

Weed species, not mulching, affect web-building spiders and their prey in organic fruit orchards in South Africa

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Citation: Arvidsson, F., P. Addison, M. Addison, C. R. Haddad, and K. Birkhofer. 2020. Weed species, not mulching, affect web-building spiders and their prey in organic fruit orchards in South Africa. *Ecosphere* 11(3):e03059. 10.1002/ecs2.3059

Abstract. Weed infestation affects economically relevant orchard properties, including tree performance, yield, and fruit quality negatively, and weeds are therefore often controlled by herbicide application in conventional farming. The addition of organic mulch below tree canopies has been proposed as an alternative reliable practice to suppress weeds and preserve soil moisture in organic farming. Mulching, however, may also affect arthropod pest and natural enemy populations, which highlights the need for simultaneously assessing weed, natural enemy, and animal pest communities in mulch experiments. This study addresses the limited knowledge about nonchemical ground cover management strategies for the control of plant and animal pests in orchards as a major constraint for organic growers. Here, we hypothesize that decisions about ground cover management practices in organic temperate fruit orchards affect the composition of web-building spider communities and their functional role as natural enemies of pest arthropods through effects on weed and insect pest communities. We studied weed, prey, and spider communities, as well as spider diet composition, in four temperate fruit types (apricot, peach, plum, and quince) on a single farm in the Western Cape, South Africa. We established experimental plots with and without addition of dead organic mulch under fruit tree canopies. Addition of organic mulch did not significantly affect weed cover under trees or the taxonomic composition of weed or spider communities over the eight-month study period. However, independent of mulching, the taxonomic composition of weed communities was significantly related to the composition of potential prey and spider communities. These relationships indirectly affected the prey composition of web-building spiders. These results suggest that the identity of weed species in the study orchards had a pronounced effect on the diet composition and functional role of web-building spiders. Future research should focus on the value of individual plant species for the promotion of pest control services provided by spiders across larger spatial scales and with higher levels of replication to allow for wider generalizations. The expected results would not only be relevant for weed control but could also be considered during the development of future flower strips in orchards.

Key words: Araneae; biodiversity; biological control; ground cover management; habitat preference; microhabitat; mulch; organic farming; pest control; predation.

Received 6 January 2020; accepted 8 January 2020. Corresponding Editor: Uffe Nielsen.

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INTRODUCTION

The limited availability of nonchemical strategies for pest control is one of the major constraints for organic temperate fruit production (Wyss et al. 2005, Peck et al. 2006, Wooldridge et al. 2013). Two major groups of economically important pests in orchards in South Africa are herbivorous insects (Prinsloo and Uys 2015) and agricultural weeds (Ferrara et al. 2015). Conventional farmers primarily rely on synthetic insecticides and herbicides to control these organisms, whereas organic farmers need to rely on alternative solutions (Zehnder et al. 2007). In peach orchards, for example, weed infestations are known to affect numerous economically relevant aspects, including tree growth, yield, and fruit quality (Majek et al. 1993). High weed cover is particularly disadvantageous to fruit trees in areas where water is limited and irrigation is expensive (Ames and Kuepper 2004), and hampers the control of nonflying pest insects, such as weevils and ants. In order to reduce negative effects of competition between fruit trees and weeds, organic farmers often rely on intensive mechanical cultivation, which may negatively impact soil structure, soil faunal communities, and nutrient cycling (Hoagland et al. 2008). A less disruptive strategy, which has proven effective in reducing weed cover in orchards, is mulching with dead organic mulch, for example, by covering the ground surrounding tree trunks with organic debris (Rifai et al. 2000, Hoagland et al. 2008). In Spanish citrus orchards, mulch was equally effective in reducing weed cover compared to applications of the herbicide glyphosate (Verdú and Mas 2007). Mulching has the additional benefit of reducing runoff and evaporation, important advantages in areas with limited precipitation and high water costs (Bennie and Hensley 2001).

Insect pests reduce yields in orchards by attacking the fruit directly and lowering its quality or appearance (Hoyt and Burts 1974), by reducing overall tree vigor, by feeding on various plant parts, and by acting as vectors for viruses (Dedryver et al. 2010). To control insect pests, fruit growers may actively promote natural enemies through habitat management (Michalko et al. 2017, Happe et al. 2019, Michalko and Košulić 2019). Web-building spiders are an

important natural enemy group in agroecosystems (Nyffeler and Sunderland 2003, Birkhofer et al. 2013, Nyffeler and Birkhofer 2017). Spiders are generalist predators, which attack and consume a wide range of prey organisms in terrestrial ecosystems (Birkhofer and Wolters 2012) and in orchards in particular (Cross et al. 2015). Spiders prey on various insects, including pests such as aphids, leafhoppers, and thrips (Miliczky and Calkins 2001, Nyffeler and Sunderland 2003, Birkhofer et al. 2016, Michalko et al. 2019). Previous studies suggest that individual spider species may not sufficiently control pest species, but that multiple species feed on the same pest (Michalko and Pekár 2015, Lefebvre et al. 2017) and can contribute to pest suppression (Cahenzli et al. 2017). In South Africa, previous surveys of arboreal spiders in orchards have found 11 web-building families in avocado orchards (Dippenaar-Schoeman et al. 2005), ten families in pistachio orchards (Haddad et al. 2004, 2005), nine families in unsprayed citrus orchards (Van den Berg et al. 1992), and six in macadamia orchards (Dippenaar-Schoeman et al. 2001).

