



Flowering plants in open tomato greenhouses enhance pest suppression in conventional systems and reveal resource saturation for natural enemies in organic systems

M. Scarlato^{a,b,*}, L. Bao^a, W.A.H. Rossing^b, S. Dogliotti^a, P. Bertoni^a, F.J.J.A. Bianchi^b

^a Faculty of Agronomy, Universidad de la República del Uruguay, Montevideo, Uruguay

^b Farming Systems Ecology, Wageningen University and Research, Wageningen, the Netherlands

ARTICLE INFO

Keywords:

Conservation biological control
Agroecology
Integrated pest management
Farm management
Biodiversity
Vegetable production

ABSTRACT

Vegetable production in open greenhouses is often associated with high inputs of synthetic pesticides. Introducing flowering plants into such greenhouses may promote the top-down pest suppression by natural enemies and reduce the reliance on pesticide use. However, it is not known how effective this practice is in organically and conventionally managed greenhouse crops. We assessed the influence of introducing flowering plants into open greenhouses with organically and conventionally managed tomato crops on the abundance of pests, natural enemies (NE), pollinators, and crop yield. We monitored tomato crops during two years in two greenhouses at four organic farms and four conventional farms that used integrated pest management (IPM). On each farm one greenhouse contained flower islands of basil (*Ocimum basilicum*), marigold (*Tagetes patula*) and alyssum (*Lobularia maritima*), and the other greenhouse served as a control. Organic farms had yields comparable to conventional farms, a lower abundance of pests, less pest injury, and a higher abundance of NE. The cumulative pest: NE ratio was 9 for organic and 38 for conventional management. The effect of introducing flowering plants on arthropods depended significantly on the type of farm management. Conventionally managed tomato crops in greenhouses with seven flower islands per 100 m² had 18% lower pest abundance compared to the control greenhouses without flowers, while flower islands did not significantly influence arthropod abundances in organically managed tomato crops. Tomato plants had a higher abundance of pests than the three introduced plant species in conventionally managed greenhouses, while marigold had a higher abundance of pests than tomato in organically managed greenhouses. Alyssum supported a relatively low pest abundance and high abundance of NE and pollinators. Our findings indicate that NE in IPM-conventionally managed greenhouses can benefit from resources provided by flowering plants, resulting in reduced pest abundance, while in organically managed greenhouses the conditions are already favourable for the suppression of pests and addition of floral resources does not further improve the effectiveness of NE. This finding highlights the potential of agroecological and organic management to reduce the reliance on synthetic pesticides without yield reduction.

1. Introduction

Vegetable cultivation in (semi-)open greenhouses is often associated with the extensive applications of synthetic pesticides (van Lenteren, 2000), which can have adverse effects on the environment and human health (Mahmood et al., 2016; Tifton et al., 2016; UNCTAD, 2017). Moreover, pest populations can quickly develop resistance against pesticides, triggering further pesticide use and potentially giving rise to a pesticide treadmill (Bommarco et al., 2011; van Lenteren, 2020). While approaches that strengthen biological control can reduce the reliance on

chemical insecticides in vegetable greenhouse production (van Lenteren, 2000), growers often still lack context-specific and actionable knowledge of implementing such approaches on their farms.

There have been several examples of successful biological control in closed greenhouses by introducing natural enemies (Bueno, 2005; van Lenteren et al., 2020, 2018), so-called classical or augmentative biological control strategies (Stenberg et al., 2021). However, in many parts of the world, greenhouses are open structures with an active exchange of arthropods with the surroundings. In open greenhouses, crop production is influenced by the agroecosystem within the greenhouse and the

* Correspondence to: Facultad de Agronomía, Universidad de la República, Camino Folle km 35.500, Progreso, CP. 90000 Canelones, Uruguay.
E-mail address: mscarlato@fagro.edu.uy (M. Scarlato).

<https://doi.org/10.1016/j.agee.2023.108389>

Received 8 July 2022; Received in revised form 12 January 2023; Accepted 25 January 2023

Available online 1 February 2023

0167-8809/© 2023 The Author(s). Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

surrounding landscape that may act as a source for potential pests, natural enemies, and pollinators (Arduany et al., 2022; Aviron et al., 2016; Castañé et al., 2004; Gabarra et al., 2004; Messelink et al., 2021; Tschardt et al., 2012; van Lenteren, 2000). In this context, conservation biological control (CBC) based on plant and habitat diversification is a promising approach to enhance natural enemy populations and disfavours pests (Stenberg et al., 2021), but has received limited attention for open greenhouse cultivation (Li et al., 2021).

Habitat manipulation is a cornerstone of CBC (Begg et al., 2017), which involves the provision of shelter and food, pollen and alternative prey/hosts to support effective populations of natural enemies (Landis et al., 2000; Messelink et al., 2014). Introducing flowering plants providing pollen, nectar, and shelter can be a promising strategy to attract and enhance the activity of natural enemies in greenhouses (Wäckers et al., 2005). This may be especially important for crops, such as tomato, that do not provide sufficient floral food resources to support effective natural enemy populations (Wäckers and van Rijn, 2012). The efficacy of several flowering plant species to enhance natural enemies has been assessed under controlled conditions (Arnó et al., 2018; Conboy et al., 2019; Kopta et al., 2012; Sivinski et al., 2011), but it is not clear how this unfolds under commercial open-greenhouse conditions (but see Li et al., 2021) and what flowering plant species are best suited for the specific agroecological context. In open greenhouses, the effectiveness of CBC strategies is influenced by farm management (Aviron et al., 2016; Balzan et al., 2016; Begg et al., 2017). For instance, the introduction of flowering plants may play out differently in conventional systems where synthetic pesticides and synthetic fertilisers are used than in organic systems. Furthermore, within organic (Marliac et al., 2016; Pépin et al., 2021) or conventional management (Scarlato et al., 2022; Sumberg and Giller, 2022) there is a great diversity of management practices that could influence pest and natural enemy dynamics, such as crop diversity and vegetation management (Yang et al., 2021; Zehnder et al., 2007; Marliac et al., 2016), nutrients (Hsu et al., 2009; Stavisky et al., 2002) and soil management (Altieri et al., 2012; Magdoff and van Es, 2009). Moreover, the efficacy of CBC strategies in open greenhouse settings may be modulated by landscape complexity (Tschardt et al., 2016, 2012). Following the intermediary landscape-complexity hypothesis proposed by Tschardt et al. (2005, 2012) the effectiveness of biodiversity-based management interventions should be higher in simple, intermediately complex landscapes than in extremely simplified landscapes where additions to the impoverished species pool are not sufficient to instigate a meaningful response in the short term, or in highly complex landscapes where there is no discernible effect of adding more diversity (Tschardt et al., 2005, 2012). The wide variation in production situations calls for context-specific and actionable knowledge to support the design and adoption of more sustainable farm management (Altieri, 2002; Duru et al., 2015 a,b; Rossing et al., 2021).

This study assessed the influence of flowering plants in organically and conventionally managed greenhouse tomato on the abundance of pests, natural enemies and pollinators, and crop performance. To do so, we first characterised the management practices in organically and conventionally managed tomato greenhouses and the surrounding landscape. We then compared for each management system how the addition of flower islands influenced the abundances of pests, predators, parasitoids, pollinators and other phytophagous arthropods. Finally, we assessed the abundances of these arthropod groups on the flowering plant species.

2. Materials and methods

2.1. Study area and research approach

The study was conducted in the department of Canelones in the south of Uruguay, where most vegetable production is concentrated (34°21' S to 34°57' S – 55°40' W to 56°40' W). The climate is humid subtropical,

with an average mean temperature of 17 °C (minimum: 11 °C, maximum: 23 °C) and light frosts between May and September. Mean annual precipitation is 1200 mm, evenly distributed throughout the year but with significant variation between years (Castaño et al., 2011). The main soil types are Mollic Vertisols (Hypereutric), Luvic/Vertic Phaeozems (Pachic), and Luvic Phaeozems (Abruptic/Oxyaquic) (Alliaume et al., 2013).

The south of Uruguay comprises 350 ha of greenhouse crops, where tomato is the main crop (DIEA-MGAP, 2017). Typical greenhouses are "open greenhouses" made of wooden posts covered with transparent polyethylene plastic, where ventilation is manually controlled through opening and closing the plastic cover on the sides. Greenhouses typically comprise areas between 380 and 1000 m², and crops are cultivated in the soil (Fig. 1). Greenhouse tomato is produced in short (200 days or less) or long (more than 200 days) cycles. The typical short cycle in spring is transplanted in August or September and harvested until January or February (Berrueta et al., 2019). In this short cycle, greenhouse whitefly (*Trialeurodes vaporariorum* Westwood, Hemiptera: Aleyrodidae) and tomato leaf miner (*Tuta absoluta* (Meyrick), Lepidoptera: Gelechiidae) are major pests that can reduce tomato yield (Berrueta et al., 2019). Occasional pests are thrips (*Frankliniella occidentalis* Pergande, and *F. schultzei* (Trybom), Thysanoptera: Thripidae), aphids (*Macrosiphum euphorbiae* (Thomas) and *Aphis gossypii* Glover, Hemiptera: Aphididae), red spider mite (*Tetranychus urticae* Koch, Acari: Tetranychidae), tomato russet mite (*Aculops lycopersici* (Tryon), Acari: Eriophyidae), stinkbug (*Nezara viridula* L., Hemiptera: Pentatomidae), and cucumber beetle (*Diabrotica speciosa* (Germar), Coleoptera: Chrysomelidae) (Bentancourt and Scatoni, 2010).

We used a participatory research approach where farmers and technicians were closely involved in problem identification and execution of the research. Farmers and technicians expressed their interest to explore the potential of flowering plants in greenhouses to enhance beneficial arthropods during a workshop in December 2017. Field days were organised in farms that used sown flowers in greenhouses to discuss the management and experiences in 2018. During September 2019 and December 2020, preliminary results and adjustments of the experiment were discussed with farmers and technicians during two workshops, and farmers involved in the experiment had weekly interactions with the research team (see below).

2.2. Experimental design

The experiment was conducted at four organically certified and four conventionally managed farms in Canelones. The organic farms were certified and implemented agroecological management for more than five years. The conventional farms implemented biological control and integrated pest management (IPM) for at least three years (Table 1). The criteria for farm selection were: (i) tomato had been an important crop for more than five years; (ii) each farm comprised at least two greenhouses with short cycle spring tomato with similar size, soil type, surrounding vegetation, management (tomato variety, planting date, plant density, soil and fertilisation management), and previous crop; (iii) farmers were willing to engage in the participatory research process. At each farm, we selected two paired greenhouses. In one randomly selected greenhouse, flower islands were established (treatment), while the other greenhouse did not receive flower islands (control). In total, sixteen greenhouses (2 greenhouses x 8 farms) were included. The experiment was conducted during two growing seasons: from October to January 2018–2019 ("Year 2018") and from October to January 2019–2020 ("Year 2019"). Year 2018 had more rain and a greater number of rainy days, less radiation and lower temperatures than 2019 (Appendix A).

The plant species selected for the flower islands were *Lobularia maritima* (L.) Desv. (alyssum, Brassicaceae), *Tagetes patula* L. (marigold, Asteraceae), and *Ocimum basilicum* L. (basil, Lamiaceae). These species were selected because (i) some organic farmers were already using these

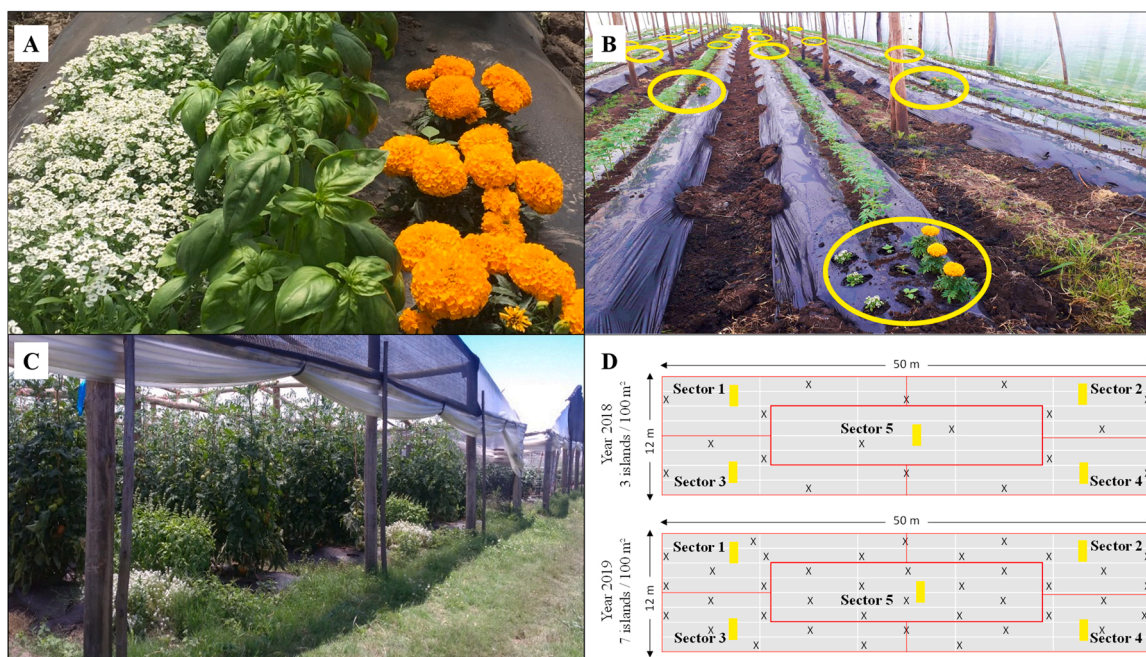


Fig. 1. Flower island composition with three plants of basil in the middle and three marigold and alyssum plants on each side (A), flower islands at ten days post-transplanting (B), flower islands located in the borders of the greenhouse at the onset of tomato harvest (C), schematic overview of a greenhouse of 600 m² divided into five sectors, with locations of yellow sticky traps (yellow quadrangles) and flower islands (crosses) in 2018 and 2019 (D).

