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Plant–herbivore–natural enemy trophic webs in date palm agro-ecosystems

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Abstract

Understanding the composition and dynamics of ecological communities is challenging because of the large number of organisms present and their numerous interactions. Among agricultural systems, intercropping considerably increases the complexity of communities compared to monocultures and alternative host plants can influence insect pest damage. Using literature records, we construct and analyse connectance trophic webs of date palm (*Phoenix dactylifera*) agro-ecosystems, including and excluding intercrops. Estimates of connectance (community complexity) are relatively low and little affected by consideration of intercrops. Plant–herbivore overlap is relatively high, suggesting that herbivores are typically not specialists. Herbivore–natural enemy overlap is greater when intercrops are considered, suggesting that diffuse apparent competition regulates pest populations. We pay particular attention to how trophic web structure might affect *Batrachedra amydraula* (Lesser date moth), an important economic pest. Records indicate it having 15 species of natural enemies and sharing 9 of these with other herbivores; these may maintain populations of natural enemies when the moth is seasonally rare, contributing to pest suppression. The estimated potential for apparent competition between the lesser date moth and other herbivores is higher when intercrops are considered. The consequent expectation of less severe infestations in plantations that are intercropped compared to monocultures matches empirically derived reports. Further, comparing results obtained from the literature on one country (Oman) and from 15 Middle Eastern countries, we find that community metric estimates are relatively little affected by the geographical scale considered. Overall, our results suggest that literature-based trophic web construction can provide an efficient and robust alternative, or in addition, to direct empirical methodologies and that the presence of intercrops will contribute to major pest suppression via indirect apparent competition.

Keywords Intercrops · Connectance · Overlap · Apparent competition · Pest control · Lesser date moth

Key message

- Community structure of date palm plus intercrops is assessed indirectly using literature records
- Community metric estimates are relatively little affected by geographical scale
- Herbivores and their natural enemies are not typically specialists
- A key specialist pest shares many natural enemies with herbivores feeding on intercrops
- Expected lower pest infestations when intercropping match direct empirical evidence

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Introduction

Understanding the composition and dynamics of ecological and agro-ecological communities is extremely challenging because of the large number of organisms present and their numerous past and present interactions (Holt and Lawton 1993; Wilson et al. 1996; Holt and Hochberg 2001; van Veen et al. 2006; Allesina and Tang 2012; Jaworski et al. 2015; Levine et al. 2017; Heleno et al. 2020). Among agricultural systems, practices such as intercropping and diversifying surrounding vegetation can considerably increase the complexity of communities compared to monocultures and the availability, density and type of alternative host plants can influence the damage caused by insect pests (Power 1987; Settle et al. 1996; Atakan and Uygur 2005; van Veen et al. 2006; Zhang et al. 2017; Nasi 2023; Vásquez-Ordóñez et al. 2023; Zemp et al. 2023). While alternative host plants may support pests during periods when their primary crop hosts are seasonally unavailable, allowing them to subsequently migrate back to damage the primary crop (Clementine et al. 2005; Goodell 2009; Saeed et al. 2015), these plants may also enhance the suppression of pests by natural enemies, such as predators and parasitoids, by promoting indirect ecological interactions such as apparent competition and diffuse apparent competition (e.g. Shameer et al. 2018). Apparent competition occurs when one host species declines due to the presence of another through the effects of a shared natural enemy, without direct resource competition occurring and diffuse apparent competition describes the same phenomenon but with many more species of hosts and natural enemies in the community; Holt and Lawton 1993; van Veen et al. 2006; Jaworski et al. 2015; Shameer et al. 2018). Intercropping can also modify the physical and ecological conditions of the agricultural field and alter the predator–prey dynamics to benefit generalist arthropod predators and promote assemblages of pollinators in the field (Järvinen et al. 2022, 2023). Although increasing agricultural diversity may enhance natural control of arthropod pests via increased provision of food resources and breeding habitats for natural enemies (Rosenheim et al. 2022; Farooq et al. 2022), increasing the size of monoculture cropping can have positive, negative, neutral, or even nonlinear effects on arthropod pest densities (Rosenheim et al. 2022).

A successful approach to describing and analysing the complexity of ecological communities has been to construct webs of interactions between members of two or more trophic levels (Memmott and Godfray 1994; Bukovinszky et al. 2008; Peralta et al. 2014; Rocca and Greco 2015; Henri and van Veen 2016; Sanders et al. 2018; Miller et al. 2021). Complex webs have been constructed for the parasitoids and secondary parasitoids of aphids (Müller et al. 1999; Lohaus et al. 2013) and for lepidopterans and their parasitoids (Henneman and Memmott 2001; Timms et al. 2012; Peralta et al. 2014; Frost et al. 2016; Shameer et al. 2018). These trophic webs (food webs) have been used to answer specific ecological questions, such as the degree to which parasitoids introduced as biocontrol agents in cropping systems are penetrating natural communities (Henneman and Memmott 2001; Jarrett and Szűcs 2022), the importance of functional complementarity and redundancy of parasitoids as determinants of parasitism rates (Peralta et al. 2014) and to quantify the importance of apparent competition (Frost et al. 2016). Incorporating a consideration of parasitoids into network-based analyses, such as trophic webs, has wide applications in assessing ecosystem services within agro-ecosystems (Miller et al. 2021).

Trophic webs may be constructed directly, for instance by collecting immature herbivores, in the field and rearing them in the laboratory to establish whether they have been attacked by parasitoids (Henneman and Memmott 2001), which generates accurate, and often quantitative, information on community structure. This approach is, however, labour-intensive, in terms of collection, rearing and taxonomic identification of biological material, and results may be site-specific. An alternative, and relatively rapid, approach is to construct trophic webs using prior literature records of plant–herbivore and herbivore–natural enemy associations (Shameer et al. 2018). Such webs will typically apply across large-scale agro-ecosystems and thus may not represent given local communities and are also constrained to be non-quantitative 'connectance webs' (Memmott and Godfray 1994). Connectance webs may nonetheless indicate the relative importance of direct and indirect competitive interactions between species occupying a given trophic level and, for cropping systems, the potential for the presence of intercrops to promote the suppression of pest herbivores by their natural enemies (Shameer et al. 2018).