Unlike annual crops which form part of a rotation, orchards provide more stable habitats with a higher permanency of food-web structure (Simon et al. 2011). Pest control levels through natural enemies are often higher in perennial compared to annual crops (Hall and Ehler 1979, Risch et al. 1983). Altering the vegetation characteristics in an area (e.g., plant diversity or cover) affects spider activity and community composition (Rypstra et al. 1999, Diehl et al. 2013). The addition of mulch may, for example, benefit spider populations by providing structures for web-building (Rypstra et al. 1999; but depending on mulch type, Sereda et al. 2015) and by regulating microclimatic conditions such as temperature and humidity (Riechert and Bishop 1990, Thomson and Hoffmann 2007). However, by reducing the weed cover, potential habitats for natural enemies may be lost (Kozar et al. 1994).

Here, we hypothesize that mulching with organic mulch affects the taxonomic composition of web-building spider communities and their functional role in organically managed orchards in the Western Cape Province of South Africa. We studied web-builders and their prey in four major types of organically farmed temperate fruits (plum, quince, peach, and apricot) in five orchards

on a single farm under two different ground cover managements (with and without addition of mulch under the tree canopy) and in three microhabitats (canopy, below canopy, and work row). The aims of our study were to (1) compare how web-building spider communities and their prey differ between the four fruit types and different orchard microhabitats, (2) identify effects of mulching on web-building spider communities and their prey in organic orchards, and (3) understand whether effects of ground cover management depend on fruit type or microhabitat.

METHODS

Study site and treatment

South Africa is among Africa's largest organic producers, but temperate fruits are currently only cultivated under organic certification in a very small area of approximately 77 ha (Willer and Lernoud 2019). Due to the very limited availability of organically certified temperate deciduous fruit orchards in the Western Cape Province, our selection was constrained to five orchards at the same farm. The study plots were located at Tierhoek Farm in the Western Cape Province, South Africa (33°43'43.9" S 19°47'33.3" E). The farm has been organically certified since 2005, and 24–30 ha of the farm area out of a total farm size of 180 ha is used for fruit production. The grower cultivates temperate fruits with 6 ha of apricots, 2 ha plum, 1.5 ha quinces, and 1.4 ha peaches. All orchard plots are irrigated on demand throughout summer with drippers (apricot, plum, and quince) or micro-jets (peach). Certified organic fertilizer, chicken manure, and liquid guano are applied as fertilizers.

The two ground cover treatments that were established between 3 and 14 October 2016 in all orchards were (1) mowing with 4–5 manual cuts of vegetation below tree canopies and 1–2 cuts in the working rows (hereafter called "control") per year with the cut material left distributed across work rows and canopy areas, vs. (2) mow and blow, 4–5 cuts under the canopy and 1–2 cuts in the working rows, with addition of all cut material as dead organic mulch below tree canopies (hereafter called "treatment"). All mowing was performed mechanically by weed eaters (hand-held machines) as part of the standard management routine, and placement of mulch was

performed manually by raking mown material into the tree row.

Subplots were established in five individual orchards with a minimum distance of 30 m between subplots within an orchard: one apricot (cultivar Imperial, 1.75 ha, planted 2005), one plum (cultivars Southern Belle, Angelino, and Sogold, 1.14 ha, planted 2002), and one peach (cultivar Neethling, 1.49 ha, planted 1992) orchard, and two smaller quince orchards (cultivar Portuguese, 0.75 and 0.39 ha, both planted 2007). In each of the apricot, plum, and peach orchards, two control and two treatment subplots (20 × 20 m) were established. Each of the two quince orchards only had one control and one treatment subplot due to their smaller size. This resulted in a total of 16 study subplots (eight treatment and eight control plots) in four different orchard types (apricot, plum, peach, and quince).

Mulch cover in the treatment subplots was measured between 31 October and 4 November 2016 and between 22 June and 7 July 2017 below the canopy of five randomly selected trees per treatment subplot (excluding dead trees). To derive an estimate of mulch cover, the two maximum horizontal dimensions (orthogonal to each other) and the maximum cover height were measured. The mulch covered an average area of $112 \pm 5 \times 109 \pm 8$ cm under trees, with an average height of 25 ± 1 cm at the time of sampling, 2–3 weeks after treatment establishment (mean \pm SE). Approximately eight months after mulch establishment in 2017, the mulch covered an average area of $81 \pm 2 \times 71 \pm 2$ cm, with an average height of 8.8 ± 1 cm.

Sampling

To determine the long-term effect of both ground cover management strategies on weeds below fruit tree canopies and in adjacent work rows, the percentage weed cover and the plant species composition and frequency of each species were determined between 4 and 5 December 2017 in one 1-m² quadrat adjacent to the tree trunk (on the southern side) and in one 1-m² quadrat one meter away from the tree trunk in each subplot. Species were recorded from these quadrats based on estimates of their percentage cover. In the apricot orchard, only one treatment and one control subplot were sampled for plants due to logistical problems.