Table 1
Overview of farms, type of management, resource endowment and greenhouses size.

Farm number	Type of management ¹	Farm size (ha) ²	Mechanisation level ³	Total labour (FTE) ⁴	Family labour (proportion of Total labour)	Annual farm area vegetable crops (ha)	Greenhouse area vegetable crops (ha)	Irrigated area ⁵	Average individual greenhouse size (m ²)
F1	Organic (since 1991)	26	5	9.1	0.22	5.8	0.77	3	750
F2	Organic (since 1995)	90	5	15.6	0.19	9.5	1.77	2	840
F3	Organic (since 1992)	27	4	12.2	0.30	9.0	0.40	2	700
F4	Organic (since 2014)	27	4	15.8	0.27	6.0	1.14	2	588
F5	Conventional (BC since 2015)	42	4	8.0	0.30	2.9	2.90	3	980
F6	Conventional (BC since 2016)	26	3	3.2	0.63	10.2	0.82	2	1050
F7	Conventional (BC since 2016)	2.2	3	3.1	1	0.7	0.34	3	396
F8	Conventional (BC since 2016)	9	3	2.9	1	0.5	0.48	3	480

¹ BC: biological control. In all cases, farmers used entomopathogenic fungus to control whitefly and used selective insecticides when possible.

² Farm size corresponded to the total area managed by the farmer.

³ Scale 1–5: 1: no tractor or 1 tractor but no tractor sprayer, greenhouse sprayer, mulching machine, disc ridger, rotary tiller, cultivator; 2: 1 tractor and one implement mentioned in 1; 3: 1 tractor and 2 or more implements, or 2 tractors and 2 implements; 4: 2 tractors and more than two implements; 5: 3 or more tractors and 2 or more implements.

⁴ Full-time equivalent (FTE). 1 FTE = 300 days of work and 8 h per day = 2400 h per year of labour.

⁵ Scale 1–3: 1: less than 50% of the annual vegetable area under irrigation, 2: between 51% and 80% of the annual vegetable area under irrigation, 3: 100% of the annual vegetable area under irrigation.

plant species; (ii) these plant species attract natural enemies without attracting potential pests or hosting tomato viruses (Ambrosino et al., 2006; Balzan and Wäckers, 2013; Jankowska, 2010; Lu et al., 2014; Song et al., 2010); (iii) the flowering periods coincide with the tomato crop cycle; and (iv) the plants were readily available from local nurseries.

Each flower island contained three basil, alyssum and marigold plants, for a total of nine plants (Fig. 1-A). The area of the flower islands was approximately 1 m², with a distance of approximately 30 cm

between plants. In the first year, we established three islands per 100 m² greenhouse, with a maximum distance of 8 m between islands and two islands on each greenhouse border (Fig. 1-B, C, D). After discussing first-year results with farmers and technicians, the number of islands in the second year was increased to seven islands per 100 m² greenhouse and three islands on each greenhouse border (Fig. 1-D).

2.3. Data collection

2.3.1. Crop and farm management and tomato yield

Farmers were interviewed to assess their farm and greenhouse management. During the study, the farmers kept records of the pesticide applications (product, dose, date) and other management practices in the greenhouses (soil tillage, fertilisation, irrigation, plant management). We recorded tomato plant density, tomato variety, planting and transplanting date, harvest period, and the preceding crop in the greenhouses. Crop yield was calculated from farmer records of weekly harvests. Soils were characterised through a description of the soil profile and soil analysis. Composite soil samples were taken from the top layer (0–20 cm). We determined soil organic carbon using the Walkley-Black method described by Nelson and Sommers (1996), extractable phosphorus (P, Bray and Kurtz, 1945), exchangeable potassium (K) (atomic absorption spectrophotometry following ammonium acetate 1 M extraction at pH 7 (Isaac and Kerber, 1971), and nitrate content (colorimetry, Mulvaney, 1996). Leaf N concentration was assessed by the Kjeldahl method (Bremner and Mulvaney, 1982) at the start of harvest in the second year on a sample of 15 randomly selected young fully-grown leaves in each greenhouse. Temperature and relative humidity in the greenhouse during the crop cycle were recorded in the second year with a Datalogger (MX2301) placed in the middle of each greenhouse at 2 m height. The percentage of ground cover of weeds in the pathways of the greenhouses was assessed using a ground cover estimation sheet (McNaught et al., 2008). The weed cover assessment was conducted at twenty random plots of 625 cm² (25 × 25 cm) in the pathways of each greenhouse at each sampling round during the first year and at the last four rounds in the second year. Weed cover was classified into three levels: low (less than 20% soil cover during the entire season), medium (between 20% and 50% soil cover in at least half the sampling rounds), and high (more than 50% in at least half the sampling rounds).

2.3.2. Surrounding vegetation

The vegetation around each greenhouse was mapped at two scales: within 3 m and within 150 m. Within 3 m of the greenhouse border, we assessed (i) the type of vegetation (grass, grass and shrubs, bare soil); (ii) the average vegetation height (<20 cm, 20–50 cm, >50 cm); (iii) the number of plant species (<10, 10–20, >20); (iv) the identity of the two or three main plant species; and (v) the type of management or use (mowing, pathway, no management). We classified the area into 4 quality levels: Very low: ≥ 50% bare soil; Low: full vegetation cover with vegetation height < 20 cm and less than ten plant species; Medium: full vegetation cover with vegetation height ≥ 20 cm or more than ten plant species; and High: full vegetation cover with vegetation height ≥ 20 cm and more than ten plant species. In a 150 m radius around the greenhouse, we recorded the type of land use (field crops, vegetable greenhouse crops, pastures, and non-cultivated land) and the type of vegetation (crop species and semi-natural habitat type(s): pasture and/or shrubs and/or trees). The surroundings were classified into three levels of complexity: Low: > 75% arable land and greenhouses; medium: 50–75% arable land and greenhouses; and high: < 50% arable land and greenhouses.

2.3.3. Yellow sticky traps

The abundance of pests, natural enemies, and pollinators in the greenhouses was assessed using yellow sticky traps. Each greenhouse was divided into five sectors, and one sticky trap was placed in the middle of each sector (Fig. 1-D). The sticky traps (15 × 20 cm) had thirty-six quadrants (2 × 2 cm) on each side. Traps were placed above the tomato plants by attaching them to the beams of the greenhouse at approximately two meters height. In 2018, four 14-day sampling rounds were conducted from mid-November (starting dates: mid-November, early December, mid-December, and early January). In 2019, one earlier round was included (early November) for a total of five sampling

rounds.

Upon collection, the traps were wrapped in plastic clingfilm and put in a freezer until processing. Eight of the thirty-six quadrants (32 cm²) on one side of the sticky trap were inspected (one quadrant in each corner, two quadrants left from the centre and two quadrants right from the centre of the sticky trap). The arthropods in the eight quadrants were identified under a microscope to order, family or species level and divided into six functional groups: tomato pests, other phytophagous arthropods, predators, parasitoids, pollinators, and other arthropods. Natural enemies (NE) comprised predators and parasitoids. The group "other arthropods" consisted of arthropods that did not belong to any of the other functional groups or that we could not classify with certainty (e.g. Diptera and ants; Appendix B).

2.3.4. Pest infestation levels on tomato plants

In each sampling round, twenty tomato plants were randomly selected per greenhouse to visually assess whitefly abundance and tomato leaf miner injury. Whitefly adults were counted on the three top leaves of each plant. Tomato leaf miner injury was assessed by counting the number of tunnels on three leaves per plant, at the top, middle, and bottom stratum of plants, respectively. In addition to the sampling rounds described for sticky traps, in 2019 one extra late round of tomato plant assessment was included in mid-January, for a total of four rounds in 2018 and six rounds in 2019.

2.3.5. Visual observation of flower islands

We assessed flower visitation by arthropods during 15-minute observation periods, divided into 5 min per flowering plant species. Observations were made on one randomly selected flower island in each of the five sectors per sampling round in 2018 and three randomly selected islands per greenhouse per sampling round in 2019. Because many arthropods are sensitive to motion, the observer remained motionless during observation and did not cast a shadow on the flower island (Ambrosino et al., 2006). Sampling rounds coincided with yellow sticky traps rounds, for a total of four in 2018 and five in 2019. The arthropods were recorded per plant species, and we used the same arthropod groups as for the yellow sticky traps.

2.3.6. Suction sampling

Arthropods on the flowering plant species in 2018 and 2019 and tomato plants in 2019 were sampled using a handheld aspirator (PK-VC404, 80 W) (Swart et al., 2017). Following the visual observation of flower islands, each flowering plant species and the three tomato plants nearest to each island were sampled for ten seconds. Arthropods were collected in bags and put in a freezer until processing. The arthropods were identified and classified in the same functional groups used for the yellow sticky traps.

2.3.7. Quality assessment of flower islands

Flower island quality was assessed by recording the number of plants per species and their development stage (vegetative or flowering). During each round, the quality of each sampled flower island was recorded. All islands in a greenhouse were assessed at harvest initiation and the end of the tomato cycle.

2.4. Data analysis

We conducted the analysis in four steps. First, the 16 greenhouses were grouped according to their crop and farm management practices, not considering management type. The following variables were included: the amount of organic, synthetic and total N, P, K inputs (kg per ha); the number of synthetic and organic insecticide applications, fungicide applications, and the total number of pesticide applications; biological and alternative products applications; soil organic carbon (percentage) and relative active soil organic matter (proportion); previous crop (tomato, other solanaceous, or other not solanaceous crops);

the presence of other crops in the greenhouse (yes or no); weed cover (low, medium, high); vegetation in the 3 m radius (very low, low, medium, high) and the 150 m radius (low, medium, high); crop diversity in the 150 m radius and over the year (number of crops); plant density (plants m⁻²), greenhouse size (m²), nylon black mulch use (yes or no), and tomato variety type (hybrid, no hybrid). In total 27 variables were included. Factor analysis of mixed data (FAMD) was used to transform categorical variables into continuous principal components and combine and reduce the number of variables (Kassambara, 2017). Hierarchical cluster analysis on the first seven dimensions of the FAMD output was conducted (principal components, HCPC), which explained 88% of the variance. Clusters were defined according to the proportion of the total explained variability and agronomic criteria, and were characterised by the significant active variables used in the partition (Kassambara, 2017). The tomato yield among clusters was compared using the Kruskal-Wallis test.

Second, we assessed how the arthropod abundances per functional group on the yellow sticky traps, and whitefly abundance and leaf miner injury on tomato plants were influenced by the presence or absence of flower islands and the farm management type. We only used data from greenhouses of which 80% of the flower islands still contained at least two flowering plants per species at tomato harvest, resulting in the exclusion of data from farms F1 (organic) in 2018 and F4 (organic) and F5 (conventional) in 2019. We also excluded F6 (conventional) in 2018 because the tomato crops in the two greenhouses were subject to different pesticide application regimes. We used generalised linear models and principal component analysis (PCA) and analysed each year separately. For the generalised linear model analysis, response variables were the abundance of pests, other phytophagous arthropods, parasitoids, predators, natural enemies, pollinators, other arthropods, and total number of arthropods on the yellow sticky traps, number of adult whitefly individuals and number of leaf mines per tomato plant. Explanatory variables were management (organic or conventional), treatment (flowers or control), sampling round, and their two-way interactions. Arthropod abundances and tomato leaf miner injury were treated as count data, and we tested the Poisson, negative binomial, zero-inflated Poisson, and zero-inflated negative binomial error distributions. We selected the negative binomial error distribution for all response variables and both years because models with this error distribution had the lowest Akaike Information Criterion (AICc) value. Residual plots confirmed that the models met homogeneity of variance criteria (Zuur and Ieno, 2016; Zuur et al., 2010). We applied a model selection procedure using the dredge approach, which calculates all possible factor combinations and sorts the models according to the value of AICc. Then we used full model averaging in the cases where we had more than one model within an envelope of 2 delta AICc points (Burnham and Anderson, 2007; Feld et al., 2016; Grueber et al., 2011). For the PCA analysis, we used the summed number of arthropods of all sampling rounds for each functional group, whitefly individuals, and number of tomato leaf mines per tomato plant.