Here we construct connectance trophic webs from prior literature records of the date palm (*Phoenix dactylifera* L., Arecales: Arecaceae) agro-ecosystem, both including and excluding consideration of intercrop species. These webs summarize the presence or absence of trophic interactions between crop and intercrop plants with their herbivores and between these herbivores and their natural enemies. The host plant ranges of the herbivores and the host or prey ranges of the natural enemies combine to indicate the likely importance of direct interspecific competition between crop pest herbivores and of diffuse apparent competition that may contribute to the control of these pests. We pay particular attention to how trophic web structure might affect populations of the lesser date moth (LDM: *Batrachedra amydraula* Meyrick), which is considered as one of its most important economic pests of date palm. Further, we assess effects of the geographic scale at which trophic webs are constructed by comparing results obtained when considering literature records on the agro-ecosystem in one country, Oman, within the Middle East and from wider consideration of literature from across 15 Middle Eastern countries (Table 1).

The date palm agro-ecosystem

Date palm has current economic importance as well as being one of the main historical elements of civilization in the Middle East. There are many countries that cultivate date palm, with a total cultivated area estimated at 1.1 million ha (FAO 2022; Alotaibi et al. 2023; Table 1). In the Sultanate of Oman, date palm is the most important crop, with an estimated 25,630 ha under cultivation (FAO 2022, Table 1), which accounts for 78.32% of the total area cultivated with fruit trees (Ministry of Agriculture and Fisheries 2014). There are an estimated 8.5 million date palm trees in Oman, of which around 7.5 million are grown in agricultural holdings, with the annual production of dates amounting to 316,000 tonnes (Ministry of Agriculture and Fisheries 2014). While Middle Eastern and North African countries are the main date production areas (El-Shafie et al. 2017; FAO 2022), date palm cultivation has recently been introduced to many further countries, such as India, Pakistan, Australia, USA, Chile, Peru, Argentina and Brazil, in areas that are characterized by arid and semi-arid climates, with long summers, high temperatures and low rainfall (Zaid 2002; Reilly 2012; El-Shafie et al. 2017; Escobar and Valdivia 2015). Date palm trees are affected by a large number of pests attacking their leaves, fruits, trunk and roots (El-Shafie et al. 2017). Key arthropod pests causing economic damage include the old-world date mite (*Oligonychus afrasiaticus*), the red palm weevil (*Rhynchophorus ferrugineus*), the Dubas bug (*Ommatissus lybicus*) and the lesser date moth (LDM: *Batrachedra amydraula* Meyrick) (Al Khatri 2009; Al Sarai 2015; Al-Khayri et al. 2015; Al-Yahyai and Khan 2015; El-Shafie et al. 2017). LDM is considered one of the most important economic pests as it is a date palm specialist (El-Shafie et al. 2017), attacking fruits and causing up to 70% yield loss (Michael 1970; Abdel-Wahab 1974; Eitam 2001; Abbas et al. 2008; Shayesteh et al. 2010; Kinawy et al. 2015; Alyousuf 2018).

LDM has many species of natural enemies: a field survey conducted by the Ministry of Agriculture and Fisheries (MAF) in Oman in 2006 found six species of parasitoids and two species of predators. The hymenopteran parasitoids were *Goniozus omanensis* (Bethylidae), *Bracon* sp. (Braconidae), *Apanteles* sp. (Braconidae), *Euderus* near *arenarius* (Eulophidae), *Pediobius* sp. (Eulophidae) and *Eurytoma* sp. (Eurtomidae), and the predators were *Anthocorid* sp. (Hemiptera: Anthocoridae) and *Chrysoperla carnea* (Neuroptera: Chrysopidae). Among these natural enemies, *G. omanensis* was numerically dominant, with the potential to be actively used as a biocontrol agent (Abbas et al. 2008, 2014; Abbas 2012; Polaszek et al. 2019). There is little available information on the field activity of *G. omanensis* when LDM larvae are not available, from June to February each year (Michael 1970; Abdel-Wahab 1974; Eitam 2001; Abbas et al. 2008; Al Khatri 2009; Kinawy et al. 2015; Alyousuf 2018), but parasitoid populations may, in general, be maintained on alternative lepidopteran hosts that attack other crops or naturally available plant species.

Table 1 Area under date palm cultivation in the 15 Middle Eastern countries, including Oman, considered in this study and numbered in decreasing order of area of date palm cultivation (Source: FAOSTAT 2022)

Rank	Country	Area under date palm cultivation (1000 ha)	Total agricultural area (1000 ha)	Total land area (1000 ha)
1	Iraq	245.03	9250	43,412.8
2	Iran	154.15	47,013	162,250
3	Saudi Arabia	152.71	173,595.91	214,969
4	Egypt	50.84	3922	99,545
5	UAE	38.42	390.4	7102
6	Oman	25.63	1461.4	30,950
7	Yemen	15.04	23,452	52,797
8	Israel	5.33	638.4	2164
9	Kuwait	3.67	150	1782
10	Turkey	3.58	37,716	76,963
11	Jordan	3.24	1036.5	8879.4
12	Bahrain	2.47	8.6	78.3
13	Qatar	2.22	74	1149
14	Palestine	0.72	103.49	602
15	Syria	0.41	13,921	18,363