Web-building spiders and their prey were sampled in two sampling periods from 1 to 29 November 2016 and from 12 June to 8 July 2017, with two different orchards sampled each day. The temporal gap between spider and weed community sampling was partly caused by the necessity to identify weed plants at times of flowering. Weed communities in the study orchards were not expected to show drastic phenological shifts within one growing season. First, orchards were irrigated, providing relatively stable water supply over the growing season. Second, orchards were not treated with herbicides, thereby not causing dramatic weed community changes. Each subplot was sampled once in the morning and once in the afternoon per sampling period. No sampling was performed 24 h after or during rainfall events, as this would have affected the detectability of spider webs. Each plot was visually searched by the same researcher (FA) for 1.5 h with all web-building spiders, webs, and prey remains being collected, while recording the specific microhabitat: in the canopy of the tree (branches and bark), below the canopy (on the ground or the bark), or in work rows (see also Diehl et al. 2013) using approximately equivalent amounts of time between microhabitats. All samples were later identified with a stereomicroscope: Prey items were identified to order level (in a few cases to suborder or family level if possible), leading to 18 distinguishable prey taxa (realized prey). Spiders (63 taxa) were identified to species (25), genus (20), or morphospecies (18) level at the University of the Free State in Bloemfontein. Prey availability (potential prey) was sampled with three commercially available yellow sticky traps (10 × 24 cm) (Chempac Pty., Simondium, South Africa) positioned at 30 cm height and with a vertical orientation below tree canopies in each plot (Greenstone 1984, Diehl et al. 2013). A total of 16 sticky traps out of 48 were damaged or removed by baboons during the prey availability survey. All potential prey individuals were identified to the same taxonomic levels as realized prey items from spider webs. Yellow traps are known to cause a bias toward insect taxa with preferences for the color (e.g., aphids), so our estimate of prey composition may be biased toward certain prey taxa. There is unfortunately no single unbiased method to estimate the density of flying

prey as other passive methods (e.g., pan traps or sticky traps with different colors) or active methods (e.g., D-Vac suction sampling or sweep netting) would also have caused a bias.

Statistical analyses

Permutational analysis of variance (PERMANOVA) was used for all factorial models due to its flexibility to analyze both uni- and multivariate data given the choice of an appropriate resemblance measure and due to the fact that it can analyze factorial designs even if they lack or are limited in replication (Anderson et al. 2008). The following section provides details on the analyses of each respective dataset.

The percentage of weed cover was analyzed with permutational analysis of variance (PERMANOVA; Anderson 2001) based on Euclidean distances between percentage values under each tree and adjacent work rows using the fixed factors orchard type (levels: apricot, quince, peach, or plum), treatment (levels: control or mulch treatment), and microhabitat (levels: canopy, below canopy, or in work rows).

All data on the taxonomic composition of local communities (for plants, spiders, and potential and realized prey) were analyzed with permutational analyses of variance (PERMANOVAs; Anderson 2001) based on Bray-Curtis similarities. The effect of orchard type, treatment, and microhabitat on plant species composition was analyzed based on recording frequencies of each plant species in each plot. For prey availability sampled with sticky traps, the number of potential prey items from 11 insect orders was compared based on $\log(x + 1)$ -transformed numbers of each order per sticky trap for the factors orchard type and treatment. Transformation was applied to weigh down the impact of the numerically most dominant prey taxa. For spider community composition and realized prey composition in spider webs, the effect of orchard type, treatment, and microhabitat (levels: canopy, below canopy, or in work rows) was analyzed based on Bray-Curtis similarities. Post hoc tests were performed as pairwise PERMANOVAs providing t-statistics. Rank-based nonparametric Mantel tests (based on Spearman's coefficients) were used to test for the relationships between the taxonomic composition of weed, spider, and potential and realized prey communities.

Principal coordinate analysis (PCO; Anderson et al. 2008) ordination was used to show resemblances between subplots based on the multivariate taxonomic composition of web-building spider and prey communities in different orchard types and microhabitats.

All means in the text are given with standard errors of the mean, and correlations are performed based on Spearman's correlation coefficients. All statistical analyses were performed with PRIMER 7 version 7.0.13 and the PERMANOVA + 1 add-on (PRIMER-e, Quest Research Limited, Auckland, New Zealand).

RESULTS

Weeds

The percentage of weed cover below canopies and in working rows did not differ significantly between treatment and control plots (Pseudo- $F_{1,44} = 1.26$; $P = 0.269$), but did differ between orchard types (Pseudo- $F_{3,44} = 13.13$; $P < 0.001$). The effect of orchard type on weed cover depended on treatment level (Pseudo- $F_{4,44} = 6.23$; $P = 0.002$). The percentage of weed cover decreased from peach (mean \pm SE: $58.9 \pm 7.0\%$) to quince ($29.5 \pm 2.4\%$) to plum ($26.2 \pm 5.2\%$) and apricot ($24.8 \pm 5.3\%$). Subplots in mulch treatments had a higher percentage of weed cover compared to control plots in the peach orchard ($75.7 \pm 7.4\%$ vs. $42.2 \pm 7.0\%$). The species composition of plant communities differed significantly between orchard types (Pseudo- $F_{3,44} = 6.87$; $P < 0.001$), but not between control and treatment plots (Pseudo- $F_{1,44} = 0.97$; $P = 0.477$) or microhabitats (Pseudo- $F_{1,44} = 1.27$; $P = 0.212$).

Potential prey

Based on 11181 potential prey individuals sampled with sticky traps, the availability of prey differed significantly between orchard types (Pseudo- $F_{3,23} = 3.26$; $P = 0.001$), but not between treatment and control plots (Pseudo- $F_{1,23} = 1.19$; $P = 0.311$). Coleoptera numbers were significantly higher in plum than in peach ($t_{1,12} = 3.29$; $P = 0.006$) or quince ($t_{1,12} = 4.58$; $P = 0.001$) plots (Fig. 1a). Hemiptera numbers were significantly lower in apricot than in peach ($t_{1,12} = 3.28$, $P = 0.003$), quince ($t_{1,12} = 2.55$, $P = 0.019$), or plum ($t_{1,12} = 5.39$, $P < 0.001$) plots (Fig. 1b). Apricot plots had significantly higher numbers

of Diptera than peach ($t_{1,12} = 2.58$, $P = 0.027$) or quince plots ($t_{1,12} = 2.72$, $P = 0.009$; Fig. 1c). All other prey taxa did not differ significantly in estimated density between orchard types ($P > 0.05$).

