et al. 2011). Ants engage in mutualistic relationships with hemipterans and they protect them against their enemies in exchange for honeydew (Styrsky and Eubanks...
Spiders show a striking variety of activity patterns and foraging styles (Jocqué and Dippenaar-Schoeman 2006). It is therefore to be expected that the effects of spider predators and competitors vary according to the identity of the spiders involved in these interactions (Sanders and Platner 2007; Piñol et al. 2010) and that these potentially contrasting effects modify the taxonomic composition of spider assemblages. However, most experimental studies simplify the study of spider assemblages by classifying spiders into guilds—e.g. hunters versus web-builders—if not by treating the whole species assemblage as a single category (Halaj et al. 1997; Mooney 2006, 2007). Moreover, classifications of spiders according to guild are necessarily inaccurate due to the lack of knowledge about the biology of the great majority of spider species (Cardoso et al. 2011).

Because arthropod groups are hyper-diverse taxa, species-level identifications of large samples are costly and time-consuming, leading many researchers to adopt a taxonomic sufficiency approach, which involves identifying organisms to a level of taxonomic resolution sufficient to find the patterns revealed by species-level data. The use of higher-level identifications is widespread in aquatic assemblages (Williams and Gaston 1994; Bertasi et al. 2009; Carassou et al. 2012) and is receiving increasing attention in terrestrial communities, especially in ant assemblages (Schnell et al. 2003; Groc et al. 2010). However, the suitability of higher taxa surrogates in spiders has only been used to predict species richness patterns (Cardoso et al. 2004; Lin et al. 2012). Thus, it remains to be tested whether higher-level identifications are also useful in detecting the effects of experimental manipulations.

We tested the impact of ants on the spider assemblage of a Mediterranean organic citrus grove. We performed single-year ant exclusions on tree canopies each year for 8 years. We already knew from another study in the same setting by Piñol et al. (2012a) that ants have a strong influence on the abundance of different arthropod groups, including spiders. In the present study, we tested (1) whether ants changed the taxonomic composition of the canopy spider assemblage, and we then investigated (2) which spider species were most affected by ant presence. We also tested (3) whether identification at the family level was an adequate surrogate for effects detected with species-level data.

### Materials and methods

#### Study site

The grove is located in La Selva del Camp (Catalonia, NE Spain; 41°13’07”N, 1°8’35”E). The climate is Mediterranean, with a rainy spring and autumn and a dry winter and summer. The grove consists of ca. 300 Clementine trees (Citrus clementina var. clemenules) grafted on to the hybrid rootstock Carrizo citrange (Poncirus trifoliata (L.) Raf. × Citrus sinensis (L.) Osb.). The trees are watered during dry periods. Grasses and other weeds form a permanent ground cover that is mowed regularly. The grove was converted from conventional to organic agriculture in 2004, but pesticides and herbicides ceased to be applied in 2001 and 2002, respectively. For more details, see Piñol et al. (2012a).

#### Experimental design

Experimental trees were randomly selected from an area with 69 trees and randomly assigned to two treatments: control trees and banded trees, to which a glue band was applied on the trunk to prevent ants climbing up to the canopies. Sample size was the same between treatments (except in 2002) and varied slightly between years: in 2002, \( n = 8 \) in control trees and \( n = 7 \) in banded trees; \( n = 8 \) in 2003–2008; \( n = 9 \) in 2009. The band consisted of a polybutene-based sticky ring applied on plastic film tightly attached over a padded cylinder in contact with the trunk (Samways and Tate 1985). Trees were inspected weekly, and if ants were detected in the canopy, tall weeds were cut down or more glue was added to the barrier. The trunk barrier effectively excluded ants from the canopies most of the time (Piñol et al. 2012a). Treatments were established in January (February in 2002) and trees were sampled every month until December. The experiment was repeated for 8 years (2002–2009), using a different set of experimental trees each year. Reuse of the trees for experiments was not restricted except in consecutive years. Because assignment to treatments was completely random, some trees assigned to the “control” treatment in a given year could become “banded” trees further on, and vice versa.

The sticky barrier was also effective against other crawling insects in the grove, such as earwigs Forficula spp. (Piñol et al. 2009). This ant-exclusion experiment therefore has to be interpreted as one involving the exclusion of both ants and earwigs. For the sake of brevity, the term ant exclusion is used throughout the paper.