The date palm agro-ecosystem in Oman, especially in the agricultural oases, is characterized by multi-crop fields, as farmers have responded to a lack of suitable land and limited supplies of water by intercropping fruits, vegetables and other field crops with date palm trees throughout the year (Siebert et al. 2007) (Supplementary Fig. 1). Intercropping, without incurring substantial yield loss (Letourneau et al. 2011; Iverson et al. 2014), is possible due to the height of date palm trees and the orientation of their leaves allowing sufficient solar radiation to reach smaller annual and perennial crops grown among them (as is the case with other palms, such as Coconut, Nelliat et al. 1974). From experiments on date palm, carried out at a local scale, intercropping has been reported to enhance yield (by around 35% when intercropped with barley, sorghum or alfalfa, cereals compared to non-intercropped plantations with no chemical control), reduce damage by pests (including the LDM) and also enhance numbers of beneficial arthropods (Rahnama and Latifian 2013). In the present study, we take a complimentary approach: we use literature records of plant, insect herbivore and natural enemy associations, gathered at both the national (Oman) and regional (Middle East) scales, to construct trophic webs representing plant–insect communities in date palm agro-ecosystems. From these, we assess the potential importance of crop diversity to pest population suppression, by comparing trophic webs with and without intercrops included. We also assess whether estimates of community structure differ when records are drawn from one country or from across a wider region. While our investigation concerns a wide array of plant and insect species, we pay particular attention to the question of how trophic web structure might affect populations of the LDM. By maintaining populations of alternative hosts, intercrops may, for instance, influence the survival of natural enemies of LDM, when LDM larvae are seasonally absent.

We take a broad and indirect approach to the assessment of the influence of crop diversity on the potential for natural enemies to suppress pests of economic importance. The trophic webs are constructed to show the probable structure of communities concerned without claiming that these communities are described exactly. Our ultimate purposes are, specifically, to provide information on the plant–pest–natural enemy complex in date palm agro-ecosystems that will be useful for future pest control strategies and, broadly, to develop the literature-based approach as an addition, or an alternative, to directly empirical methodologies for community structure assessment.

Materials and methods

Construction of trophic webs

An extensive literature survey was carried out to compile field records for insect species associated with date palm grown in Oman and in the other Middle Eastern countries indicated in Table 1 and Supplementary Fig. 2. Literature records were obtained following the methodology of Shameer et al. (2018): we inspected annual reports, agricultural census reports, journal papers and reviews available in print and online from 2005 to 2022 and extracted information regarding the presence of pests and natural enemies. Information on trophic associations (herbivory, parasitism and predation) was obtained from the publications of the Department of Agriculture, Sultanate of Oman (e.g. Kinawy 1991, 2005a, b; Mokhtar 2005; Ministry of Agriculture Annual Report 2008a, b; Agricultural Census by the Directorate General of Planning and Development, Ministry of Agriculture and Fisheries, Oman 2014). We also used monographs on pests and natural enemies, such as CAB Reviews (e.g. El-Shafie et al. 2017), journal papers (e.g. Polaszek et al. 2019, 2021; Rakhshani et al. 2019) and authentic websites such as CAB International Invasive Species Compendium (CABI 2021), Universal Chalcidoidea Database (Noyes 2015), www.fao.org (FAO 2022) and Plant Pests of the Middle East Database of the Hebrew University of Jerusalem, Israel (Gerson and Applebaum 2019) to collect information on pests and natural enemies for Oman and all other countries studied. When we found leads to further reports cited within the literature we inspected, we followed these up until no further records could reasonably be found, resulting in a comprehensive set of information. A full list of literature sources used is given in the supplementary material (Supplementary Reference List). We found numerous errors in the reported names and taxonomic positions of both herbivores and their natural enemies, especially in governmental reports, and we corrected these for use in this study by cross-referencing between sources before carrying out further analysis. In cases where species names have synonyms, we use the current taxonomic nomenclature.

Intercrop species with substantial areas of cultivation in Oman (Ministry of Agriculture and Fisheries 2014) were only included in the study if there were Omani records available for their herbivores and natural enemies (e.g. Ficus and Olive crops were excluded on this basis). We considered all the insect pests of date palm and its intercrops, including the stored products pests that infest ripening fruits prior to harvest, and most of the insect natural enemies (predators and parasitoids) of the considered pests. We excluded termites (Isoptera: Blattodea) and non-insect arthropods, such as mites and spiders.

These literature records were used to construct composite connectance trophic webs (Memmott and Godfray 1994; Sunderland et al. 2005, 2023; Shameer et al. 2018) of plant–herbivore and herbivore–natural enemy interactions within the date palm agro-ecosystem. Four trophic webs were constructed for separate, but related, analyses at different geographical scales, with and without intercrops considered. Two webs considered only date palm and directly associated insects: (A) date palm and its herbivores and their natural enemies in Oman and (B) date palm and its herbivores and their natural enemies throughout the Middle East. Two webs considered date palm plus intercrops: (C) date palm and its intercrops plus herbivores and their natural enemies in Oman and (D) date palm and its intercrops plus herbivores and their natural enemies throughout the Middle East. Web A is a subset of Web B, while Web B and Web C form different subsets of Web D, the overall trophic web.

Illustration of trophic interactions

Visualizations of Webs A to D were created using the package 'bipartite' (Dormann et al. 2008) within R (2021). We show webs in the least-complex form possible, achieved by allowing the package to determine the sequence in which species are arranged within each trophic level and by illustrating only two trophic levels at a time. Webs A and C are shown as bi-trophic (herbivores and natural enemies) because only one plant species, date palm, is considered and the lowest trophic level is visually redundant. Webs B and D are shown for all three trophic levels considered, but in two parts in order to present each set of trophic interactions (plant–herbivore, herbivore–natural enemy) in their simplest forms (i.e. the order in which herbivores are shown is allowed to differ between the two component parts of the tri-trophic web). Webs B and D are shown in alternative formats in the supplementary materials, i.e. as single tri-trophic webs, with all species constrained to be ordered numerically. In each trophic web illustrated, the width of the rectangular bar associated with each species is shown as proportional to the interaction strength, i.e. the number of trophic interactions that species has relative to those of other species at the same trophic level (using the 'plotweb' function within 'bipartite', Dormann et al. 2008). Following Müller et al. (1999), we also show visualizations of the overall potential for apparent competition between all herbivores within each constructed trophic web (using the 'plotPAC' function within 'bipartite', Dormann et al. 2008).