Web-building spiders

Both orchard type (Fig. 2a) and microhabitat (Fig. 2b) affected the overall abundance of web-building spiders (orchard type Pseudo- $F_{3,24} = 6.12$; $P = 0.004$; microhabitat Pseudo- $F_{2,24} = 19.32$; $P < 0.001$). Only microhabitat affected the taxonomic richness of spider communities significantly (Pseudo- $F_{2,24} = 37.82$; $P < 0.001$), but independent of orchard type (Pseudo- $F_{6,24} = 0.90$; $P = 0.509$) and with no significant mulch treatment effect (Pseudo- $F_{1,24} = 0.04$; $P = 0.849$; Fig. 2c).

Orchard type (Pseudo- $F_{3,24} = 4.97$; $P < 0.001$) and microhabitat (Pseudo- $F_{2,24} = 15.06$; $P < 0.001$) both affected the taxonomic composition of web-building spiders significantly, with a significant interaction term between both factors (Pseudo- $F_{6,24} = 2.16$; $P < 0.001$). Mulch treatment did not affect the composition of spider communities significantly (Pseudo- $F_{1,24} = 0.26$; $P = 0.981$). Morphospecies 2 and 15 (both Theridiidae) were abundant on trees of apricot, peach, and plum plots, and *Gandanameno* sp. (Eresidae) individuals were abundant in the canopy of all orchard types and under the canopy in plum and quince (Fig. 3). *Cyclosa insulana*, *Larinia bifida* (both Araneidae), *Agyneta habra*, *Metaleptophantes familiaris*, and *Microlinyphia sterilis* (all Linyphiidae) were common in work rows. *Benoitia* sp. (Agelenidae), *Tidarren* sp. (Theridiidae), and *Uloborus* sp. (Uloboridae) were more characteristic for microhabitats below the canopy in quince and peach, compared to plum and apricot plots.

Realized prey

Out of 974 sampled web-building spiders, 488 had 2335 prey items in webs, with the number of items ranging from 1 to 89 per web. The number of total prey items per orchard was not significantly related to the overall number of spiders sampled per orchard ($N = 8$, $R = -0.57$, $P = 0.142$). The most common prey orders were Hymenoptera ($N = 1053$ individuals), Coleoptera ($N = 302$), Hemiptera ($N = 286$), Thysanoptera ($N = 268$), Diptera ($N = 154$), and Psocoptera ($N = 129$).

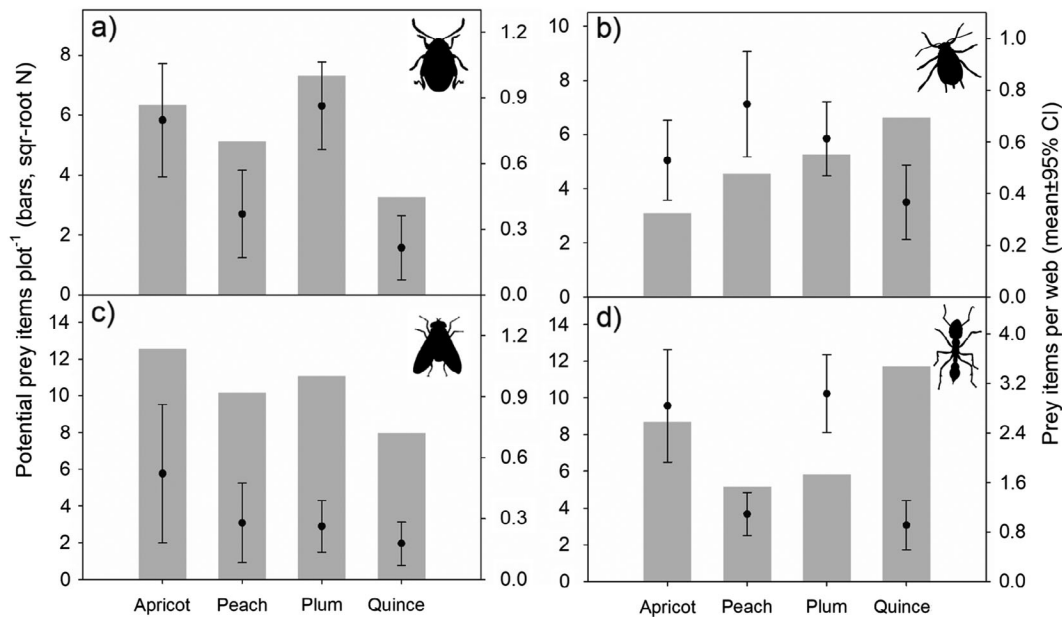


Fig. 1. Average density of potential prey available to web-building spiders (gray bars, left axis) and realized prey items per spider web (means \pm 95% confidence intervals, right axis) for (a) Coleoptera, (b) Hemiptera, (c) Diptera, and (d) Hymenoptera prey in different orchard types.

The prey composition of web-building spiders (average number of prey items per prey order and per web) differed significantly between orchard types (Pseudo- $F_{3,6} = 5.46$; $P = 0.001$) and microhabitats (Pseudo- $F_{2,6} = 13.25$; $P < 0.001$), with a significant interaction between both factors (Pseudo- $F_{6,6} = 3.22$; $P = 0.002$). Spiders in work rows had fewer Coleoptera and Hymenoptera prey than spiders below and in the canopy. Spiders in the canopy of quince trees and under the canopy of peach trees more frequently caught mites and less frequently caught Diptera prey (Fig. 4).