Third, we assessed whether tomato yield was related to management type and the presence or absence of flowers. We used linear models including yield as response variable, and year, management type, flower treatment and their two-way interactions as fixed effects. Residual plots confirmed that the models met homogeneity of variance criteria (Zuur and Ieno, 2016; Zuur et al., 2010). First, we performed the analysis excluding farms F1 and F6 in 2018, and F4 and F5 in 2019 (24 greenhouses). As the flower treatment was not significant, we performed an analysis with the full dataset (32 greenhouses; 2 years).

Fourth, we analysed the arthropod abundance data obtained by suction sampling and visual observation of the three flowering plant species. We used suction sampling data at the functional group level on marigold, alyssum, basil in 2018 and 2019, and tomato in 2019. For visual observations, we used data at the arthropod functional group level on marigold, alyssum and basil in both years. We used generalised linear models and PCA. In the generalised linear models, the response

variables were the abundance of arthropods in each functional group. Pollinators in the suction sampling were discarded because the numbers were too low for a meaningful analysis. The explanatory variables were: farm management type (organic or conventional), plant species (marigold, alyssum and basil for both methods, including tomato in suction data in 2019), year, and round. Model selection and validation were conducted in a similar way as described for step 2. For all functional groups, a negative binomial error distribution was used. For the PCA analysis, we considered the cumulative number of arthropods per functional group (sum of all sampling rounds).

Data analyses were conducted using R 3.6.3 (2020–02–29). The R-packages "factoextra" (Kassambara and Mundt, 2020) and "FactoMineR" (Le et al., 2008) were used for FAMD, HCPC and PCA analyses. The R-packages "MASS" (Venables and Ripley, 2002), "pscl" (Jackman, 2020) and "car" (Fox and Weisberg, 2019) were used for analyses with generalised linear models, and "MuMin" (Barton, 2020) for model selection and averaging. The R-packages "lattice" (Sarkar, 2008), "ggplot2" (Wickham, 2016), "ggpubr" (Kassambara, 2020) and "HH" (Heiberger, 2020) were used for data visualization.

3. Results

3.1. Characterisation of farm management types

The first partition of the HCPC analysis explained 31% of the total variability and resulted in two clusters coinciding with the two farm management types: one cluster included all the organically managed greenhouses, while the other included all the conventionally managed greenhouses (Table 2, Appendix C). Organic management was characterised by a higher number of crops (ranging from 12 to 30 in organic versus 1 to 5 in conventional, $p < 0.001$) and higher soil organic carbon ($p < 0.001$). Both management types used organic manure, but conventional farms combined it with synthetic fertilisers. Organic farms had lower organic and total N, P and K fertilizer input than conventional farms ($p < 0.001$). Both farm management types had a similar total number of pesticide applications, but differed in the type of products used (Table 2, Appendix C). Synthetic pesticides were not used in organic management, but the application of organic insecticides in organically managed greenhouses exceeded those of conventionally managed greenhouses ($p < 0.05$). Organically managed greenhouses had a higher weed cover than conventional ones ($p < 0.01$). Organically managed farms had high and medium vegetation quality in the 3 m area around greenhouses, while conventional farms had low and very low vegetation quality ($p < 0.01$). Conventional farms had a higher proportion of high-quality vegetation within a 150 m radius, while organic farms had more medium quality vegetation ($p < 0.05$, Table 2). Tomato crop yield was not significantly different between organically and conventionally managed greenhouses (Kruskal-Wallis tests $p = 0.676$, Table 2).

3.2. Arthropod sampling in greenhouses and flower islands

Across the two years, 49,073 arthropods were captured on sticky traps in the 16 greenhouses (2018: 19,922; 2019: 29,151). While we captured a higher number of arthropods in 2019 than in 2018, the distribution of the arthropods across functional groups and the main pests, NE and pollinators, were roughly similar. Pests comprised 78% of the total number of arthropods, followed by NE (10%) and other arthropods (9%) (Table 3). Suction sampling of the flowering plants and tomato in the 16 greenhouses resulted in 9804 arthropods, and 4531 arthropods were recorded during visual observation of flowering plants (Table 3). Suction samples were dominated by "other arthropods" (62% of the individuals), pests (19%) and NE (11%, Table 3). In visual observations, "other arthropods" accounted for 39% of the individuals, followed by NE and pollinators in 2018 and NE and pests in 2019 (Table 3). The main pests, NE and pollinators, were the same in both years (Table 3).

Table 2

Characterisation of management across the 32 greenhouses and identification of clusters based on HPCP analysis. Two clusters were identified: one cluster included all greenhouses of conventional farms, while the other included all the organic ones. NA is not applicable. Statistically significant differences are indicated in bold, ns: not significant.

Indicator	Units	Cluster 1: Conventional					Cluster 2: Organic					p-value HPCP analysis
		Number	Average	S.D	Min	Max	Number	Average	S.D	Min	Max	
Yield ¹	kg/m ²	16	9.1	1.9	6.0	12.0	16	8.7	2.3	5.5	12.0	NA
Synthetic insecticide applications	Number of applications	16	3.1	3.2	0	9	16	0	0	0	0	< 0.001
Organic insecticide applications	Number of applications	16	0.1	0.3	0	1	16	3.0	4.0	0	10	< 0.05
Fungicide applications	Number of applications	16	2.7	2.8	0	9	16	2.9	4.0	0	10	ns
Total number of pesticide applications	Number of applications	16	4.3	2.7	1	9	16	3.6	3.9	0	10	ns
Biological and alternative applications ²	Number of applications	16	4.1	3.3	0	10	16	3.6	5.0	0	15	ns
Soil organic carbon	%	16	1.83	0.37	1.31	2.45	16	2.69	0.49	2.13	3.63	< 0.001
Relative active soil organic carbon³	Proportion	16	0.41	0.24	0.15	0.95	16	0.71	0.19	0.49	1.16	< 0.01
N input-organic source	g/m ²	16	10.0	3.8	6	19	16	6.3	3.4	3	10	< 0.01
P input-organic source	g/m ²	16	9.4	5.4	3	22	16	4.3	2.6	2	8	< 0.01
K input-organic source	g/m ²	16	41.4	23.7	8	93	16	22.8	13.3	10	43	< 0.01
N input – synthetic source	g/m ²	16	2.3	2.4	0	6	16	0	0	0	0	< 0.01
P input – synthetic source	g/m ²	16	0	0	0	0	16	0	0	0	0	ns
K input – synthetic source	g/m ²	16	12.3	16.9	0	40	16	0	0	0	0	< 0.05
N input – total	g/m ²	16	12.0	3.8	9	21	16	6.3	3.4	3	10	< 0.001
P input – total	g/m ²	16	9.4	5.4	3	22	16	4.3	2.6	2	8	< 0.01
K input – total	g/m ²	16	53.5	24.9	18	96	16	22.8	13.3	10	43	< 0.001
NO ₃ -soil at harvest initiation	ppm	8	236	106	116	376	8	181	81	96	314	NA
N-leaf at harvest initiation	%	8	2.8	0.2	2.5	3	8	2.6	0.6	1.8	3.6	NA
Average air temperature	°C	8	22.5	1.7	20.0	26.0	8	22.7	1.6	19.7	25.4	NA
Average relative humidity	%	8	68.3	4.9	56.5	77.7	8	69.0	5.1	58.2	81.0	NA
Plant density	Number of plants / m ²	16	2.64	0.22	2.22	3.07	16	2.37	0.38	1.87	3.45	ns
Greenhouse size	m ²	16	686	314	320	1080	16	724	115	528	870	ns

Indicator	Units	Number	Median	Min	Max	Number	Median	Min	Max
Number of crops in 150 m radius	Number of crops	16	2	1	5	16	19	12	30
Number of crops per year in the farm	Number of crops	16	6	2	8	16	41	28	48

Indicator	Classes	Number	Number of cases per class	Number	Number of cases per class
Vegetation quality in the 3 m radius⁴	High / Medium / Low / Very Low	16	0 high, 2 medium, 6 low, 8 very low	16	6 high, 10 medium, 0 low, 0 very low
Proportion of uncultivated land in 150 m radius⁵	High / Medium / Low	16	9 high, 7 medium, 0 low	16	3 high, 12 medium, 1 low
Previous crop in the greenhouse	Tomato / Other Solanaceae / Other	16	5 tomato, 5 other Solanaceae, 6 other	16	6 tomato, 6 other Solanaceae, 4 other
Diverse crops inside the greenhouse	Only tomato / Combined	16	16 only tomato	16	9 only tomato, 7 combined
Weed cover inside greenhouse⁶	High / Medium / Low	16	0 high, 8 medium, 8 low	16	8 high, 4 medium, 4 low
Nylon black mulch	Yes/ No	16	6 yes, 10 no	16	12 yes, 4 no
Tomato variety ⁷	Hybrid / Non-hybrid	16	16 hybrid	16	12 hybrid, 4 mixture hybrid-non-hybrid

¹ Estimated based on weekly records of the farmers. Not significantly different for organically and conventionally managed greenhouses (Kruskal-Wallis tests $p = 0.676$).

² Entomopathogenic fungus, milk and bicarbonate, vegetable oil.

³ Relative Active Soil Organic Carbon (RASOC) = ((Actual SOC – Min SOC)/(Max SOC – Min SOC)) * 100 (Dogliotti et al., 2014).

⁴ Vegetation quality in the 3 m radius: High: soil full covered, more than 20 sp and more than 10 sp., Medium: soil full covered, more than 20 cm or more than 10 sp, Low: soil full covered, less 20 cm high, less than 10 species, Very low: with 50% or more soil no covered.

⁵ Proportion of uncultivated land in 150 m radius: High: < 50% crop fields and greenhouses, Medium: 50–75% crop fields and greenhouses, Low: > 75% crop fields and greenhouses.

⁶ Weeds cover: High: more than 40% in at least half sampling rounds, Medium: between 10% and 40% in at least half sampling rounds, Low: less than 10% soil cover during all season.

⁷ Tomato genetic: Hybrid: Belfast, Etere, Ichiban, Barteza, Santa Paula; Non-hybrid: farmer's seeds of heirloom tomatoes

Detailed information can be found in [Appendix D](#).

3.3. Influence of flower islands and farm management

Organically managed tomato supported a significantly lower abundance of pests ($p < 0.001$), lower population densities of greenhouse whitefly ($p < 0.05$ – 0.001 depending on the round), and lower tomato leaf miner injury levels ($p < 0.001$) than conventionally managed tomato, and this was consistent for 2018 and 2019, and for yellow sticky

trap data and observed pest infestation levels on tomato plants (Figs. 2-A and 2-C, Table 4). Pest populations, dominated by greenhouse whiteflies, increased exponentially in conventional farms, while in organic farms, populations only increased slightly or remained stable along crop cycle (Fig. 3, Appendix E).

In 2018 the establishment of flower islands did not significantly influence the abundance of pests on sticky traps (Table 4, Fig. 2-B) or observed pest infestation levels on tomato plants (Fig. 2-B, Appendix E). Similarly, in 2019, greenhouse whitefly abundance assessed by visual

Table 3
Number of arthropods collected by three sampling methods, distribution among functional groups and main orders/families of dominant groups.