#### Sampling methodology

Arthropods from the canopy were sampled every month using beating trays (0.5 m\(^2\)), with three blows in opposite
directions on the tree crowns; they were then captured with entomological aspirators and preserved in 70 % ethanol. Sampling was comparable throughout the 8 years because the area covered by each of the sampled canopies was sufficiently large, from the start of the study, to contain all the beating trays (mean ± SE canopy area: 2.3 ± 0.1 m^2 in 2002).

Taxonomic identifications

Spiders were identified to species, using mainly the keys of Roberts (1985a, b) and Heimer and Nentwig (1991). We used additional keys to determine individuals belonging to the families Anyphaenidae (Urones et al. 1995), Corinnidae (Bosselaers et al. 2009), Linyphiidae (Wunderlich 1980; Bosmans and Abrous 1990) and Salticidae (Alicata and Cantarella 1994). Some juveniles could only be identified to the genus level. Nevertheless, juveniles from a given genus were assigned to the same species as adults if that species was the sole representative of that genus in the grove, but not all juvenile linyphiids could be classified. We followed the nomenclature given in Platnick (2011). Ants were also identified to species using Collingwood (1978) and Seifert (1992). The most common ants in the trees were the aphid-tending species Lasius grandis Forel (60 % of individuals) and Formica rufibarbis Fabricius (15 %), followed by the nectarivorous Plagiolepis pygmaea (Latreille) (9 %). A general overview of the remaining arthropod orders sampled from the canopies is given in Piñol et al. (2012a).

Statistical analyses

The response variable was the average number of spiders in each tree from February (March in 2002) to December of each year. We did not use data from the January samples (February in 2002) because the experimental exclusion of ants started the following month.

For each year, we tested for differences between treatments on the taxonomic composition of the canopy spider assemblage with permutational multivariate ANOVAs (PERMANOVA) on the square-root-transformed averages, using the Bray–Curtis index of similarity, with “ant exclusion” (control, band) as a fixed factor. PERMANOVA is a non-parametric analogue to MANOVA that does not require multivariate data to be normality distributed. PERMANOVA is thus particularly suitable for analysing data on assemblage species composition, which rarely satisfy multivariate normality. We conducted the analyses at species and family levels to test the influence of taxonomic resolution on the detection of effects.

When the PERMANOVA analysis for a given year was significant, we ran univariate permutational ANOVAs on the square-root-transformed abundances of the most common spider species or families in that year using the Euclidean distance, resulting in a permutational equivalent of classical ANOVAs (Anderson et al. 2008). These univariate analyses served as posteriori statistical tests that allowed us to detect which species were causing the differences in assemblage composition between ant-excluded and control trees. To adjust the level of significance, we used the step-up false discovery rate (FDR) by Benjamini and Hochberg (1995). We considered that the set of univariate analyses derived from each significant PERMANOVA analysis constituted a family of tests (García 2004).

We analysed differences in species richness (S) between treatments for each year with univariate permutational ANOVAs on S, using the Euclidean distance. The response variable was the average spider richness in each tree from February (March in 2002) to December of each year. Since we could not identify all the spiders to species, the estimate of S was conservative.

To test the relationship between the spider and the ant assemblages, we conducted a RELATE analysis—a multivariate analogue to simple regression—on the square-root-transformed total yearly abundances of all the spider and ant species averages, with the Bray–Curtis index of similarity. We used the Spearman correlation (statistic ρ). We repeated the analysis without the ant L. grandis, to test its influence on the spider assemblage, as this species seemed to play a major role in determining the abundances of arthropods in the tree canopies (Piñol et al. 2012a). We conducted the RELATE analyses at species and family levels to test again the influence of taxonomic resolution on the detection of effects. All analyses were conducted with the software PERMANOVA+ for PRIMER v.6 (Anderson et al. 2008).

Results

The spider assemblage

A total of 13,460 spiders were captured from the canopies with beating trays. Seventy-seven species from 21 families were sampled, the most abundant being Theridiidae (34.0 % of all individuals), Philodromidae (21.6 %), Araneidae (13.4 %), Salticidae (8.3 %), Clubionidae (6.1 %), and Thomisidae (3.9 %). Each of these families was dominated by one species (Philodromidae: 83.3 % Philodromus cespitum; Araneidae: 80.8 % Neoscona subfuscata; Salticidae: 62.2 % Icius hamatus; Thomisidae: 66.4 % Xysticus sp; Theridiidae: 26.1 % Anelosimus vittatus); or genus (Theridiidae: 41.8 % Theridion spp.). Clubiona leucaspis was the only clubionid species in the grove. The genus Theridion comprised three species, namely T.
**Table 1** Summary of the PERMANOVA table of the effect of ant exclusion on the spider assemblage from 2002 to 2009, at the species and family level.