The effect of mulch treatment on prey composition depended on orchard type (Pseudo- $F_{3,464} = 1.63$; $P = 0.046$), as it was only significantly different in peach plots ($t_{1,116} = 1.72$; $P = 0.028$). Individual spiders in peach control plots had 2.4 times higher numbers of Hemiptera prey compared to treatment plots (1.0 ± 0.2 vs. 0.4 ± 0.1 Hemiptera prey items per web).

Relationships between weeds, prey, and spiders

The taxonomic composition of weed communities was not significantly related to the composition of realized prey, but was significantly

related to the composition of spider communities and potential prey (Fig. 5). Among the most common weed and spider species (occurrence in at least six out of 18 plots), significant positive relationships were observed between eight spider species and eight weed species (Fig. 6). Six of these spider species had on average at least 0.5 potential pest prey items per web. All these weed species with the exception of *Senecio burchelli* are alien species to South Africa. Significant relationships were also observed between the abundance of several common prey and weed taxa (occurrence in at least four out of eight treatment \times fruit type combinations, Table 1).

Both the composition of spider communities and the composition of potential prey were significantly related to the composition of realized prey (Fig. 5). For three prey orders, the abundance of available prey correlated significantly with the number of realized prey items: Coleoptera (Fig. 1a; $R = 0.98$, $P < 0.001$), Diptera (Fig. 1c; $R = 0.92$, $P = 0.001$), and Hymenoptera (Fig. 1d; $R = 0.81$, $P = 0.015$). The abundance of the following common spider species and realized prey were significantly positively correlated: *A. habra* and Diptera; *Larinia bifida* and Diptera; *Leucauge*

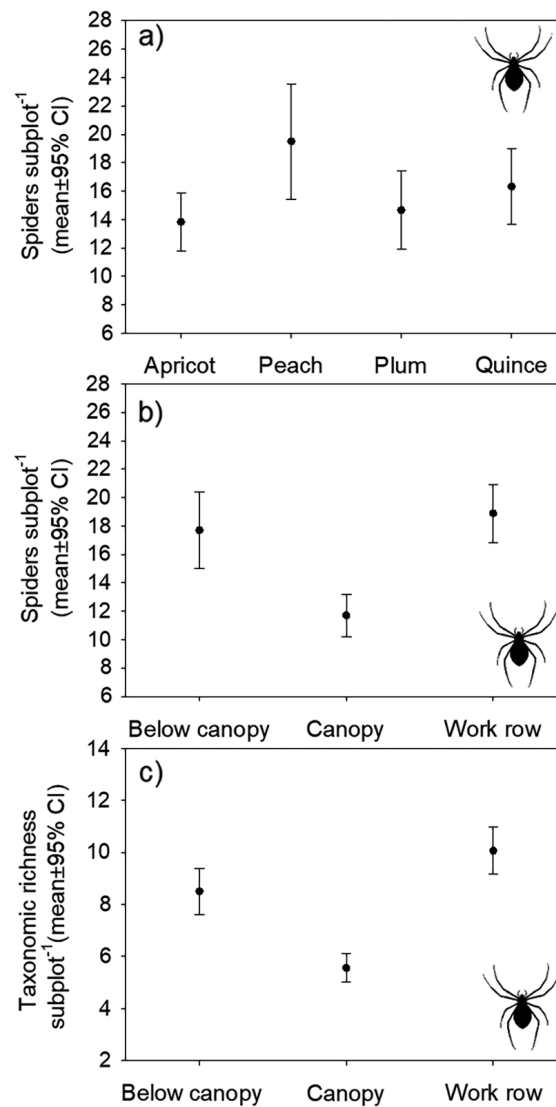


Fig. 2. Web-building spider abundance in (a) orchard types, (b) microhabitats, and (c) the taxonomic richness of web-building spiders in microhabitats (means \pm 95% confidence intervals).

sp. and Diptera; *Tidarren* sp. and Araneae, Gastropoda, Hymenoptera, and Psocoptera; and morphospecies 3 (Theridiidae) and Acari.

DISCUSSION

The treatment with organic mulch did not significantly affect weed cover or the taxonomic composition of weed or spider communities. However, independent of mulch treatments, the taxonomic composition of weed communities

was significantly related to the composition of potential prey and spider communities in orchard subplots. These relationships indirectly affected the prey composition of web-building spiders, suggesting that individual weed species in the organic study orchards have a pronounced effect on the diet composition and functional role of web-building spiders.

Management practices that increase the structural complexity of habitats, such as the addition of mulch, may enhance the density and diversity