Method	Total number of arthropods	Distribution among the functional groups (%) and main order/family identified within each functional group (%)					
		Pests	Natural enemies (NE)		Pollinators	Other phytophagous	Other
			Parasitoids	Predators			
Sticky traps	49073	78 Greenhouse whitefly (Hemiptera: <i>Aleyrodidae</i> , 80%) thrips (Thysanoptera: <i>Terebrantia</i> , 17%)	8 microhymenoptera (74%)	2 longlegged flies (Diptera: <i>Dolichopodidae</i> , 8.5%)	3 houseflies (Diptera: <i>Muscidae</i> , 38%) wasps (Hymenoptera: <i>Vespidae</i> , 33%)	1	8
Suction sampling of flowering plants and tomato	9804	19 thrips (Thysanoptera: <i>Terebrantia</i> , 63%) aphids (23%)	6 microhymenoptera (51%) spiders (33%)	5	0	8	62
Visual observation of flowering plants	4531	17 stinkbugs (Hemiptera: <i>Pentatomidae</i> , 55%) thrips (Thysanoptera, 37%)	13 microhymenoptera (44%) hoverflies (Diptera: <i>Syrphidae</i> , 26%) spiders (8%)	14	9 houseflies (72%) wasps (17%)	8	39

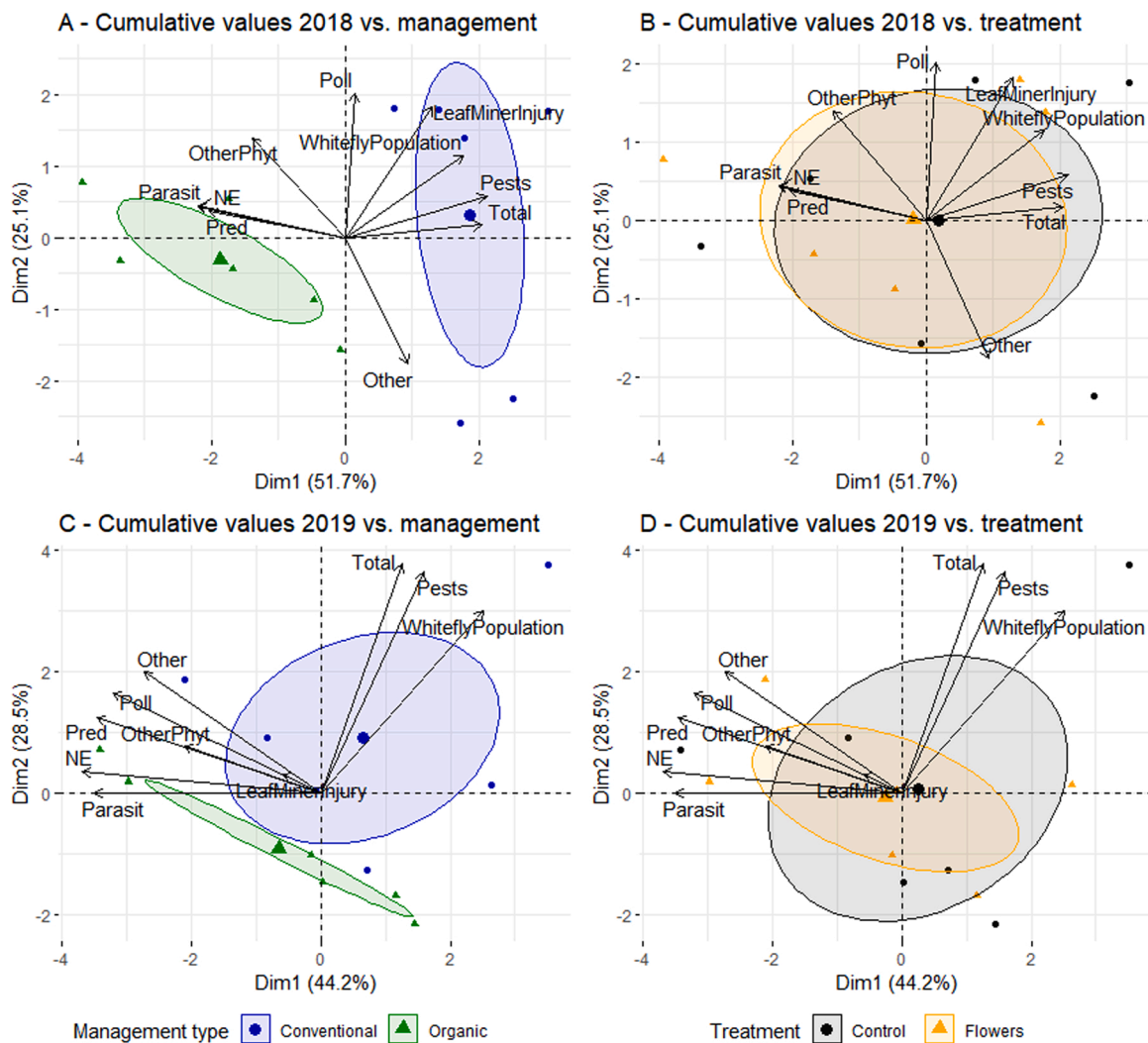


Fig. 2. Principal component analysis of total number of arthropods captured per greenhouse during the growing cycle in sticky traps: pests, parasitoids (Parasit), predators (Pred), natural enemies (NE), pollinators (Poll), other phytophagous (OtherPhyt), other arthropods (Other) and total whitefly population and tomato leaf miner injury in tomato plants. Separate analyses were conducted for 2018 (A and B) and 2019 (C and D). Management type (A, C) and flower treatment (B, D) are indicated with specific markers. For both years, N = 12 greenhouses, and the total variation explained by the first two principal components was in all cases more than 70%.

Table 4

Results of the model averaging procedure (based on $\Delta AICc < 2$) to assess the effects of farm management type (conventional versus organic), presence or absence of flower islands, and sampling round on the abundance of pests, natural enemies (NE) and pollinators on yellow sticky traps, and greenhouse whitefly abundance and tomato leaf miner injury on tomato plants. All models included a negative binomial error distribution. NA is not applicable. A dash (/) indicates that the variable was not included in the final model. Estimates are shown, with the standard error between brackets and statistical significance in bold and with asterisks. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; $^{\dagger} p < 0.1$.

Variable	2018					2019				
	Pests	NE	Pollinators	Whitefly	Leaf miner	Pests	NE	Pollinators	Whitefly	Leaf miner
Organic	-0.30 (0.20)	0.95 (0.20) ***	-0.05 (0.10)	0.28 (0.49)	-3.34 (0.70)***	0.62 (0.23) **	0.39 (0.13) **	-0.08 (0.12)	-2.61 (1.17)*	-2.98 (0.26)***
Flowers	-0.02 (0.06)	0.04 (0.2)	-0.01 (0.06)	/	/	-1.26 (0.24) ***	0.09 (0.13)	0.08 (0.12)	/	/
Round2	NA	NA	NA	NA	NA	0.23 (0.26)	0.42 (0.14) **	0.92 (0.21) ***	2.41 (1.10) *	-1.13 (0.51)*
Round3	0.81 (0.19) ***	0.62 (0.22) **	/	1.75 (0.48) ***	-0.36 (0.00)	2.14 (0.25) ***	0.18 (0.14)	0.53 (0.21)* *	2.22 (0.97) *	1.14 (0.45) *
Round4	1.48 (0.19) ***	0.56 (0.22) *	/	2.64 (0.48) ***	1.68 (0.84)*	2.90 (0.26) ***	0.46 (0.14) ***	0.48 (0.21)* *	3.35 (1.04) **	1.08 (0.45) *
Round5	2.14 (0.19) ***	1.12 (0.21) ***	/	3.80 (0.48) ***	2.41 (0.83)**	3.13 (0.25) ***	1.09 (0.13) ***	0.62 (0.21)* **	3.30 (0.99) ***	-0.20 (0.47)
Round6	NA	NA	NA	NA	NA	NA	NA	NA	2.89 (0.68) ***	2.33 (0.45) ***
Organic:Flowers	/	-0.00 (0.16)	/	/	/	0.36 (0.17) *	-0.13 (0.19)	/	/	/
Flowers:Round2	NA	NA	NA	NA	NA	1.13 (0.31) ***	/	/	/	/
Flowers:Round3	/	-0.09 (0.24)	/	/	/	0.88 (0.30) **	/	/	/	/
Flowers:Round4	/	-0.12 (0.24)	/	/	/	1.05 (0.30) ***	/	/	/	/
Flowers:Round5	/	-0.02 (0.23)	/	/	/	1.30 (0.30) ***	/	/	/	/
Flowers:Round6	NA	NA	NA	NA	NA	NA	NA	NA	/	/
Organic:Round2	NA	NA	NA	NA	NA	-0.65 (0.31) *	/	/	-1.74 (1.73)	/
Organic:Round3	-0.83 (0.28)**	-0.20 (0.24)	/	-1.68 (0.69) *	/	-1.84 (0.30) ***	/	/	-1.22 (1.30)	/
Organic:Round4	-1.30 (0.28)***	0.18 (0.24)	/	-2.98 (0.69) ***	/	-2.31 (0.30) ***	/	/	-1.47 (1.50)	/
Organic:Round5	-1.40 (0.27)***	-0.45 (0.23)	/	-3.11 (0.68) ***	/	-2.44 (0.30) ***	/	/	-1.27 (1.34)	/
Organic:Round6	NA	NA	NA	NA	NA	NA	NA	NA	-0.38 (0.79)	/
Number models averaged	2	2	3	1	1	2	3	4	2	1
AICc	2129.7	1356.5	982.5	451.6	146.2	2596.3	1598.5	1030.4	679.0	403.0

Model references: Management: conventional, Treatment: control, Round: 2 in 2018, 1 in 2019.

observation and tomato leaf miner injury on tomato plants were not significantly influenced by the presence of flower islands (Appendix E). For sticky trap catches, however, there was a significant interaction between the farm management type and treatment in 2019 ($p < 0.05$), indicating that pest abundance was lower in greenhouses with flowers on conventional farms but not on organic farms (Table 4, Fig. 2-D, Fig. 3). In the three conventional farms included in the analysis in 2019, the summed number of pests of all sampling rounds of the greenhouse with flowers was $18 \pm 8\%$ lower than the control greenhouse.

In both 2018 and 2019, NE abundance on yellow sticky traps was significantly higher in organically than in conventionally managed tomato ($p < 0.001$ in 2018, $p < 0.01$ in 2019) (Figs. 2-A and 2-C, Fig. 3, Table 4), both for parasitoids ($p < 0.001$ in 2018, $p < 0.01$ in 2019) and predators ($p < 0.001$ in 2018, $p < 0.05$ in 2019) (Figs. 2-A and 2-C, Appendix E). The presence of flower islands did not significantly influence NE abundance (Table 4, Fig. 3). NE abundance increased in rounds 3, 4 and 5 in 2018 and 2, 4 and 5 in 2019 for both management types and flower treatments (Table 4, Fig. 3).

Pollinator abundance on yellow sticky traps was not significantly influenced by management type or flower treatment in both years and showed an increase in sampling rounds 2 to 5 in 2019 (Table 4). The abundance of other phytophagous arthropods was not significantly influenced by any explanatory variable in 2018 and only by sampling round in 2019 (Appendix E). The abundance of other arthropods

decreased during the crop cycle ($p < 0.001$) and was lower on organic than conventional farms in 2019 ($p < 0.05$, Appendix E).

Tomato yield was not significantly influenced by management type (linear model $p = 0.730$; and cluster's comparison Section 3.1), the presence or absence of flower islands ($p = 1.000$) or year ($p = 0.931$).

3.4. Influence of flowering plant species

Visual observations of arthropods on flowering plants indicated that organic farms had a higher abundance of arthropods visiting the flowering plants than conventional farms ($p < 0.001$), including higher numbers of pests ($p < 0.05$), predators ($p < 0.05$), and other arthropods ($p < 0.001$) (Table 5, Appendix F). Alyssum had a lower abundance of pests than basil and marigold ($p < 0.001$, Table 5), a higher abundance of other phytophagous ($p < 0.05$) and other arthropods ($p < 0.001$, Fig. 4-A, Appendix F). Alyssum supported the highest abundance of NE ($p < 0.001$), caused by a higher number of parasitoids than marigold ($p < 0.001$) and a higher number of predators than basil and marigold ($p < 0.001$) (Fig. 4-A, Table 5). Alyssum also had a higher abundance of pollinators than basil ($p < 0.05$) and marigold ($p < 0.001$, Fig. 4-A, Table 5).