<table>
<thead>
<tr>
<th>Years</th>
<th>Species</th>
<th>Pseudo-(F)</th>
<th>(P) (perm)</th>
<th>Family</th>
<th>Pseudo-(F)</th>
<th>(P) (perm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2002</td>
<td>1.70</td>
<td>0.076</td>
<td>1.67</td>
<td>0.13</td>
<td>0.012</td>
<td>0.45</td>
</tr>
<tr>
<td>2003</td>
<td>1.31</td>
<td>0.23</td>
<td>1.76</td>
<td>0.11</td>
<td>0.002</td>
<td>0.012</td>
</tr>
<tr>
<td>2004</td>
<td>1.29</td>
<td>0.20</td>
<td>1.13</td>
<td>0.36</td>
<td>0.0002</td>
<td>0.0002</td>
</tr>
<tr>
<td>2005</td>
<td>3.28</td>
<td>0.0007</td>
<td>3.13</td>
<td>0.0046</td>
<td>0.002</td>
<td>0.002</td>
</tr>
<tr>
<td>2006</td>
<td>4.16</td>
<td>0.0006</td>
<td>5.62</td>
<td>0.0002</td>
<td>0.0097</td>
<td>0.0097</td>
</tr>
<tr>
<td>2007</td>
<td>2.99</td>
<td>0.0016</td>
<td>2.82</td>
<td>0.0097</td>
<td>0.0008</td>
<td>0.0008</td>
</tr>
<tr>
<td>2008</td>
<td>4.02</td>
<td>0.0003</td>
<td>6.01</td>
<td>0.0008</td>
<td>0.0097</td>
<td>0.0097</td>
</tr>
<tr>
<td>2009</td>
<td>5.17</td>
<td>0.0002</td>
<td>9.86</td>
<td>0.0002</td>
<td>0.0097</td>
<td>0.0097</td>
</tr>
</tbody>
</table>

**Fig. 1** Abundance of the most common spider species in the grove over the 8 years of study (02–09), in control (Ants) and banded (No ants) trees. Species are ordered by decreasing abundance. Mean ± SE are shown, \(n = 8\) (\(P < 0.05\); *significant after FDR correction)
were more abundant in ant-free trees in at least one of the years. The negative effect of ants was especially strong on the *K. aulica*, *P. tincta*, *Theridion* spp. (Theridiidae), and on *Xysticus* sp. (Thomisidae), as their abundances were affected in 3 or 4 years, while the other species were affected in only 1 year. On the contrary, *I. hamatus (Salticidae)* was more abundant in control trees in 2008 (*P* = 0.00074).

Ant exclusion increased spider richness in 2006, 2007 and 2009 (*P* < 0.032; Table 2). There was a correlation between the spider and the ant assemblages (*r* = 0.55, *P* = 0.004), but the relationship vanished when the ant *L. grandis* was removed from the analysis (*r* = 0.21, *P* = 0.075).

**Monthly variations in species abundance**

The negative effect of ants on most of the analysed spider species was reflected by their changes in abundance between control and ant-free trees over the months. Spider abundances were similar in both treatments in winter and early spring. In May–June, coinciding with the start of intense ant activity in the canopies, abundances became higher in the banded trees than in the controls (Online resource 4). In contrast, abundances of most species reached a minimum in May–June, increased abruptly in July and peaked in late summer. Notable exceptions to this seasonal trend were *O. lineatus* and *Xysticus* sp.; these

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**Fig. 1 continued**

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**Table 2** Summary of the ANOVA table of the effect of ant exclusion on spider richness (S) from 2002 to 2009

<table>
<thead>
<tr>
<th>Years</th>
<th>Ants Mean (SE)</th>
<th>No ants Mean (SE)</th>
<th>ANOVA Pseudo-F</th>
<th>P (perm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2002</td>
<td>3.80 (0.34)</td>
<td>2.91 (0.53)</td>
<td>1.10 0.35</td>
<td></td>
</tr>
<tr>
<td>2003</td>
<td>4.06 (0.13)</td>
<td>3.97 (0.22)</td>
<td>0.21 0.64</td>
<td></td>
</tr>
<tr>
<td>2004</td>
<td>4.58 (0.34)</td>
<td>4.99 (0.29)</td>
<td>0.99 0.33</td>
<td></td>
</tr>
<tr>
<td>2005</td>
<td>3.70 (0.25)</td>
<td>3.32 (0.22)</td>
<td>1.26 0.27</td>
<td></td>
</tr>
<tr>
<td>2006</td>
<td>3.83 (0.34)</td>
<td>5.82 (0.29)</td>
<td>14.94 0.0007</td>
<td></td>
</tr>
<tr>
<td>2007</td>
<td>5.52 (0.22)</td>
<td>6.49 (0.33)</td>
<td>5.86 0.032</td>
<td></td>
</tr>
<tr>
<td>2008</td>
<td>6.58 (0.38)</td>
<td>7.21 (0.37)</td>
<td>1.32 0.26</td>
<td></td>
</tr>
<tr>
<td>2009</td>
<td>5.58 (0.19)</td>
<td>6.95 (0.27)</td>
<td>16.92 0.0009</td>
<td></td>
</tr>
</tbody>
</table>
species appeared in the citrus canopies in late spring, peaked in June-July and almost vanished thereafter.