Analysis of trophic webs

We calculated connectance (a proportional measure of community complexity) as the number of recorded plant–herbivore or herbivore–natural enemy interactions divided by the number of possible interspecific trophic interactions (Sunderland et al. 2005, 2023; Rocca and Greco 2015). We also quantified herbivore overlap and natural enemy overlap to indicate the degree to which sharing host plants and sharing natural enemies with intercrop herbivores might influence the pest populations of date palm. Overlap was calculated as the number of pairs of species of plant, or herbivore, that shared at least one herbivore, or natural enemy, divided by the total possible number of such links (Sunderland et al. 2005, 2023). We also recorded the numbers of herbivore, or natural enemy, species that were shared between each linked pair of plants or herbivores, providing quantitative measures of overlap (van Veen et al. 2008; Shameer et al. 2018). A measure of the potential for apparent competition (PAC) was obtained using the PAC function in 'bipartite' package (Müller et al. 1999; Dormann et al. 2008; Frost et al. 2016). For this metric we focused on the lesser date moth: when LDM shares one or more natural enemies with other herbivore species within a trophic web, its separate pairwise (LDM-other herbivore) PAC values sum to 1 (Müller et al. 1999). One component of this sum represents LDM being attacked by a natural enemy that developed from LDM and remaining components combine to provide the metric we report representing apparent competition: the proportion of instances that LDM is attacked by a natural enemy that developed on another species of herbivore.

Our analyses are largely descriptive, i.e. we chiefly report metrics rather than performing statistical hypothesis tests. However, we provide some tests using values for Webs B and D, the most complete and wide-ranging webs. We note that comparisons of Webs A and B or C and D provide information on the effects of considering a more complex array of plant categories (including or excluding intercrops) within a given area while comparisons of Webs A and C or of B and D can indicate the effects of considering the same plant categories at a greater geographical scale.

Results

Date palm pests and natural enemies in Oman (Web A)

The literature records indicated the presence of 44 species of insect herbivores, belonging to the Orders Coleoptera, Diptera, Hemiptera, Lepidoptera, Orthoptera and Thysanoptera feeding on date palms in Oman (Table 2 and Supplementary Table 1). The connectance of the herbivore–natural enemy trophic web was 0.026 (Table 2), indicating that community structure is far less complex than its potential (Fig. 1). The following 25 herbivore species did not have any natural enemies reported in Oman: *Arenipses sabella* Hampson, *Cadra calidella* Guenee, *Cadra elutella* Hübner, *Cadra figulilella* Gregson, *Ephestia dowsoniella* (Richard & Thompson), *Plodia interpunctella* (Hübner), *Phonopate frontalis* Fahraeus, *Julodis euphratica* Castelnau and Gory, *Acanthophorus arabicus* Thomson, *Jebusea hammerschmidti* Reiche, *Macrocoma* sp., *Carpophilus dimidiatus* (Fabricius), *Carpophilus hemipterus* (Linnaeus), *Oryctes rhinoceros* (Linnaeus), *Strategus julianus* Burmeister, *Drosophila melanogaster*

Table 2 Properties of trophic webs constructed for insect communities associated with date palm and with the date palm intercropping system at two geographical scales

Metric	Oman		Middle East	
	Date palm (Web A)	Date palm + intercrops (Web B)	Date palm (Web C)	Date palm + intercrops (Web D)
All crop plants and herbivores				
Plants	1	50	1	70
Herbivores	44	80	52	112
Herbivores per plant (mean) [Herbivore load]	44	3.54	52	4.43
Plants fed on (mean per herbivore) [Herbivore diet breadth]	–	2.14	–	2.77
Plant–herbivore connectance	–	0.043	–	0.040
Plant–herbivore overlap	–	0.18	–	0.224
Plants not sharing any herbivores	–	18	–	11
Herbivores shared by linked plants (mean)	–	4.14		4.81
All herbivores and natural enemies				
Herbivores without natural enemies	25	25	23	23
Natural enemies per herbivore (mean) [Natural enemy load]	1.66	2.65	2.86	3.56
Predators per herbivore (mean) [Predator load]	0.61	0.91	1.36	1.31
Parasitoids per herbivore (mean) [Parasitoid load]	1.05	1.74	1.5	2.25
Natural enemies (total)	63	127	119	197
Predators	23	37	58	67
Parasitoids	40	90	62	131
Herbivores attacked per natural enemy (mean) [Natural enemy diet breadth]	1.14	1.60	1.22	1.93
Herbivores attacked per predator (mean) [Predator diet breadth]	1.13	1.76	1.24	1.99
Herbivores attacked per parasitoid (mean) [Parasitoid diet breadth]	1.15	1.53	1.19	1.90
Herbivore–natural enemy connectance	0.026	0.020	0.023	0.017
Herbivore–natural enemy overlap	0.011	0.051	0.0151	0.080
Prey–predator overlap	0.0042	0.034	0.0090	0.035
Host–parasitoid overlap	0.0063	0.021	0.0068	0.052
Natural enemies shared by linked herbivores (mean)	2.29	3.11	2.24	3.75
Predators shared by linked herbivores (mean)	2.5	3.15	2.3	4.47
Parasitoids shared by linked herbivores (mean)	2.2	3.10	2.2	3.45
Lesser date moth				
Plants fed on	1	1	1	1
Plants shared with other herbivores	1	1	1	1
Natural enemies	10	10	15	15
Predators	2	2	2	2
Parasitoids	8	8	13	13
Natural enemies shared with other herbivores	3	4	7	9
Predators shared with other herbivores	1	1	1	2
Parasitoids shared with other herbivores	2	3	6	7
Potential for apparent competition with other herbivores (PAC)	0.183	0.290	0.233	0.489

Values for plants, herbivores and natural enemies refer to numbers of species. Connectance values are the number of recorded trophic interactions divided by the number of possible interspecific trophic interactions in a given web. Overlap values are the number of pairs of species at one trophic level that share at least one species that feeds on them divided by the total possible number of such links in a given web. Metrics are provided for trophic webs overall and for the lesser date moth in particular

Meigen, *Ceratitis capitata* Wied, *Asterolecanium phoenicis* (Ramachandra Rao), *Perindus binudatus* Emeljanov, *Fiorinia linderae* Takagi, *Vespa orientalis* L., *Anacridium melanorhodon arabafrum* Dirsh, *Schistocera gregaria* (Forskal), *Adiheteothrips jambudvipae* Ramok and *Franklinella schultzei* (Trybom).