There was a significant interaction between plant species and management type in the suction samples, indicating that the abundance of pests on conventionally managed tomato plants was higher than on

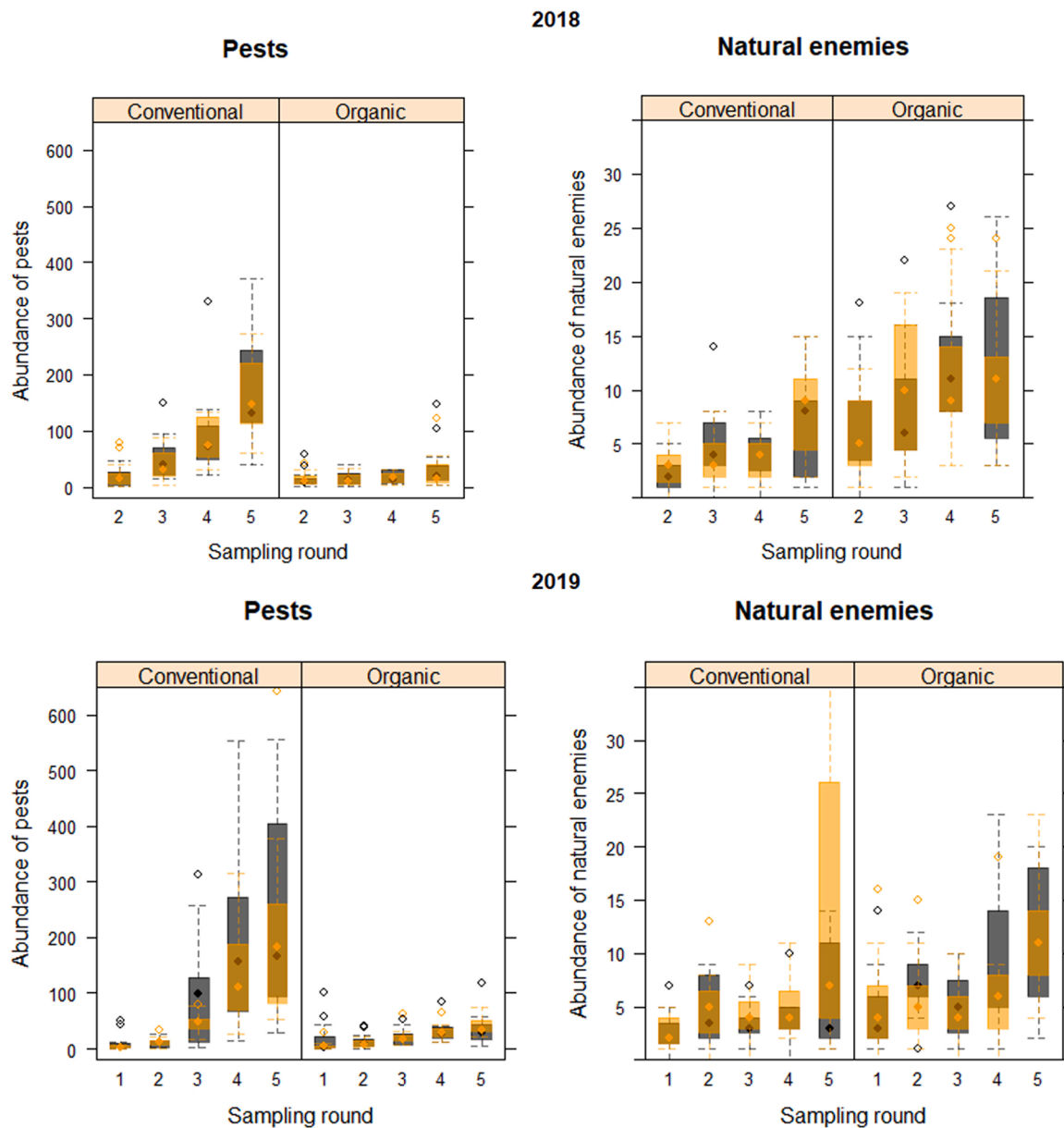


Fig. 3. Boxplots of the development of pest and natural enemies abundance in conventionally and organically grown tomatoes in greenhouses with (orange) and without flower islands (black) in 2018 (top) and 2019 (bottom). The Y-axis shows the abundance of pests or natural enemies on yellow sticky traps. Sampling rounds 1: early Nov, 2: mid-Nov, 3: early Dec, 4: mid-Dec, and 5: early Jan. Organically managed tomato had significantly lower pest abundance than conventional greenhouses from round 3 to 5 in 2018 and 2 to 5 in 2019 ($p < 0.05$ to < 0.001 depending on the round), and higher NE abundance ($p < 0.001$ in 2018, $p < 0.01$ in 2019). Conventionally managed tomato crops with flower islands in 2019 had a significantly lower pest abundance than without flower islands ($p < 0.05$).

allyssum, basil, and marigold. In contrast, in organically managed tomato, marigold had a higher abundance of pests than tomato and alyssum ($p < 0.001$, Fig. 4-B, Table 5), which was mainly caused by the presence of thrips and aphids. In both farm types, basil had the lowest abundance of pests ($p < 0.001$). Alyssum supported the highest abundance of NE ($p < 0.001$), caused by a higher abundance of parasitoids than tomato, basil and marigold ($p < 0.001$), and a higher abundance of predators than basil and tomato ($p < 0.001$), irrespective of farm type (Fig. 4-B, Table 5).

Both visual observation and suction sampling of flowering plant species indicated that the abundance of pests ($p < 0.001$), other phytophagous ($p < 0.001$), parasitoids ($p < 0.001$), predators ($p < 0.001$), and other arthropods ($p < 0.001$) was higher in 2019 than in 2018 (Table 5, Appendix F). The number of observed pollinators was significantly higher in 2018 than in 2019 ($p < 0.001$). NE, other

phytophagous and other arthropods increased during the sampling rounds, while the abundance of pests increased in rounds 3 and 4 ($p < 0.01$) as assessed by suction sampling, but not by visual observation (Table 5, Appendix F).

4. Discussion

This study assessed the effect of introduced flowering plants and farm management (organic and conventional) on the abundance of pests, natural enemies, and pollinators in commercial greenhouse tomato crops in the south of Uruguay. We reported three key findings. First, organic farms had a lower abundance of pests and pest injury levels and a higher abundance of natural enemies than conventional farms, resulting, on average, in a pest:NE ratio of 9 in organically and 38 in conventionally managed greenhouses. Moreover, while pests

Table 5

Results of the model averaging procedure (based on $\Delta AICc < 2$) to assess the effects of the plant species (PlantSp: marigold, alyssum and basil), farm management type (conventional and organic), year (2018 and 2019) and sampling round on the abundance of pests, natural enemies (NE), parasitoids, predators and pollinators assessed by suction sampling and visual observation. Suction sampling data also contain arthropod abundances on tomato. All models included a negative binomial error distribution. NA is not applicable. A dash (/) indicates that the variable was not included in the final model. Estimates are shown, with standard error between brackets and statistical significance in bold and asterisks: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; † $p < 0.1$.

Variable	Suction sampling				Visual observation				
	Pests	NE	Parasitoids	Predators	Pests	NE	Parasitoids	Predators	Pollinators
Year2019	0.49 (0.12) ***	1.21 (0.14) ***	1.42 (0.20) ***	1.03 (0.16) ***	1.61 (0.16) ***	1.65 (0.11) ***	4.51 (0.40) ***	0.83 (0.11) ***	-0.89 (0.16) ***
Organic	-0.38 (0.16) *	0.02 (0.07)	-0.01 (0.09)	0.11 (0.14)	0.30 (0.14) *	0.11 (0.09)	-0.01 (0.08)	0.23 (0.10)*	-0.05 (0.11)
Basil	-0.72 (0.17) ***	-1.58 (0.16) ***	-1.62 (0.22) ***	-1.53 (0.20) ***	1.00 (0.17) ***	-0.51 (0.11) ***	0.04 (0.17)	-0.86 (0.13) ***	-0.36 (0.16)*
Marigold	-0.03 (0.16)	-0.63 (0.13) ***	1.10 (0.20) ***	-0.16 (0.14)	1.22 (0.18) ***	-0.81 (0.12) ***	-0.62 (0.18) ***	-0.80 (0.13) ***	-1.78 (0.26) ***
Tomato	0.67 (0.19) ***	-2.52 (0.23) ***	-2.60 (0.31) ***	-2.47 (0.32) ***	NA	NA	NA	NA	NA
Round2	-0.45 (0.19)	0.42 (0.28)	0.74 (0.42)	0.14 (0.33)	-0.79 (0.26)**	1.14 (0.19) ***	0.43 (0.27) ***	1.36 (0.24) ***	1.28 (0.48)**
Round3	0.48 (0.18) **	1.35 (0.25) ***	1.77 (0.38) ***	0.91 (0.28) **	-0.23 (0.24)	1.01 (0.19) ***	0.96 (0.25) ***	1.05 (0.24) ***	1.41 (0.47)**
Round4	0.77 (0.17) ***	1.49 (0.24) ***	2.05 (0.67) ***	1.02 (0.27) ***	-0.02 (0.24)	1.36 (0.18) ***	1.26 (0.24) ***	1.35 (0.23) ***	1.09 (0.48)*
Round5	0.32 (0.18)	1.84 (0.24) ***	2.14 (0.38) ***	1.57 (0.28) ***	0.11 (0.25)	1.15 (0.19) ***	1.47 (0.26) ***	1.00 (0.25) ***	1.69 (0.47) ***
Organic: Basil	0.10 (0.25)	/	/	/	/	/	/	/	/
Organic: Marigold	0.46 (0.23)*	/	/	/	/	/	/	/	/
Organic: Tomato	-1.01 (0.27) ***	/	/	/	NA	NA	NA	NA	NA
Round: PlantSp	/	/	/	/	/	/	/	/	/
Management: Round	/	/	/	/	/	/	/	/	/
Number of models averaged	1	2	2	2	1	2	2	1	2
AICc	2736.7	1773.7	1276.3	1216.2	1560.1	2018.9	1162.33	1579.2	1150.9

Model references: Year: 2018, Management: conventional, Plant species: Alyssum, Round: 1

Figure captions

increased exponentially during the growing season in conventional farms, they remained constant or increased slightly in organic farms. Second, the effect of flowering plants on arthropods depended on the type of farm management. In conventional farms, tomato crops with flower islands had, on average, an 18% lower pest abundance during the growing season than the controls, while flower islands did not affect arthropod abundance in organic farms. This interaction was significant in the second year when we doubled the number of flower islands per greenhouse as compared to 2018. Third, alyssum, basil, and marigold had a lower proportion of pests and a higher proportion of NE than tomato plants. However, while tomato had a higher abundance of pests than the three introduced plant species in conventionally managed greenhouses, marigold had a higher abundance of pests than tomato in organically managed greenhouses. Alyssum had the lowest abundance and proportion of pests and the highest abundance and proportion of NE and pollinators.

Organic farms achieved tomato yield levels similar to conventional farms, but had a lower pest pressure and more natural enemies than conventional farms. The presence of NE early in the season when pest densities are still very low, as we found in organic greenhouses, is essential for the suppression of pests, in particular for greenhouse whitefly, the dominant pest, which has the potential for exponential population increase (Jaworski et al., 2019; van Lenteren et al., 1996). Moreover, in conventionally managed tomato more insecticides with lower selectivity and higher toxicity on natural enemies of the main pests of the crop were applied than in organic tomato (Appendix C, Table C2), which can disrupt natural biological control and lead to secondary pest outbreaks (Janssen & van Rijn, 2021). Frequent insecticide applications can also trigger resistance development in pest populations, such that insecticides are no longer effective in controlling pests (Bommarco et al., 2011; van Lenteren, 2000). The patterns in pest

and natural enemy populations in the conventionally managed greenhouses in our study were compatible with the patterns that can be expected from insecticide-mediated disruption of biocontrol and resistance development in pest populations. In addition, the conventional farms involved in this study were already in a transition process towards integrated pest management (IPM) for at least three years and had a substantially lower number of pesticide applications (4.3 on average) than the average of 11 applications in short cycle tomato in the south of Uruguay (Scarlato et al., 2022). Thus, the pest problems in conventional farms in this study may be relatively low as compared to the mainstream conventional farms based on the number of applications and may not reveal the full extent of the pesticide induced problems.

Besides pesticide use, organically and conventionally managed greenhouse tomato differed in many other aspects. The conventional farms applied IPM and substituted synthetic pesticides by less harmful products when possible (Deguine et al., 2021). The organic farms involved in this study applied agroecological management (Deguine et al., 2021; Nicholls et al., 2016), which influenced resource availability and host plant finding for herbivores in various ways (bottom-up effects). For instance, relatively high levels of crop diversity, vegetation quality around the greenhouses (Sarhou et al., 2014; Yang et al., 2021; Zehnder et al., 2007), and weed abundance and richness (Bretagnolle and Gaba, 2015; Marshall et al., 2003; Ryelandt et al., 2017; Storkey and Neve, 2018) reduce the potential of herbivores to find host plants. Furthermore, high soil organic matter levels (Altieri et al., 2012; Magdoff and van Es, 2009), absence of synthetic fertilisers and lower levels of nutrient application reduce the host plant quality for herbivores and the associated potential for population increase (Hsu et al., 2009; Jauset et al., 2000; Stavisky et al., 2002). The absence of synthetic pesticides and crop and wild plant diversification also influenced the amount, diversity and proximity of natural enemies (top-down effects).