Influence of taxonomic resolution on the detection of effects

At family level, the spider assemblage was significantly affected by ant exclusion in the years 2005–2009 (pseudo-$F_{1,14} = 2.82$, $P < 0.0097$; Table 1; Online resource 5). After adjusting the level of significance for each year, univariate permutational ANOVAs showed that Araneidae ($P = 0.0092$; Fig. 2; Online resource 6), Clubionidae ($P = 0.015$), Miturgidae ($P = 0.0023$), Oxyopidae ($P = 0.011$), Theridiidae ($P < 0.0046$), and Thomisidae ($P < 0.0033$) were more abundant in trees without ants in at least one of the years. Gnaphosidae ($P = 0.014$) and Salticidae ($P = 0.0033$) were more numerous in control trees in 2008. The spider assemblage analysed at family level was related to the ant assemblage ($q = 0.62$, $P = 0.02$), but when *L. grandis* was removed from the analysis the relationship became weaker ($q = 0.31$, $P = 0.033$).

**Discussion**

Our 8-year study revealed that ants had a widespread influence on the spider assemblage, although the effect was only evident in the last 5 years of experiments (2005–2009).
Analyses at the family level were effective in detecting assemblage differences between treatments, but they concealed contrasting responses to ant exclusion in related species.

Effect of ants on the spider assemblage

From 2005 to 2009, we detected a severe negative effect of tree-foraging ants on spiders: in the trees with ants, 10 of the 17 species analysed had lower abundances and species richness was lower than in ant-free trees. While other studies have also found that ants decrease the abundances of canopy spiders (Philpott et al. 2004; Vanek and Potter 2010; Piñol et al. 2012a), to our knowledge no removal experiments in other systems have ever previously analysed the effects of predators or competitors on the individual spider species constituting an assemblage. In three studies conducted in the canopies of North American pine stands, Halaj et al. (1999) and Mooney (2006, 2007) classified spiders into two guilds (hunters, web-weavers) and reported a substantial negative impact of ants on hunters, and a slight effect on web-wavers (Mooney 2007). In the studied Mediterranean citrus grove, we found that ants foraging on canopies strongly reduced the abundances of both hunting (C. mildei, C. leucaspis, M. nidicolens, O. lineatus, Xysticus sp.) and web-building species (A. vittatus, K. aulica, N. subfuscus, P. tineta, Theridion spp.). The diversity of lifestyles within these two broad categories (Uetz et al. 1999; Cardoso et al. 2011) indicates that the attack of ants is indiscriminate and that these species do not share any trait that makes them especially vulnerable to the activity of ant workers. Nevertheless, the spiders most affected (K. aulica, P. tineta, Theridion spp., Xysticus sp.) were all sit-and-wait predators (Foelix 2010), which suggests that sedentary habits may make individuals more susceptible to ant foraging.

By contrast, the species I. hamatus, Dipoena melanogaster and Aphantaulax trifasciata were more common in ant-frequented trees in almost all the years, although the trends were only significant for I. hamatus. One plausible explanation is that ants are the preferred prey of these species, as shown in Dipoena and Icicus spiders (Umeda et al. 1996; Pekár et al. 2012). Similarly, previous experiments have reported a decrease in the abundance of Zo-dariidae (Gibb 2003) and Gnaphosa (Moya-Laraño and Wise 2007) following ant exclusion, because these spiders prey on ants. Although unlikely, ant presence may also be boosting the densities of some unknown prey of these spiders and thus indirectly benefiting them.