The remaining herbivore species were reported to be attacked by a total of 63 species of natural enemies: 40 were

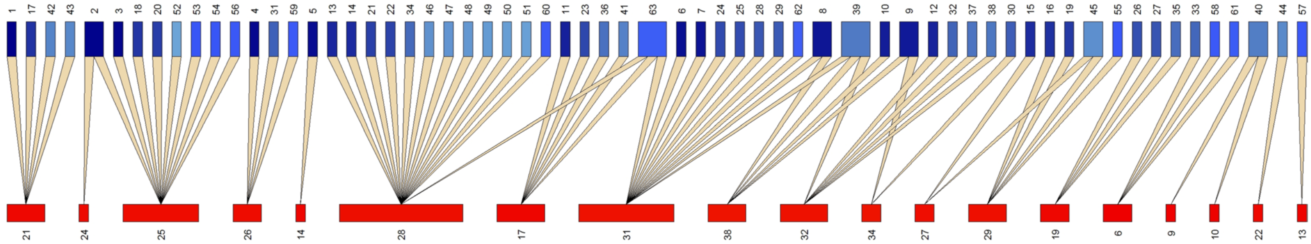

Fig. 1 Trophic interactions between herbivores and natural enemies (parasitoids and predators) of date palms in Oman: composite connectance web summarizing natural parasitism and predation (Web A). The lower (red) row represents the 19 species of herbivores of date palm (from a total of 44 reported herbivore species) that are recorded to have natural enemies in Oman. The upper (blue) row represents the species of natural enemies (1–40 are parasitoids and 41–63 are predators) attacking these herbivores. The width of the bar for each species is proportional to the number of trophic interactions that species has relative to those of other species at the same trophic level. In both rows, species are ordered in such a way as to produce the visually simplest trophic web possible, rather than according to their numerical labels. Herbivore and natural enemy species identities are given in Supplementary Tables 1 and 2, respectively; herbivore 31 is the lesser date moth

parasitoids, mainly belonging to the order Hymenoptera, and 23 were predators belonging to the orders Coleoptera, Dermaptera, Diptera, Hemiptera and Neuroptera (Table 2 and Supplementary Table 2). Some of the important pests of the date palm are attacked by many parasitoids and predators (e.g. LDM, 8 parasitoids and 2 predators; pomegranate butterfly, 5 parasitoids; carab moth, 4 parasitoids; dubas bug, 3 parasitoids and 2 predators; spherical mealybug, 5 parasitoids and 8 predators; *Parlatoria* scale, 4 parasitoids and 4 predators; citrus mealybug, 2 parasitoids and 3 predators) (Fig. 1). The mean number of natural enemy species per herbivore (including those that were not attacked by any species of natural enemy), or 'natural enemy load' was 1.66, with the parasitoid load averaging around twice the value of the predator load (Table 2). Conversely, the mean number of herbivores attacked per natural enemy (natural enemy diet breadth) was 1.14, with similar diet breadths between predators and parasitoids (Table 2).

Of the 63 species natural enemies, only 7 were shared between two or more herbivores. The overall proportion of natural enemy overlap between the herbivore species was 0.011, while parasitoid overlap was 0.0063 and predator overlap was 0.0042 (Table 2, Supplementary Table 3). The potential for apparent competition between all herbivores within Web A is relatively low (Fig. 2), and the PAC value for LDM is the lowest among all webs constructed (Table 2).

Date palm pests and natural enemies across the Middle East (Web C)

There were records of 52 species of herbivores of date palm throughout the Middle East belonging to the Orders Coleoptera (15), Diptera (2), Hemiptera (18), Lepidoptera (12), Orthoptera (2) and Thysanoptera (3) (Supplementary Table 4). Twenty-three of these species did not have any reported species of natural enemies. The others were reported to be attacked by a total of 119 species of natural enemies (61 parasitoids and 58 predators, Table 2, Fig. 3 and Supplementary Table 5). The mean number of natural enemy species per herbivore (including those that were not attacked by any species of natural enemy), or 'natural enemy load' was 2.86, with the predator load lower than the parasitoid load (Table 2). Among the hymenopteran parasitoids, the majority belonged to the families Aphelinidae (7), Braconidae (9), Encyrtidae (10), Eulophidae (4) and Trichogrammatidae (10). Among the predators, 45 species belonged to the Coleoptera, of which 34 belonged to the Family Coccinellidae (Supplementary Table 5).

The connectance of the herbivore–natural enemy trophic web was 0.023, similar to the value when only records from Oman were considered (Table 2, Fig. 3). Some of the herbivores were attacked by more parasitoids and predators across the Middle East than in Oman alone; e.g. the lesser date moth, 13 parasitoids compared to 8 (Table 2, Fig. 3). The mean number of herbivores attacked per natural enemy (natural enemy diet breadth) was 1.22, with similar diet breadths between predators and parasitoids (Table 2). The proportion of the overall natural enemy overlap between herbivore species was 0.0151, the parasitoid and predator overlap values separately being 0.0068 and 0.009, respectively (Table 2, Supplementary Table 6). Twenty-one of the 119 natural enemies were shared between two or more herbivores. The potential for apparent competition between all herbivores within Web C (Fig. 4) and the PAC value for LDM are both higher than when only records from Oman are considered (Table 2).