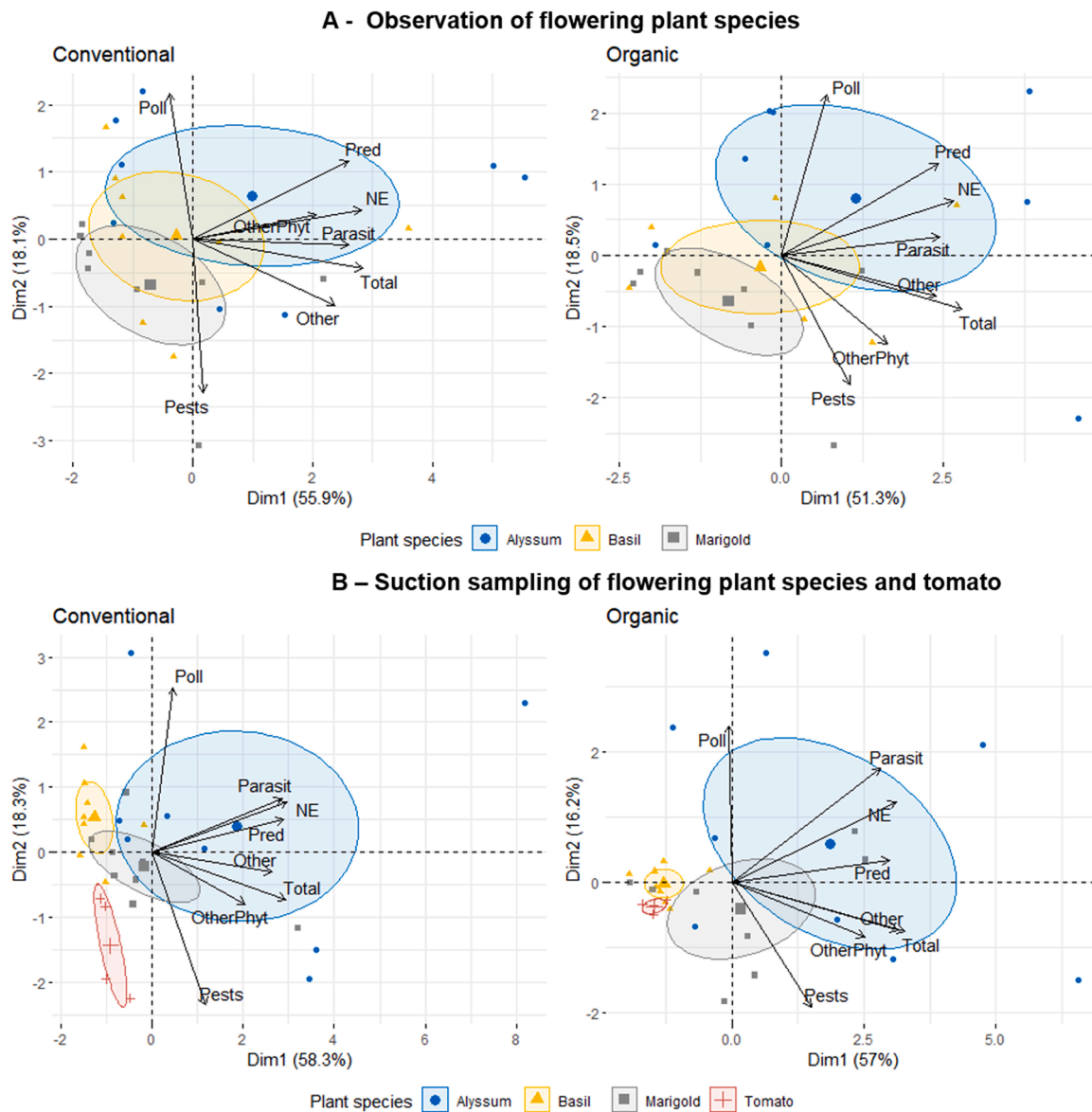


Fig. 4. Principal component analysis of total number of arthropods per functional group: pests, parasitoids (Parasit), predators (Pred), natural enemies (NE), pollinators (Poll), other phytophagous (OtherPhyt), other arthropods (Other). (A) Observed among flowering species (N = 56), and (B) captured with suction sampling among flowering species and tomato (N = 48) during the growing cycle according to management type. Plant species are indicated with specific markers. The total variation explained by the first two principal components in both analysis was more than 70%.

While our experimental setup did not allow assessing the contribution of these various aspects to pest suppression in organically managed farms, they likely influenced the capacity for bottom-up and top-down pest suppression mechanisms (Bianchi, 2022). We hypothesise that the pest suppressive environment of the organic systems was created by various management practices that had been implemented simultaneously for more than five years, rather than by a single practice. Thus, quick fixes and “silver bullet” approaches have limited potential (Lewis et al., 1997), highlighting the need for a more holistic management approach to reduce the reliance on synthetic pesticides (Deguine et al., 2021; Lewis et al., 1997; Nicholls et al., 2016).

Our finding of a significant reduction of pest abundance by increasing floral resources in conventional management but not in organic management indicates that the potential of flowering plants to enhance biocontrol in open greenhouse tomato is moderated by farm management and landscape context (Balzan et al., 2016; Begg et al., 2017; Tscharntke et al., 2016, 2012). The “intermediate landscape-complexity hypothesis” proposed by Tscharntke et al. (2012)

postulates that the efficacy of biodiversity-based management interventions depends on landscape complexity. Landscapes with a low complexity may be most responsive to these management practices, while for landscapes with an already high level of complexity the addition of more diversity will only have limited effect (Tscharntke et al., 2005, 2012). Our results suggest that this hypothesis may also apply to the open greenhouses in our study region. While conventional farms had a higher proportion of non-cultivated land than organic farms in a 150 m radius around greenhouses (Table 2), organic farms had a higher crop diversity in this area, reflecting more diversified crop rotations, a higher vegetation quality in the 3 m adjacent to the greenhouses, and a higher weed cover in the greenhouse. Organic systems may therefore have a higher structural complexity within and outside the greenhouse than conventional systems, and the addition of flower resources may have contributed relatively little to the resources for natural enemies that were already present (i.e. resources reached saturation levels) (Tscharntke et al., 2012). In contrast, in conventional farms with low pesticides use, the addition of flower islands made a

meaningful contribution to pest suppression, suggesting that these farm contexts reflect the responsive part of the "intermediate landscape-complexity hypothesis" curve.

The introduced flower islands significantly reduced pest abundance in the conventionally managed farms after increasing their number of islands in the second year. Pest abundance of greenhouses with flower islands decreased by on average 18% in comparison with greenhouses without flowers. The pest reduction was mainly caused by a decrease in the abundance of greenhouse whiteflies. We did not find a significant effect of flower islands on NE abundance. However, it is possible that the flower islands affected NE efficacy of pest control by providing resources that enhance NE activity (Lu et al., 2014). Indeed, we found that the flowering plants supported parasitoids and generalist predators, such as hoverfly larvae and spiders. A second explanation may be the release of volatile compounds by marigold that may deter whiteflies (Conboy et al., 2019). A third explanation could be that the placement of the yellow sticky traps at about 2 m height above the tomato plants was effective in trapping greenhouse whitefly adults located at the top of the plants (Basso et al., 2001), but underestimated the abundance of NE. For instance, parasitoids may be more abundant in the middle of the plant where eggs and immature stages of whitefly are placed (Basso et al., 2001). Our study setup did not allow testing these potential mechanisms and therefore further research is needed to elucidate this paradox.

Many flowering plant species have been tested for their potential role in enhancing biological pest control (Arnó et al., 2018; Balzan, 2017; Kopta et al., 2012; Li et al., 2021; Parolin et al., 2012; Wäckers and van Rijn, 2012). We found differences between marigold, basil, and alyssum to support tomato pests, NE, and pollinators. The three plant species had a lower proportion of pests and a higher proportion of NE than tomato plants. However, while tomato had a higher abundance of pests than the three introduced plant species in conventionally managed greenhouses, marigold had a higher abundance of pests than tomato in organically managed greenhouses. Alyssum supported the highest number of NE and pollinators and relatively few pests, confirming previous research findings (Arnó et al., 2018; Pease and Zalom, 2010; Ribeiro and Gontijo, 2017). On the contrary, marigold supported a relatively high number of pests (mainly thrips and aphids), and relatively few NE and pollinators. Marigold has earlier been reported to perform less than other flowering species such as alyssum and *Fagopyrum esculentum* Moench (Arnó et al., 2018), *Anethum graveolens* L., *Calendula officinalis* L., *Centaurea cyanus* L., *Fagopyrum esculentum* L. and *Foeniculum vulgare* (Kopta et al., 2012), and *Cosmos bipinnatus* Cav. and *Borago officinalis* L. (Li et al., 2021). Nevertheless, marigold hosted a lower abundance of pests than tomato in conventionally managed greenhouses. In contrast, marigold had a higher abundance of pests than tomato on organic farms, potentially functioning as a reservoir of pests and/or as a trap crop (Srinivasan et al., 1994). The differences among flowering plants may be related to their flower morphology, floral resources, flowering intensity, flowering period, and presence of secondary metabolites or volatiles (Wäckers and van Rijn, 2012). Alyssum had the highest intensity and most extended flowering period, basil had flowering waves, and marigold had a relatively low number of flowers and had the lowest number of plants persisting in the greenhouses. Therefore, it is important to select the flowering species according to their morphological characteristics and attractiveness while considering the practical considerations in commercial open greenhouses.

The involvement of farmers and technicians during all the stages of the research was essential for ensuring that the research findings were relevant to farmers. The participatory methodology helped to shape and improve the research substantially. In particular, after the first year of research, in June 2019, a workshop was held to discuss the first year's results and adjust or improve the experiment for the second year. In this workshop, farmers proposed to double the flower island density, which improved pest suppression in conventionally managed tomato. The farmers also identified the need for more information to explain the management effects, which led to the inclusion of an additional early

sampling round, the monitoring of temperature and relative humidity in the greenhouses, and the measurement of tomato leaf nitrogen content. Also, several ideas emerged for future management adjustments and follow-up research. For example, planting the islands earlier might provide resources for early NE colonisation of the greenhouses (Conboy et al., 2019; Jaworski et al., 2019). Moreover, flower islands inside the greenhouses could be complemented with perennial flower strips or islands at the outside borders (Arnó et al., 2018; Li et al., 2021). Finally, flowering plant species selection according to their attractiveness to NE and pests is important (Li et al., 2021; Wäckers and van Rijn, 2012). During the workshop, farmers expressed the need for more research-supported knowledge to enhance conservation biological control by managing the attractiveness of the surrounding natural vegetation and nearby crops (Bärberi et al., 2010) and the resources provided by native plants (Landis et al., 2012). Therefore, the participatory method applied promoted synergies between the context-specific empirical knowledge of farmers and technicians and the scientific knowledge of researchers that improved the research design and allowed the identification of new questions for the research agenda.

5. Conclusions

Our study revealed that organically and conventionally managed tomatoes in open greenhouses comprise clearly different agroecosystems, which had profound effects on pest and natural enemy dynamics. The differences between organic and conventional management were not only reflected by the abundances of pests and natural enemies, but also by the arthropod responses to flower islands. While the introduction of sufficient flower islands resulted in a 18% reduction of pest abundance in IPM-conventionally managed tomato, it did not further reduce pest abundance in organic tomato systems based on agroecological management, which was already low. This indicates that the introduction of flowering plants has potential as a conservation biological control strategy in conventional systems with low pesticides use, and that organic systems based on agroecological management already benefit from effective levels of functional diversity to suppress pest populations without the addition of flowers. Despite the differences between the two systems, the tomato yield levels were comparable, highlighting that there is ample room to reduce synthetic insecticides without productivity loss in Uruguayan vegetable production (Scarlato et al., 2022). Furthermore, the gap in pest densities between conventional systems with flower resources and organic systems indicates that the addition of flower resources in conventional systems alone is not enough to effectively suppress pests, and that a more holistic approach is needed.

CRedit authorship contribution statement

M. Scarlato: Conceptualization, Methodology and design, Data generation, Data handling and analysis, Writing – original draft, Writing – review & editing. **L. Bao:** Conceptualization, Methodology and design, Data generation, Writing – review & editing. **S. Dogliotti:** Conceptualization, Methodology and design, Writing – review & editing. **W.A.H. Rossing:** Conceptualization, Methodology and design, Writing – review & editing. **F.J.J.A. Bianchi:** Conceptualization, Methodology and design, Writing – review & editing. **P. Bertoni:** Data generation, Writing – review & editing.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Mariana Scarlato reports financial support and administrative support were provided by University of the Republic Uruguay. Mariana Scarlato reports article publishing charges was provided by Wageningen University & Research. Mariana Scarlato reports financial support was

provided by Netherlands Foundation of Scientific Research Institutes. Walter Rossing, Felix Bianchi reports financial support was provided by Wageningen University & Research. Leticia Bao, Paloma Bertoni, Santiago Dogliotti reports financial support was provided by University of the Republic Uruguay. Mariana Scarlato reports financial support was provided by National Agricultural Research Institute of Uruguay. Mariana Scarlato reports financial support was provided by National Research and Innovation Agency of Uruguay.

Data Availability

Data will be made available on request.

Acknowledgement

We thank the eight farmer families and the technicians involved in this research. We thank Red de Agroecología del Uruguay for its contribution in organizing the workshops. We thank MSc students Lisa Van der Graaf and Lotte Demmink for helping with data collection and processing. This work was supported by the National Research and Innovation Agency of Uruguay (grant no. POS_EXT_2016_1_134356), the National Institute of Agricultural Research of Uruguay, and the HortEco project funded by NWO-WOTRO (contract no. W 08.250.304).

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.agee.2023.108389](https://doi.org/10.1016/j.agee.2023.108389).