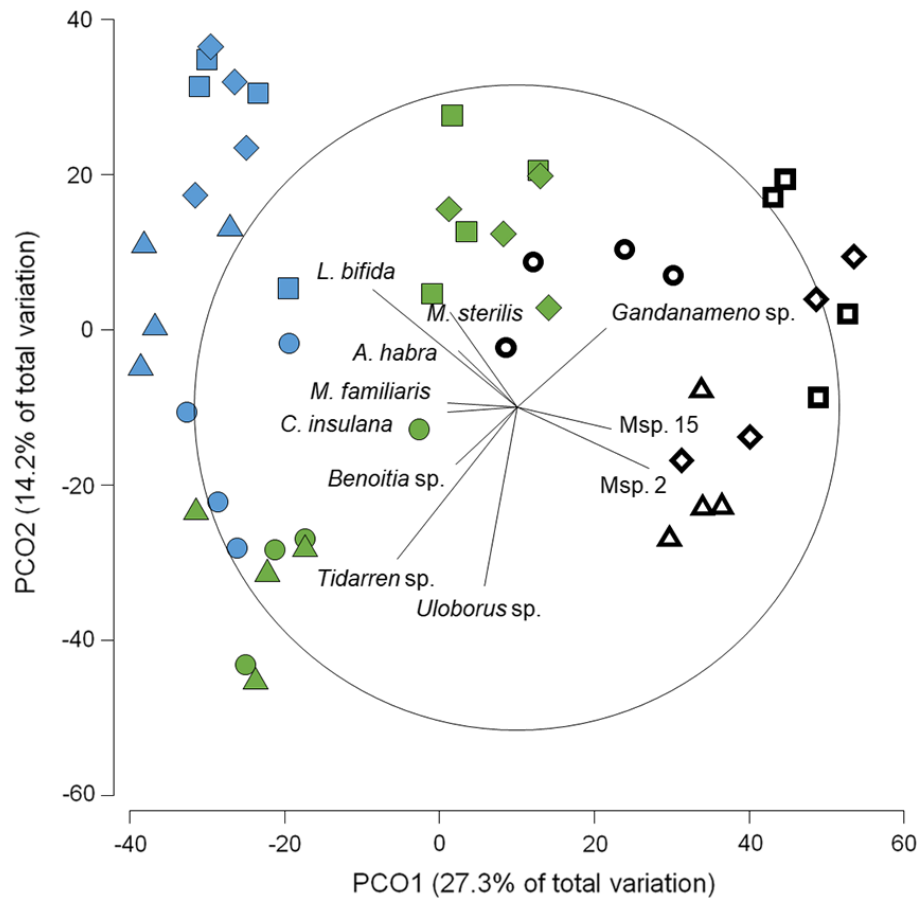


Fig. 3. Principal coordinate analysis ordination based on the taxonomic composition of web-building spider communities in apricot (diamond), peach (triangle), plum (square), and quince (circle) plots in work rows (blue), below canopies (green), and in the canopy (open). Vectors for spider species are superimposed based on multiple correlation coefficients >0.2 between plot-level spider abundances and coordinates in ordination space.

of spiders (Rypstra et al. 1999, Schmidt et al. 2004, Sereda et al. 2015). Mulch provides structures for web construction (Rypstra et al. 1999), favorable microclimatic conditions (Riechert and Bishop 1990), and protection from natural enemies (Sunderland and Samu 2000). Brown and Tworkoski (2004) observed an increase in spider abundance in temperate apple orchards after adding compost mulch. Shading created by orchard trees leads to favorable microclimatic conditions below the canopy, especially in arid climates (Belsky et al. 1993). This orchard property, together with the severe drought during the study period and the relatively short-term nature of the study, potentially limited the effects of mulch addition.

The effect of microhabitat differences on the species composition of web-builder abundance and taxonomic richness was stronger than effects of weed composition or fruit type. Spider species with a strong preference for mosquito (*L. bifida*) or aphid (*M. sterilis*) prey were frequently observed in the grassy vegetation of work rows, whereas the most common canopy spider species primarily preyed on ants in our study (*Gandanameno sp.*). The abundance and taxonomic richness of web-building spiders were higher in work rows and below the canopy compared to inside the canopy. This was likely caused by the higher structural complexity of substrates, offering a range of suitable conditions for various web types (Rypstra et al. 1999). Links between

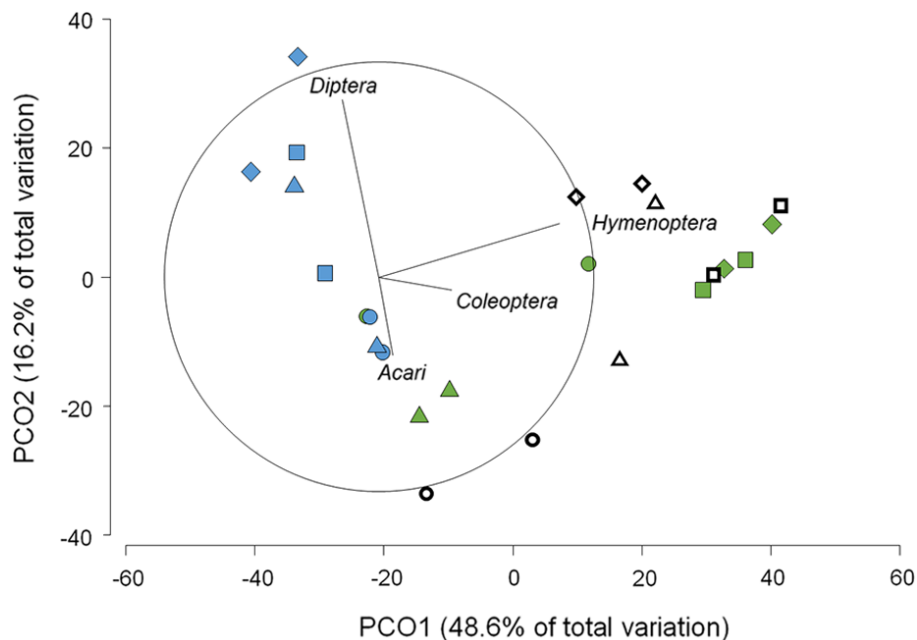


Fig. 4. Principal coordinate analysis ordination based on the average number of prey items from 11 prey orders per spider web in apricot (diamond), peach (triangle), plum (square), and quince (circle) plots in work rows (blue), below canopies (green), and in the canopy (open). Vectors for prey orders are superimposed based on multiple correlation coefficients >0.2 between the average number of prey items and coordinates in ordination space.

vegetation complexity and diversity of web-building spiders have previously been observed in agricultural (Diehl et al. 2013) and other habitats (Finch et al. 2008, Gómez et al. 2016). Correlations between individual spider and plant species have been previously documented in meadows. For example, spiders from the families Theridiidae and Linyphiidae require plants with a lot of branching for their webs, while orb-weaving Araneidae require large spaces between branches or plants to build their webs (Scheidler 1990). Our study highlights the importance of weed species identity for individual spider species and also documents the functional consequences of frequently co-occurring species pairs.