Long-term data

Until 2004, ants had no noticeable effect on the spider assemblage. Yet ants had a marked influence from 2005 onwards, coinciding with an increase in their abundance in the canopies—mostly due to L. grandis—that continued until the end of the study (Piñol et al. 2012a). Indeed, there was a highly significant relationship between the spider and the ant assemblages when L. grandis was included in the analysis, indicating that this species is possibly the main driver of the influence of ants on the spider assemblage. This link between ant abundance and the strength of the effects of ants was also found in two parallel studies about the whole arthropod assemblage (Piñol et al. 2012a) and the heteropteran assemblage of the grove (Piñol et al. 2012b). The grove itself underwent several changes between 2002 and 2009: due to its conversion to organic agriculture, agrochemicals stopped being used in 2004, and the irrigation system was improved in 2006 to boost the effect of organic fertiliser. Moreover, the trees were planted in 1999 and at that time they were small and the vegetal ground cover was scarce. However, it is difficult to ascertain a clear link between any of these agricultural modifications and the prominent changes suffered by the ant community.

The shift in ant abundance in the canopies over the experimental period allows us to divide the study into two distinct parts: a first part (2002–2004) in which the numbers of ants were too low to produce any detectable effect on spiders, and a second (2005–2009) in which ant numbers increased considerably, leading to a pervasive influence on the spider assemblage. Had we run experiments for less than 4 years, we would have missed the impact of ants on spiders in this system. Instead, the results of the second part of the study resemble those of two independent short-term experiments conducted between 2006 and 2009 in the same setting, which also showed a negative influence of ants on certain canopy spiders: theridiids and thomisids (Piñol et al. 2010), and araneids and theridiids (Mestre et al. 2012). Despite providing insight into the dynamics of species interactions, long-term manipulations in invertebrate communities are largely lacking (Schmitz et al. 2000). Not surprisingly, the changes in effects over time reported in such experiments are associated with the densities of not only the manipulated but also the target groups, which depend on the biotic and environmental conditions of the particular study system (Turchin 1999; Stein et al. 2010; Allan and Crawley 2011), highlighting the importance of long-term data in our understanding of species interactions (Briggs and Borer 2005; van Veen et al. 2006). With regard to other ant-manipulation studies, ground ants in a boreal forest had variable albeit slight effects on spiders over a 4-year period (Lenoir et al. 2003), whereas the effects of granivorous ants on other ant species over a 15-year period depended on the fluctuating densities of the latter (Valone and Kaspari 2005).

Conclusion

This study showed that the far-reaching impact of ants on the canopy spider assemblage only surfaced after the third ant-exclusion experiment. The influence of ants on spiders was negative for species with varied lifestyles but it was more prominent in sedentary spiders. Although analyses at family level satisfactorily detected assemblage differences between treatments, critical information about species-specific responses to ant exclusion was lost with this approach. Our findings reveal that the effects of experimental manipulations on ecological research can vary greatly over time, emphasising the need for long-term studies to document species interactions.

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Taxonomic resolution and detection of effects

Family-level identifications were as successful as species-level identifications in detecting shifts in assemblage composition between ant-excluded and control trees. Therefore, multivariate analyses of the canopy spider assemblage identified to family were sufficient to detect the general effect of ants. Overall, univariate analyses of families showed the same differences in abundance between treatments as analyses of the most abundant species within these families (Araneidae: N. subfusca; Clubionidae: C. leucaspis; Dictynidae: Nigma walckenaeri; Gnaphosidae: A. trifasciata; Linyphiidae: Styloctetor romanus; Miturgidae: C. mildei; Oxyopidae: O. lineatus; Thomisidae: Xysticus sp.). These equivalent results with two taxonomic resolutions probably arose because these families were clearly dominated by a single species, so the effects detected on it persisted to family level (Bertasi et al. 2009). Nevertheless, both the positive effect of ants on salticids and the negative effect on theridiids are misleading because they failed to reflect opposite responses of related species to ant exclusion: while most analysed theridiid species increased numerically in ant-free trees, D. melanogaster was less frequent in these trees, and the reduction in salticid abundance in ant-free trees was caused by the low numbers of I. hamatus, although the less common M. nidicolens was in fact more abundant in ant-excluded trees. The adequacy of family-level surrogacy is still not well established in terrestrial communities, where most studies deal with detecting environmental impacts on arthropod assemblages: family-level determinations are suitable for detecting habitat and disturbance level differences in mite and ant assemblages (Schnell et al. 2003; Caruso and Migliorini 2006), but they lose significant information in beetle and soil macroinvertebrate assemblages (Nahmani et al. 2006; Grimbacher et al. 2008). Here, we show that family level surrogacy can be used in community ecology to detect the overall effects of field experiments on arthropod (spider) assemblages.
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