Date palm, intercrops pests and natural enemies in Oman (Web B)

The literature survey provided, in addition to date palm, records for 49 intercrop species grown in Oman mainly

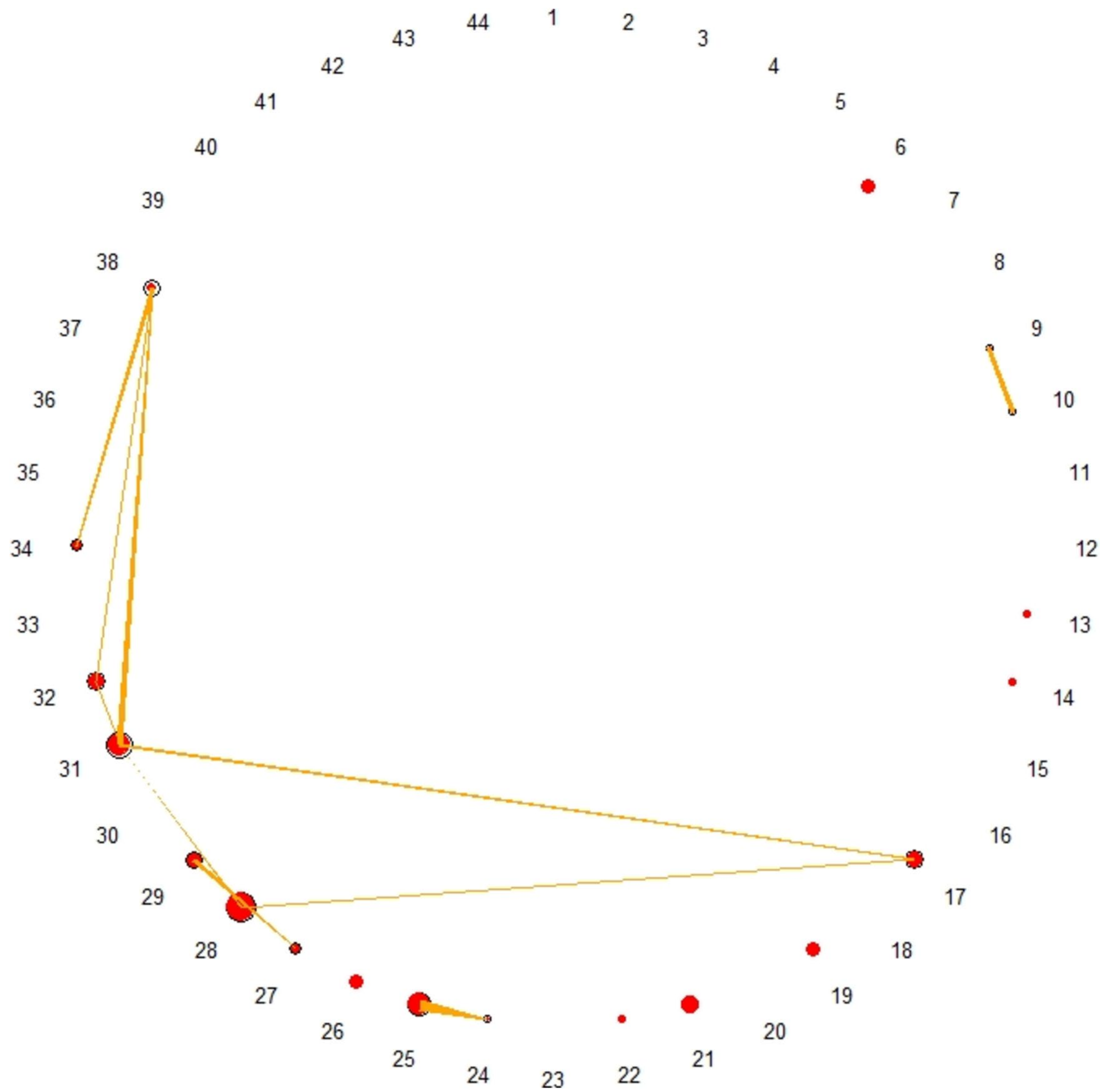

Fig. 2 Parasitoid overlap graph showing the overall potential for apparent competition between all reported herbivores of date palm in Oman (Web A). The numbers represent the herbivore species as given in Supplementary Table 1; herbivore number 31 is the lesser date moth. The circle size is proportional to the number of parasitoid species from each herbivore and lines represent sharing of parasitoids between the herbivores with thickness proportional to the number of parasitoid species

belonging to the families Brassicaceae (4), Cucurbitaceae (4), Fabaceae (4), Poaceae (6), Rosaceae (6), Rutaceae (6) and Solanaceae (3) and these were fed on by a total of 80 species of herbivores (36 hemipterans, 20 lepidopterans, 14 coleopterans and 4 dipterans) (Table 2, Fig. 5, Supplementary Tables 7 and 8, Supplementary Fig. 3). The connectance of the plant–herbivore trophic web was 0.043 (Fig. 5) and the proportion of the herbivore overlap between the constituent plant species was 0.18 (Table 2, Supplementary Table 10). Some herbivore species attacked many plants in the Omani date palm intercropping agro-ecosystem: *Bemisia tabaci* attacked 14 plant species, *Aphis gossypii* attacked 13 species, *Aleurodicus dispersus* and *Aonidiella orientalis* each attacked 6, and *Maconellicoccus hirsutus* and *Cadra cautella* each attacked 7 species, *Aleurodicus dispersus* and *Aonidiella orientalis* each attacked 6 species and *Spodoptera exempta* and *Planococcus citri* each attacked 5 species. The average diet breadth of herbivores was 2.14 and each plant species was fed on by on average 3.54 species of herbivore. Around one-third (29/80) of the herbivores shared two or more food plant species.