Temperate deciduous fruits in South Africa are attacked by a range of economically relevant pests, with aphids, flies, and thrips being important due to either direct damage to fruits or transmission of plant viruses (Prinsloo and Uys 2015). While several weed species were positively related to the abundance of such potential pest organisms in our study plots (e.g., *Senecio*

burchelli to Thysanoptera), they also were positively related to densities of spider species with considerable pest control potential (e.g., *S. burchelli* to *Tidarren* sp. with high numbers of Aphidoidea prey). Other weed species were negatively related to the density of potential pest orders (e.g., Thysanoptera to *Lepidium africanum*) and at the same time were positively related to spider species with high pest control potential (*Lepidium africanum* to *Agyneta* sp.). Previous studies suggested that the presence of weeds or cover plants draws natural predators away from crops and may thereby reduce their effectiveness as natural enemies of pests (Bugg et al. 1987, Kemp and Barrett 1989, Rodenhouse et al. 1992). Our results suggest that weeds in South African orchard systems hold the potential to play a crucial role in arthropod pest control, due to positive effects on natural enemies that are effective pest predators. It is therefore important to do further research to identify weed species that facilitate the proliferation of predators while being unfavorable hosts for pest arthropods.

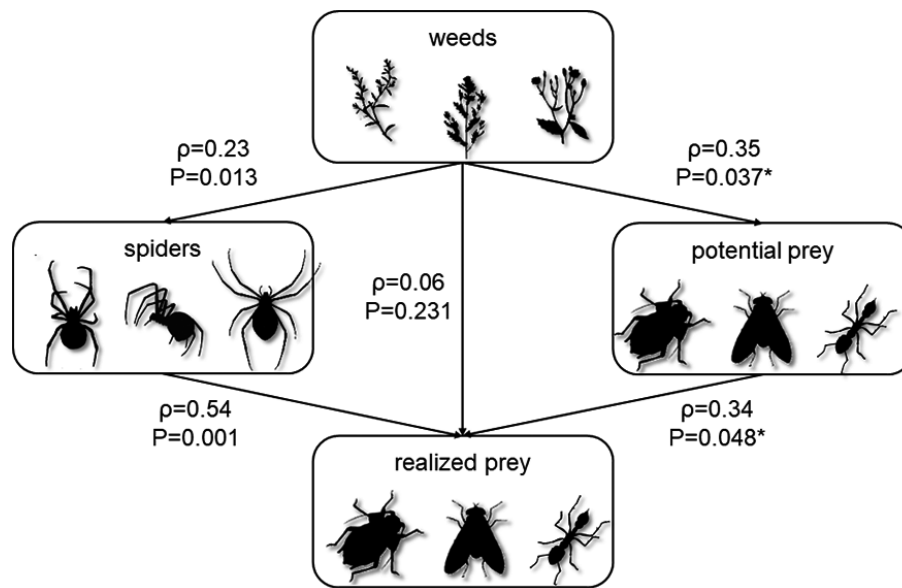


Fig. 5. The relationships between the taxonomic composition of weed, spider, and potential and realized prey communities from rank-based nonparametric Mantel tests. Values are Spearman's rank correlation coefficients (ρ) and P -values for each relationship. The sample size is 16 (four fruit types \times two replicated plots \times two treatment levels), or in the case of an asterisk, sample size is 8 (sticky traps to estimate potential prey were only analyzed for fruit type \times treatment level due to the loss of several traps).

Web-building spiders are not just aerial filters (Nentwig 1983). Several studies now document that prey composition may reflect the local availability of prey for some prey taxa, but not for others (Diehl et al. 2013, Mader et al. 2016). The density-dependent catch rates for some prey groups are probably caused by opportunistic predation, as species may feed on the most available prey, rather than targeting specific taxonomic groups (Birkhofer and Wolters 2012). In our study, some spider species were more efficient at capturing selected insect taxa than expected by the observed prey density. Spiders of the genus *Gandanameno*, for example, caught high numbers of ant prey below the canopy. In such cases, specialization for certain prey types may lead to discrimination of less preferred prey (Pekár et al. 2012). Web structure (Uetz et al. 1978) and web type (Michalko and Pekár 2016) may further determine prey composition, for example, through mesh size in orb webs. It has also been observed that competition between web-building spiders for prey or web sites affects the density and spatial arrangement of spiders (Smallwood 1993, Birkhofer et al. 2007, 2010).

Even on an individual plant, different web-building spider species will inhabit different niches, based on web height or preferences for certain plant structures (Scheidler 1990, Richardson and Hanks 2009). Web-building spider species in local communities reduce the “enemy-free space” for pests by inhabiting complementary niches, which ultimately may lead to high levels of pest control (Nyffeler and Sterling 1994, Riechert 1999, Sunderland 1999). Web-building spiders can further contribute to pest control through superfluous killing, for example, when prey trapped in webs or distasteful prey are not fed on (Riechert and Maupin 1998, Sunderland 1999). Severe declines in pest control can be mitigated by managing weeds in orchards to promote certain spider species that provide pest control services but respond differently to environmental stressors (see also Fischer et al. 2006). The strong link between the composition of weed communities and the functional role of web-building spiders in this study suggests that future research should focus on the value of individual plant species for the promotion of pest control services provided by spiders. This aspect