References

- Alliaume, F., Rossing, W.A.H., García, M., Giller, K.E., Dogliotti, S., 2013. Changes in soil quality and plant available water capacity following systems re-design on commercial vegetable farms. *Eur. J. Agron.* 46, 10–19. <https://doi.org/10.1016/j.eja.2012.11.005>.
- Altieri, M.A., 2002. Agroecología: principios y estrategias para diseñar sistemas agrarios sustentables. In: Sarandón, S. (Ed.), *Agroecología: El Camino hacia una Agricultura Sustentable*. Ediciones Científicas Americanas, pp. 49–56. (<https://drive.google.com/file/d/1Igrx9hKSpnBBarrU6AEHumtxJfwmwCUw/view>).
- Altieri, M.A., Ponti, L., & Nicholls, C.I. (2012). Soil fertility, biodiversity and pest management. In G.M. Gurr, S.D. Wratten, W.E. Snyder, & D.M.Y. Read (Eds.), *Biodiversity and Insect Pests: Key Issues for Sustainable Management* (First Edit, pp. 72–84).
- Ambrosino, M.D., Luna, J.M., Jepson, P.C., 2006. Relative frequencies of visits to selected insectary plants by predatory hoverflies (Diptera: Syrphidae), other beneficial insects, Herbiv. *Entomol. Soc. Am.* 35 (2), 394–400.
- Ardanuy, A., Figueras, M., Matas, M., Arnó, J., Agustí, N., Alomar, Ò., Gabarra, R., 2022. Banker plants and landscape composition influence colonisation precocity of tomato greenhouses by mirid predators. *J. Pest Sci.* 95 (1), 447–459. <https://doi.org/10.1007/s10340-021-01387-y>.
- Arnó, J., Oveja, M.F., Gabarra, R., 2018. Selection of flowering plants to enhance the biological control of *Tuta absoluta* using parasitoids. *Biol. Control* 122, 41–50. <https://doi.org/10.1016/j.biocontrol.2018.03.016>.
- Aviron, S., Poggi, S., Varennes, Y.D., Lefevre, A., 2016. Local landscape heterogeneity affects crop colonization by natural enemies of pests in protected horticultural cropping systems. *Agric., Ecosyst. Environ.* 227, 1–10. <https://doi.org/10.1016/j.agee.2016.04.013>.
- Balzan, M.V., 2017. Flowering banker plants for the delivery of multiple agroecosystem services. *Arthropod-Plant Interact.* <https://doi.org/10.1007/s11829-017-9544-2>.
- Balzan, M.V., Wäckers, F.L., 2013. Flowers to selectively enhance the fitness of a host-feeding parasitoid: adult feeding by *Tuta absoluta* and its parasitoid *Necremnus artynes*. *Biol. Control* 67, 21–31. <https://doi.org/10.1016/j.biocontrol.2013.06.006>.
- Balzan, M.V., Bocci, G., Moonen, A.C., 2016. Landscape complexity and field margin vegetation diversity enhance natural enemies and reduce herbivory by Lepidoptera pests on tomato crop. *BioControl* 61, 141–154. <https://doi.org/10.1007/s10526-015-9711-2>.
- Bàrberi, P., Burgio, G., Dinelli, G., Moonen, A.C., Otto, S., Vazzana, C., Zanin, G., 2010. Functional biodiversity in the agricultural landscape: relationships between weeds and arthropod fauna. *Weed Res.* 50 (5), 388–401. <https://doi.org/10.1111/j.1365-3180.2010.00798.x>.
- Barton, K. (2020). MuMIn: Multi-Model Inference. Retrieved from <https://cran.r-project.org/package=MuMIn>.
- Basso, C., Franco, J., Grille, G., Pascal, C., 2001. Distribución espacial de *Trialeurodes vaporariorum* (Homoptera: Aleyrodidae) en plantas de tomate. *Bol. San. Veg. Plagas* 27, 475–487.
- Begg, G.S., Cook, S.M., Dye, R., Ferrante, M., Franck, P., Lavigne, C., Birch, A.N.E., 2017. A functional overview of conservation biological control. *Crop Prot.* 97, 145–158. <https://doi.org/10.1016/j.cropro.2016.11.008>.
- Bentancourt, C., & Scatoni, I. (2010). *Guía de insectos y ácaro de importancia agrícola y forestal* (3rd ed.). Montevideo: Hemisferio Sur.
- Berrueta, C., Borges, A., Giménez, G., Dogliotti, S., 2019. On-farm diagnosis for greenhouse tomato in south Uruguay: explaining yield variability and ranking of determining factors. *Eur. J. Agron.* 110, 125932 <https://doi.org/10.1016/j.eja.2019.125932>.
- Bianchi, F.J.J.A., 2022. From pattern to process: towards mechanistic design principles for pest suppressive landscapes. *Basic Appl. Ecol.* 64, 157–171. <https://doi.org/10.1016/j.baee.2022.09.002>.
- Bommarco, R., Miranda, F., Bylund, H., Björkman, C., 2011. Insecticides suppress natural enemies and increase pest damage in cabbage. *J. Econ. Entomol.* 104 (3), 782–791. <https://doi.org/10.1603/EC10444>.
- Bray, R.H., Kurtz, L.T., 1945. Determination of total, organic and available forms of phosphorus in soils. *Soil Sci.* 59, 39–45.
- Bremner, J.M., Mulvaney, C.S., 1982. Nitrogen-Total. In *Methods of Soil Analyses* (2nd ed.). Soil Science Society of America, Madison, pp. 595–624.
- Bretagnolle, V., Gaba, S., 2015. Weeds for bees? A review. *Agron. Sustain. Dev.* 35, 891–909. <https://doi.org/10.1007/s13593-015-0302-5>.
- Bueno, V.H.P. (2005). Implementation of Biological Control in Greenhouses in Latin America: How Far Are We? In 2nd International Symposium on Biological Control of Arthropods (Vol. 2, pp. 531–537). Retrieved from <http://www.bugwood.org/arthropod2005/vol2/11b.pdf>.
- Burnham, K.P., & Anderson, D.R. (2007). *Model Selection and Multimodel Inference: a practical information-theoretic approach*. (K. P. Burnham & D. R. Anderson, Eds.) (2nd editio). New York: Springer-Verlag. <https://doi.org/10.1007/978-0-387-22456-5-7>.
- Castañé, C., Alomar, O., Goula, M., Gabarra, R., 2004. Colonization of tomato greenhouses by the predatory mirid bugs *Macrolophus caliginosus* and *Dicyphus tamaninii*. *Biol. Control* 30 (3), 591–597. <https://doi.org/10.1016/j.biocontrol.2004.02.012>.
- Castaña, J.P., Giménez, A., Ceroni, M., Furest, J., Aunchayna, R., 2011. Caracterización agroclimática del Uruguay 1980-2009. *Serie Técnica N° 193*. In: INIA (Ed.), (INIA). INIA, Montevideo.
- Conboy, N.J.A., McDaniel, T., Ormerod, A., George, D., Gatehouse, A.M.R., Wharton, E., Tosh, C.R., 2019. Companion planting with French marigolds protects tomato plants from glasshouse whiteflies through the emission of airborne limonene. *PLoS ONE* 14 (3), 1–21. <https://doi.org/10.1371/journal.pone.0213071>.
- Deguine, J.P., Aubertot, J.N., Flor, R.J., Lescourret, F., Wyckhuys, K.A.G., Ratnadass, A., 2021. Integrated pest management: good intentions, hard realities. A review. *Agron. Sustain. Dev.* 41 (3) <https://doi.org/10.1007/s13593-021-00689-w>.
- DIEA-MGAP. (2017). Anuario estadístico agropecuario 2016. Retrieved from <https://descargas.mgap.gub.uy/DIEA/Anuarios/Anuario2017/DIEA-Anuario2017.pdf>.
- Dogliotti, S., García, M.C., Peluffo, S., Dieste, J.P., Pedemonte, A.J., Bacigalupe, G.F., Rossing, W.A.H., 2014. Co-innovation of family farm systems: a systems approach to sustainable agriculture. *Agric. Syst.* 126, 76–86. <https://doi.org/10.1016/j.agee.2013.02.009>.
- Duru, M., Therond, O., Martin, G., Martin-Clouaire, R., Magne, M.A., Justes, E., Sarthou, J.P., 2015a. How to implement biodiversity-based agriculture to enhance ecosystem services: a review. *Agron. Sustain. Dev.* 35 (4), 1259–1281. <https://doi.org/10.1007/s13593-015-0306-1>.
- Duru, M., Therond, O., Fares, M., 2015b. Designing agroecological transitions; a review. *Agron. Sustain. Dev.* 35 (4), 1237–1257. <https://doi.org/10.1007/s13593-015-0318-x>.
- Feld, C.K., Segurado, P., Gutiérrez-Cánovas, C., 2016. Analysing the impact of multiple stressors in aquatic biomonitoring data: a “cookbook” with applications in R. *Sci. Total Environ.* 573, 1320–1339. <https://doi.org/10.1016/j.scitotenv.2016.06.243>.
- Fox, J., & Weisberg, S. (2019). *An {R} Companion to Applied Regression*. Third Edition. Gabarra, R., Alomar, Ò., Castañé, C., Goula, M., Albajes, R., 2004. Movement of greenhouse whitefly and its predators between in- and outside of Mediterranean greenhouses. *Agric., Ecosyst. Environ.* 102 (3), 341–348. <https://doi.org/10.1016/j.agee.2003.08.012>.
- Grueber, C.E., Nakagawa, S., Laws, R.J., Jamieson, I.G., 2011. Multimodel inference in ecology and evolution: challenges and solutions. *J. Evol. Biol.* 24 (4), 699–711. <https://doi.org/10.1111/j.1420-9101.2010.02210.x>.
- Heiberger, R.M. (2020). *HH: Statistical Analysis and Data Display: Heiberger and Holland*. Retrieved from <https://cran.r-project.org/package=HH>.
- Hsu, A., Hsu, Y., Shen, T., 2009. Soil fertility management and pest responses: a comparison of organic and synthetic fertilization. *J. Econ. Entomol.* 102 (1), 160–169. <https://doi.org/10.1603/029.102.0123>.
- Isaac, R.A., Kerber, J.D., 1971. *Atomic Absorption and flame photometry: techniques and uses in soil, plant and water analysis. In Instrumental Methods for Analysis of Soil and Plant Tissues*. Soil. Sci. Soc. Amer. Madison, pp. 17–37.
- Jackman, S. (2020). *pscl: Classes and Methods for R Developed in the Political Science Computational Laboratory*. Sydney, New South Wales, Australia.: United States Studies Centre, University of Sydney. Retrieved from <https://github.com/atahk/pscl/>.
- Jankowska, B., 2010. Effect of Intercropping White Cabbage with French Marigold (*Tagetes Patula* Nana) and Pot Marigold (*Calendula officinalis*) on Diamondback Moth (*Plutella Xylostella* L.) Population density and its parasitoids complex. *Veg. Crops Res. Bull.* 73, 107–117. <https://doi.org/10.2478/v10032-010-0023-x>.
- Janssen, A., van Rijn, 2021. Pesticides do not significantly reduce arthropod pest densities in the presence of natural enemies. *Ecology Letters* 1–15. <https://doi.org/10.1111/ele.13819> (February).