There were 127 species of natural enemies (90 parasitoids and 37 predators) attacking the recorded herbivores (Table 2 and Supplementary Table 9). Of the 90 species of parasitoids, 86 were hymenopterans and they mainly belonged to the families Aphelinidae (18), Braconidae (12),

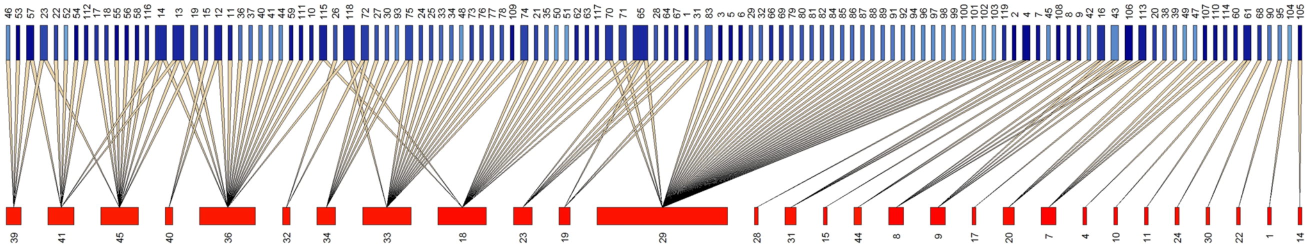

Fig. 3 Trophic interactions between herbivores and natural enemies (parasitoids and predators) of date palm across the Middle East: composite connectance web summarizing natural parasitism and predation (Web C). The lower (red) row panel represents the 29 herbivore species feeding on date palm (from a total of 52 reported herbivore species) that are recorded to have natural enemies in the Middle East. The upper (blue) panel represents the species of natural enemies (1–61 are parasitoids and 62–119 are predators) attacking these herbivores. In both rows, species are ordered in such a way as to produce the simplest trophic web possible, rather than according to their numerical labels. Herbivore and natural enemy species identities are given in Supplementary Tables 4 and 5 respectively; herbivore 36 is the lesser date moth

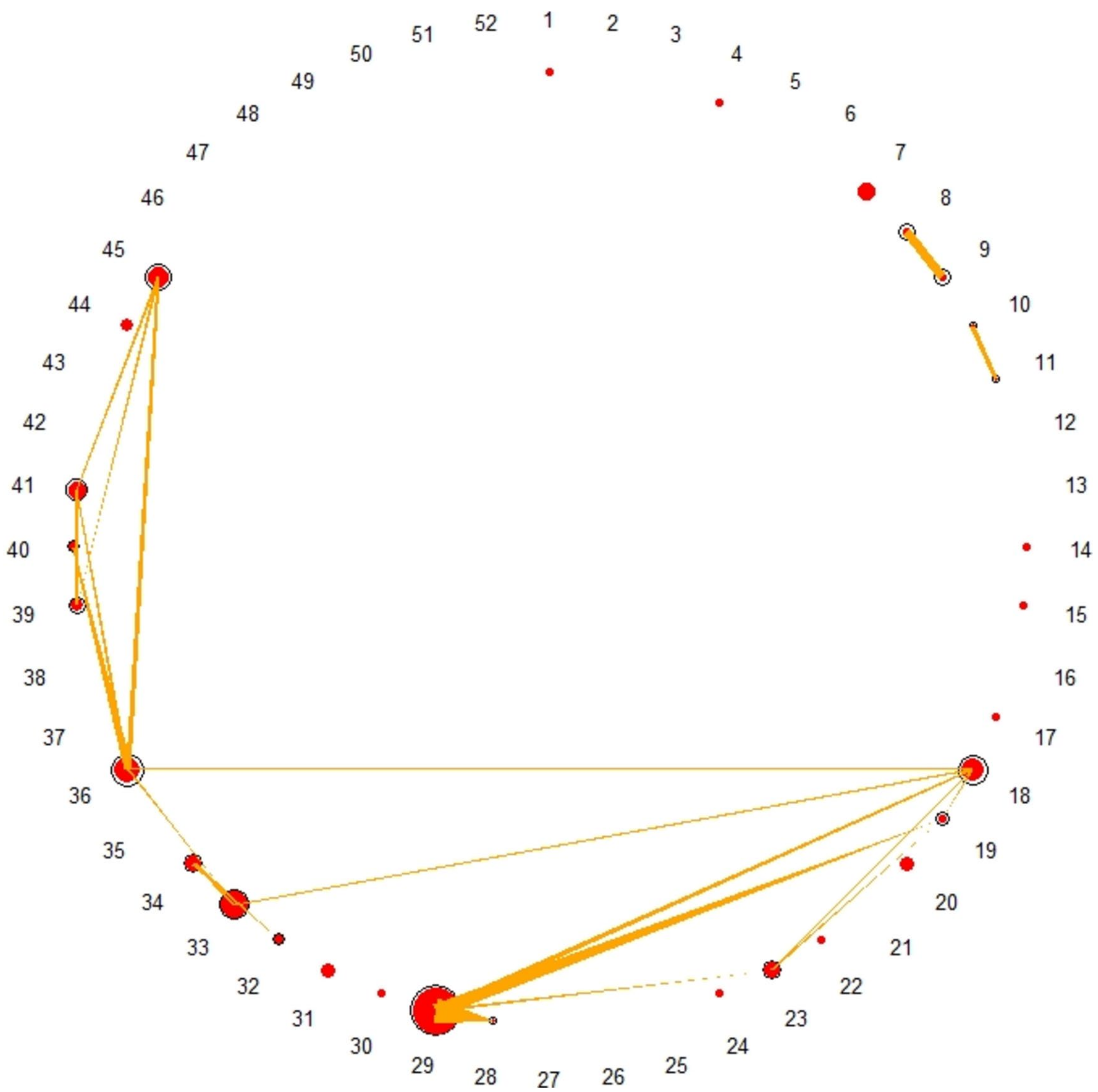

Fig. 4 Parasitoid overlap graph showing the potential for apparent competition between all herbivores of date palm in the Middle East (Web C). The numbers represent herbivore species as given in Supplementary Table 4; herbivore 36 is the lesser date moth