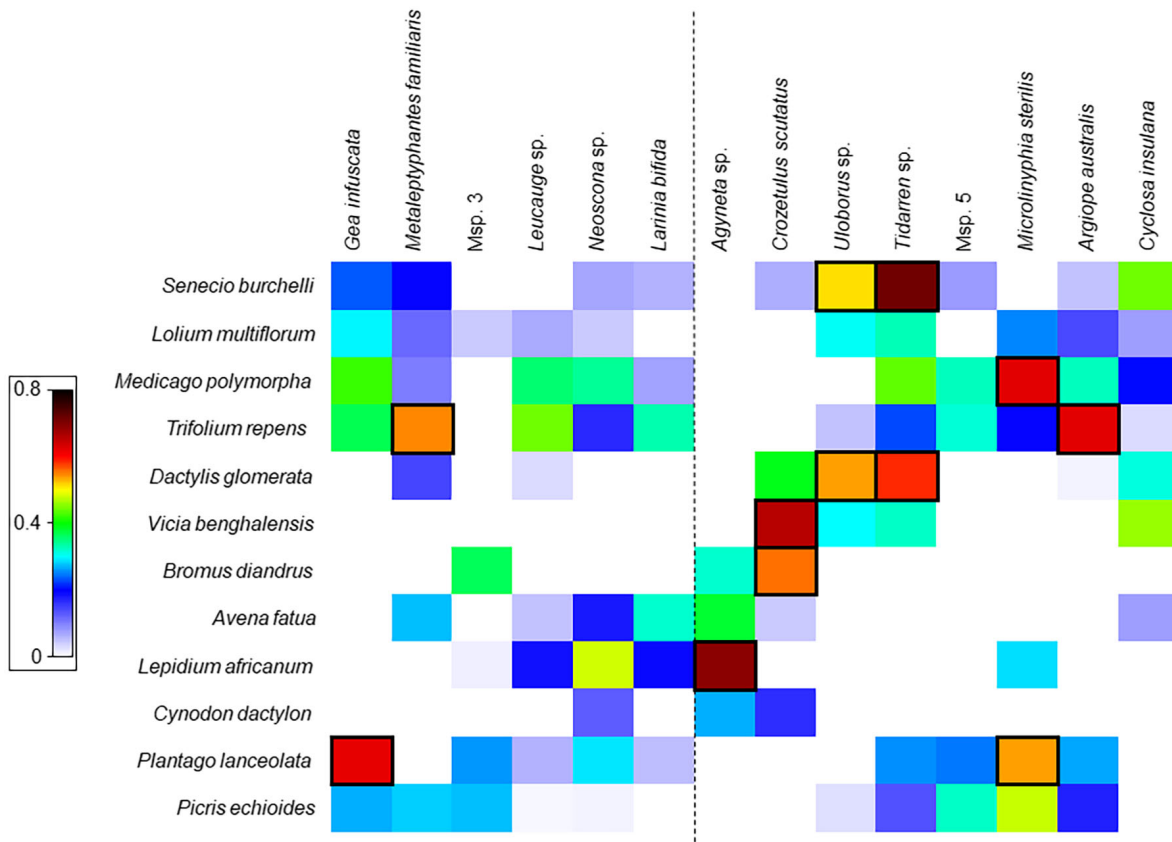


Fig. 6. Co-occurrence matrix between common weed (*y*) and web-building spider (*x*) species based on Spearman's correlation coefficients (color scale) in frequency (weeds) and abundance (spiders) across orchard subplots ($N = 16$, only species with an occurrence in at least six subplots). Web-builders are sorted from left to right based on the number of pest prey items per spider web (min = 0 items, maximum = 2.1 items per web; pest orders: Aphididae, Auchenorrhyncha, Brachycera, Psocoptera, Sternorrhyncha, and Thysanoptera). Weeds are sorted based on the Bray-Curtis similarity of species in frequency in the 16 subplots (closer species co-occur more frequently in plant communities). Significant relationships (Spearman's rank correlation) are indicated by framed boxes. Spider species that feed on pest prey with at least 0.5 pest prey items per web are located to the right side of the dotted line.

Table 1. Spearman's correlation coefficients between frequencies of common weed species and abundances of potential prey orders ($N = 8$ subplots, only taxa with an occurrence in at least four subplots)

Weeds	Potential prey				
	Coleoptera	Diptera	Hymenoptera	Orthoptera	Thysanoptera
<i>Anagallis arvensis</i> *	-0.81	-0.76	-0.81		0.74
<i>Avena fatua</i> *			0.76		
<i>Lepidium africanum</i> *		0.91			-0.82
<i>Olea europaea africana</i>			-0.75		0.91
<i>Senecio burchelli</i>	-0.74		-0.81		0.80
<i>Vicia benghalensis</i> *	-0.81				

Notes: Only combinations with significant correlation coefficients are shown. Weed species with an asterisk are alien species to South Africa.

may not only be important for weed management but could also be considered in future flower strip development for orchards. The observed local effects and relationships need to be tested over larger spatial scales and with higher levels of replication, an approach that would not be feasible in the Western Cape Province due to the limited availability of organically certified temperate fruit orchards.

ACKNOWLEDGMENTS

The authors are very grateful to the owner of the Tierhoek Organic Farm for his support. Vegetation was sampled and identified by Suzaan Kritzinger-Klopper. The authors thank Dr. Melanie Montes for assistance in the field and in editing the manuscript. We thank the Ekhaga Foundation (Ansökan 2015-11) and Volkswagen Foundation (Az.: 94646) for the financial support that allowed us to perform this study and to publish the results.

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