- Jauset, A.M., Sarasu, M.J., Avilla, J., Albajes, R., 2000. Effect of nitrogen fertilization level applied to tomato on the greenhouse whitefly. *Crop Prot.* 19, 255–261.
- Jaworski, C.C., Xiao, D., Xu, Q., Ramirez-Romero, R., Guo, X., Wang, S., Desneux, N., 2019. Varying the spatial arrangement of synthetic herbivore-induced plant volatiles and companion plants to improve conservation biological control. *J. Appl. Ecol.* 56, 1176–1188. <https://doi.org/10.1111/1365-2664.13353>.
- Kassambara, A. (2017). *Practical Guide to Principal Component Methods in R. Multivariate analysis.* Jurnal Online Internasional & Nasional (First). STHDA. Retrieved from www.journal.uta45jakarta.ac.id.
- Kassambara, A. (2020). ggpubr: “ggplot2” Based Publication Ready Plots. Retrieved from <https://cran.r-project.org/package=ggpubr>.
- Kassambara, A., & Mundt, F. (2020). factoextra: Extract and Visualize the Results of Multivariate Data Analyses. R package version 1.0.7.
- Kopta, T., Pokluda, R., Psota, V., 2012. Attractiveness of flowering plants for natural enemies. *Hortic. Sci.* 39 (2), 89–96. <https://doi.org/10.17221/26/2011-HORTSCI>.
- Landis, D.A., Wratten, S.D., 2008. Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annu. Rev. Entomology* 45, 175–201.
- Landis, D.A., Gardiner, M.M., Tompkins, J., 2012. Using native plant species to diversify agriculture (First Edit). In: Gurr, G.M., Wratten, S.D., Snyder, W.E., Read, D.M.Y. (Eds.), *Biodiversity and Insect Pests: Key Issues for Sustainable Management.* John Wiley & Sons, Ltd, pp. 276–292 (First Edit).
- Le, S., Josse, J., Hussen, F., 2008. FactoMineR: an R package for multivariate analysis. *J. Stat. Softw.* 25 (1), 1–18. <https://doi.org/10.18637/jss.v025.i01>.
- Lewis, W.J., Lenteren, J.C., Van, Phatak, S.C., Tumlinson, J.H., 1997. A total system approach to sustainable pest management. *Proc. Natl. Acad. Sci. USA* 94, 12243–12248.
- Li, S., Jaworski, C.C., Hatt, S., Zhang, F., Desneux, N., Wang, S., 2021. Flower strips adjacent to greenhouses help reduce pest populations and insecticide applications inside organic-commercial greenhouses. *J. Pest Sci.* 94 (3), 679–689. <https://doi.org/10.1007/s10340-020-01285-9>.
- Lu, Z.X., Zhu, P.Y., Gurr, G.M., Zheng, X.S., Read, D.M.Y., Heong, K.L., Xu, H.X., 2014. Mechanisms for flowering plants to benefit arthropod natural enemies of insect pests: Prospects for enhanced use in agriculture. *Insect Sci.* 21 (1), 1–12. <https://doi.org/10.1111/1744-7917.12000>.
- Magdoff, F., & van Es, H.M. (2009). *Building soils for better crops: sustainable soil management (third edit).* Sustainable Agriculture Research and Education (SARE).
- Mahmood, I., Imadi, S.R., Shazadi, K., Gul, A., & Hakeem, K.R. (2016). Effects of Pesticides on Environment. In K. R. Hakeem, M. S. Akhtar, & S. N. A. Abdullah (Eds.), *Plant, Soil and Microbes: Volume 1: Implications in Crop Science* (pp. 253–269). Cham: Springer International Publishing. https://doi.org/10.1007/978-3-319-27455-3_13.
- Marliac, G., Penvern, S., Lescouret, F., Capowiez, Y., 2016. A typology of crop protection strategies within organic farming and its consequences on the natural enemy community and predation rate. *Acta Hort.* 1137, 145–151. <https://doi.org/10.17660/ActaHortic.2016.1137.20>.
- Marshall, E., Brown, V., Boatman, N., Lutman, P., Squire, G., Ward, L., 2003. The role of weeds in supporting biological diversity within crop fields. *Weed Res.* 43, 77–89.
- McNaught, I., Thackway, R., Brown, L., Parsons, M., 2008. *A Field Manual For Surveying and mapping Nationally significant Weeds* (2nd editio). Science. Bureau of Rural, Canberra.
- Messelink, G.J., Bennisson, J., Alomar, O., Ingegno, B.L., Tavella, L., Shipp, L., Wäckers, F. L., 2014. Approaches to conserving natural enemy populations in greenhouse crops: Current methods and future prospects. *BioControl* 59 (4), 377–393. <https://doi.org/10.1007/s10526-014-9579-6>.
- Messelink, G.J., Lambion, J., Janssen, A., van Rijn, P.C.J., 2021. Biodiversity in and around greenhouses: benefits and potential risks for pest management. *Insects* 12, 933. <https://doi.org/10.3390/insects12100933>.
- Mulvaney, R.L., 1996. Nitrogen - inorganic forms. In *Methods of Soil Analysis.* Soil Science Society of America, Madison, pp. 1162–1171.
- Nelson, D.W., Sommers, L.E., 1996. Total Carbon, Organic Carbon, and Organic Matter. In *Methods of Soil Analysis.* Soil Science Society of America, Madison, pp. 961–1010.
- Nicholls, C., Altieri, M., Vazquez, L., 2016. Agroecology: principles for the conversion and redesign of farming systems. *J. Ecosyst. Ecography* 55 (010), 1–8. <https://doi.org/10.4172/2157-7625.S5-010>.
- Parolin, P., Bresch, C., Desneux, N., Brun, R., Bout, A., Boll, R., Poncet, C., 2012. Secondary plants used in biological control: a review. *Int. J. Pest Manag.* 58 (2), 91–100. <https://doi.org/10.1080/09670874.2012.659229>.
- Pease, C.G., Zalom, F.G., 2010. Influence of non-crop plants on stink bug (Hemiptera: Pentatomidae) and natural enemy abundance in tomatoes. *J. Appl. Ecol.* 134, 626–636. <https://doi.org/10.1111/j.1439-0418.2009.01452.x>.
- Pépin, A., Morel, K., van der Werf, H.M.G., 2021. Conventionalised vs. agroecological practices on organic vegetable farms: investigating the influence of farm structure in a bifurcation perspective. *Agric. Syst.* 190. <https://doi.org/10.1016/j.agsy.2021.103129>.
- Ribeiro, A.L., Gontijo, L.M., 2017. Alyssum flowers promote biological control of collard pests. *BioControl* 62 (2), 185–196. <https://doi.org/10.1007/s10526-016-9783-7>.
- Rossing, W.A.H., Marta, M., Aguerre, V., Leoni, C., Ruggia, A., Dogliotti, S., 2021. Crafting actionable knowledge on ecological intensification: lessons from co-innovation approaches in Uruguay and Europe. *Agric. Syst.* 190, 103103 <https://doi.org/10.1016/j.agsy.2021.103103>.
- Ryelandt, E., Bao, L., Scarlato, M., Rossing, W.A.H., Bianchi, F.J.J.A., 2017. Explorando las comunidades de artrópodos en especies no cultivadas en sistemas hortícolas del Sur del Uruguay. *VIII Proc. Congr. SOCLA 2020* (p. 5).
- Sarkar, D., 2008. *Lattice: Multivariate Data Visualization with R.* Springer, New York.
- Sarthou, J.P., Badoz, A., Vaissière, B., Chevallier, A., Rusch, A., 2014. Local more than landscape parameters structure natural enemy communities during their overwintering in semi-natural habitats. *Agric., Ecosyst. Environ.* 194, 17–28. <https://doi.org/10.1016/j.agee.2014.04.018>.
- Scarlato, M., Dogliotti, S., Bianchi, F.J.J.A., Rossing, W.A.H., 2022. Ample room for reducing agrochemical inputs without productivity loss: the case of vegetable production in Uruguay. *Sci. Total Environ.* 810, 152248 <https://doi.org/10.1016/j.scitotenv.2021.152248>.
- Sivinski, J., Wahl, D., Holler, T., Dobai, S., Al, Sivinski, R., 2011. Conserving natural enemies with flowering plants: estimating floral attractiveness to parasitic Hymenoptera and attraction's relationship to flower and plant morphology. *Biol. Control* 58 (3), 208–214. <https://doi.org/10.1016/j.biocontrol.2011.05.002>.
- Song, B.Z., Wu, H.Y., Kong, Y., Zhang, J., Du, Y.L., Hu, J.H., Yao, Y.C., 2010. Effects of intercropping with aromatic plants on the diversity and structure of an arthropod community in a pear orchard. *BioControl* 55, 741–751. <https://doi.org/10.1007/s10526-010-9301-2>.
- Srinivasan, K., Moorthy, P.N.K., Raviprasad, T.N., 1994. African marigold as a trap crop for the management of the fruit borer *Helicoverpa armigera* on tomato. *Int. J. Pest Manag.* <https://doi.org/10.1080/09670879409371854>.
- Stavisky, J., Funderburk, J.O.E., Brodbeck, B.V., Olson, S.M., Andersen, P.C., 2002. Population dynamics of frankliniella spp. and tomato spotted wilt incidence as influenced by cultural management tactics in tomato. *Hortic. Entomol.* 1216–1221. <https://doi.org/10.1603/0022-0493-95.6.1216>.
- Stenberg, J.A., Sundh, I., Becher, P.G., Björkman, C., Dubey, M., Egan, P.A., Viketoft, M., 2021. When is it biological control? A framework of definitions, mechanisms, and classifications. *J. Pest Sci.* 94 (3), 665–676. <https://doi.org/10.1007/s10340-021-01354-7>.
- Storkey, J., Neve, P., 2018. What good is weed diversity. *Weed Res.* 58, 239–243. <https://doi.org/10.1111/wre.12310>.
- Sumberg, J., Giller, K.E., 2022. What is 'conventional' agriculture? *Glob. Food Secur.* 32, 100617 <https://doi.org/10.1016/j.gfs.2022.100617>.
- Swart, R.C., Pryke, J.S., Roets, F., 2017. Optimising the sampling of foliage arthropods from scrubland vegetation for biodiversity studies. *Afr. Entomol.* 25 (1), 164–174. <https://doi.org/10.4001/003.025.0164>.
- Tittonell, P., Baudron, F., Klerkx, L., Félix, G., 2016. Ecological intensification: local innovation to address global challenges. In: Lichtfouse, E. (Ed.), *Sustainable Agriculture Reviews*, Vol. 19. Springer International Publishing, pp. 1–29. https://doi.org/10.1007/978-3-319-26777-7_1.
- Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I., Thies, C., 2005. Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. *Ecol. Lett.* 8, 857–874. <https://doi.org/10.1111/j.1461-0248.2005.00782.x>.
- Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batáry, P., Westphal, C., 2012. Landscape moderation of biodiversity patterns and processes – eight hypotheses. *Biol. Rev.* 87 (3), 661–685. <https://doi.org/10.1111/j.1469-185X.2011.00216.x>.
- Tscharntke, T., Karp, D.S., Chaplin-Kramer, R., Batáry, P., DeClerck, F., Gratton, C., Zhang, W., 2016. When natural habitat fails to enhance biological pest control – Five hypotheses. *Biol. Conserv.* 204, 449–458. <https://doi.org/10.1016/j.biocon.2016.10.001>.
- UNCTAD, 2017. A/HRC/34/48. Report of the Special Rapporteur on the Right to Food. FAO. <https://doi.org/10.1017/S0020818300025613>.
- van Lenteren, J.C., 2000. A greenhouse without pesticides: fact or fantasy? *Crop Protection* 375–384.
- van Lenteren, J.C., van Roermund, H.J.W., Sütterlin, S., 1996. Biological control of greenhouse whitefly (trialeurodes vaporariorum) with the parasitoid encarsia formosa: how does it work? *Biol. Control* 6, 1–10. <https://doi.org/10.1006/bcon.1996.0001>.
- van Lenteren, J.C., Bolckmans, K., Köhl, J., Ravensberg, W.J., Urbaneja, A., 2018. Biological control using invertebrates and microorganisms: plenty of new opportunities. *BioControl* 63 (1), 39–59. <https://doi.org/10.1007/s10526-017-9801-4>.
- van Lenteren, J.C., Bueno, V.H.P., Luna, M.G., & Colmenarez, Y.C. (2020). *Biological Control in Latin America and the Caribbean: Its Rich History and Bright Future.* (J. C. van Lenteren, V. H. P. Bueno, M. G. Luna, & Y. C. Colmenarez, Eds.). CAB International. <https://doi.org/doi/book/10.1079/9781789242430.0000>.
- Venables, W.N., Ripley, B.D., 2002. *Modern Applied Statistics with S.* Fourth Edition. Springer, New York. (<https://www.stats.ox.ac.uk/pub/MASS4/>).
- Wäckers, F.L., van Rijn, P.C.J., 2012. Pick and mix: selecting flowering plants to meet the requirements of target biological control insects (First Edit). In: Gurr, G.M., Wratten, S.D., Snyder, W.E., Read, D.M.Y. (Eds.), *Biodiversity and Insect Pests: Key Issues for Sustainable Management.* John Wiley & Sons, Ltd, pp. 139–165 (First Edit).
- Wäckers, F.L., Bruin, J., van Rijn, P.C.J., 2005. In: Wäckers, F.L., Bruin, J., van Rijn, P.C. J. (Eds.), *Plant-Provided Food for Carnivorous Insects: A Protective Mutualism and Its Applications.* Cambridge University Press. <https://doi.org/10.1017/CBO9780511542220>.
- Wickham, H., 2016. *ggplot2: Elegant Graphics for Data Analysis.* Springer-Verlag, New York. (<https://ggplot2.tidyverse.org/>).
- Yang, F., Liu, B., Zhu, Y., Wyckhuys, K.A.G., van der Werf, W., Lu, Y., 2021. Species diversity and food web structure jointly shape natural biological control in agricultural landscapes. *Commun. Biol.* 4 (1), 1–11. <https://doi.org/10.1038/s42003-021-02509-z>.

- Zehnder, G., Gurr, G., Kühne, S., Wade, M., Wratten, S., Wyss, E., 2007. Arthropod pest management in organic crops. *Annu. Rev. Entomol.* 52, 57–80. <https://doi.org/10.1146/annurev.ento.52.110405.091337>.
- Zuur, A.F., Ieno, E.N., 2016. A protocol for conducting and presenting results of regression-type analyses. *Methods Ecol. Evol.* 7 (6), 636–645. <https://doi.org/10.1111/2041-210X.12577>.
- Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. *Methods Ecol. Evol.* 1 (1), 3–14. <https://doi.org/10.1111/j.2041-210x.2009.00001.x>.