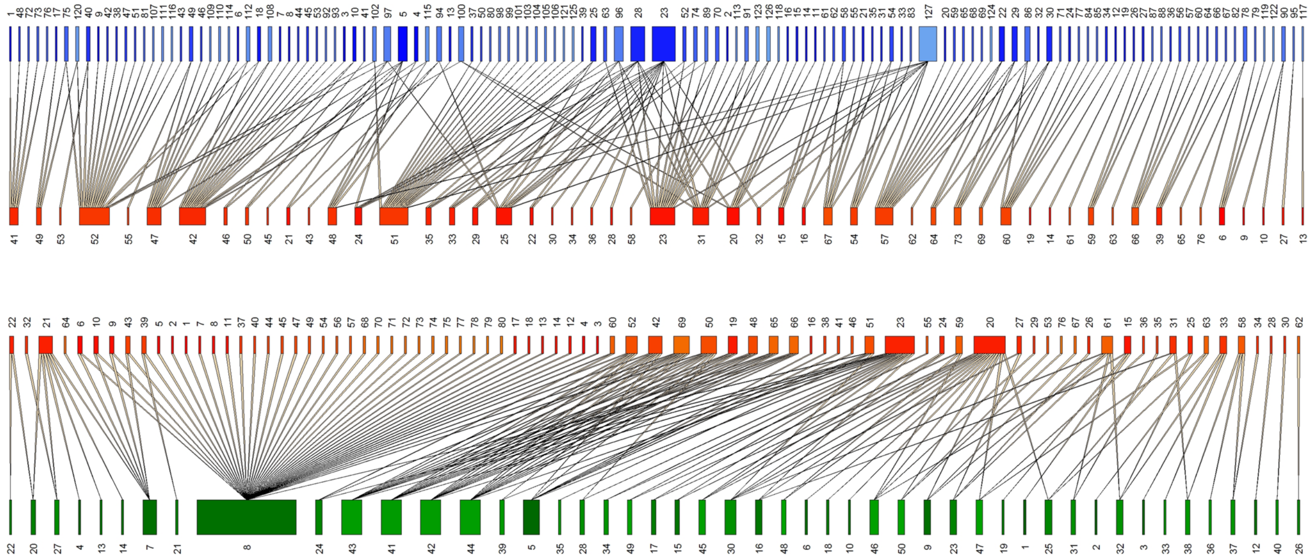

Fig. 5 Trophic interactions between plants, herbivores and natural enemies (parasitoids and predators) of date palm and intercrops in Oman: composite connectance web summarizing natural parasitism and predation (Web B). The upper panel represents interactions between herbivores (red) and their natural enemies (blue) and the lower panel represents interactions between plants (green) and their herbivores. Fewer species of herbivores (53) are shown in the upper panel than in the lower panel (80) because some reported species of herbivores had no recorded natural enemies in Oman. The lower panel represents 50 plant species including date palm, and the upper panel represents 127 species of natural enemy (1–90 are parasitoids and 91–127 are predators) attacking their herbivores. In each panel, species are ordered within rows in such a way as to produce the simplest trophic web possible, rather than according to their numerical labels: the order of herbivores thus differs between the panels. Supplementary Fig. 3 shows the same interactions as a single tri-trophic web, with all species ordered numerically. Species identities are given in Supplementary Tables 7, 8 and 9; date palm is plant species 8 (the widest bar) and herbivore 57 is the lesser date moth

Encyrtidae (17), Eulophidae (12), Pteromalidae (5) and Trichogrammatidae (4). Of the recorded predators, 28 species belonged to the Coleoptera, 23 of which were in the family Coccinellidae.

The herbivore–natural enemy connectance was 0.020, and the proportion of the natural enemy overlap between herbivores was 0.51 (Supplementary Table 11), with an average of 2.65 natural enemy species attacking each herbivore (natural enemy load). The number of parasitoids and the number of predators attacking given herbivore species were positively but marginally non-significantly correlated (Spearman's rank correlation: 0.346, $t = 1.98$, d.f. $= 53$, $P = 0.053$). The average diet breadth of natural enemies is 1.6, with similar values among predators and parasitoids (Table 2). The parasitoids that attacked many herbivores include *Aphidius* sp. (Braconidae) attacking 13 species, *Ephedrus persicae* (Braconidae) attacking 8 species and *Aphytis* sp. (Aphelinidae) attacking 5 species. Predators that attacked many herbivore species include *Chrysoperla carnea* (Neuroptera) attacking 10 species, *Coccinella undecimpunctata* (Coccinellidae) attacking 5 species and *Cryptolaemus montrouzieri* (Coccinellidae) attacking 4 species. Of the 127 natural enemy species, 36 shared two or more herbivores as hosts or prey. The parasitoid and predator overlap values were 0.021 and 0.034 respectively (Table 2). The potential for apparent competition between all herbivores within Web B appears relatively high (Fig. 6), and the PAC value for LDM is higher than among webs that do not include intercrops (Table 2).

Date palm, intercrops pests and natural enemies across the Middle East (Web D)

Considering the date palm intercropping system throughout the Middle East, literature records indicated a total of 69 intercrop species, 112 species of herbivores and 198 species of natural enemies (131 parasitoids and 67 predators, Table 2, Supplementary Tables 12, 13 and 14). Among the intercrops, the majority of the plants belonged to the following families: Asteraceae (3), Brassicaceae (5), Cucurbitaceae (4), Fabaceae (10), Poaceae (7), Rosaceae (7), Rutaceae (5) and Solanaceae (5) (Supplementary Table 12). Among the recorded herbivores, 50 belonged to the Hemiptera, 28 to the Lepidoptera, 20 to the Coleoptera and 7 to the Diptera (Supplementary Table 13). Herbivore species fed on an average of 2.77 plant species (herbivore diet breadth) and many herbivores used substantially more plants than this average: *Bemisia tabaci* attacked 15 species, *Aphis gossypii*, *Maconellicoccus hirsutus, Nipaecoccus viridis* and *Planococcus citri* fed on 13 species each, *Plutella xylostella* fed on 10 species, *Helicoverpa armigera* fed on 9 species,

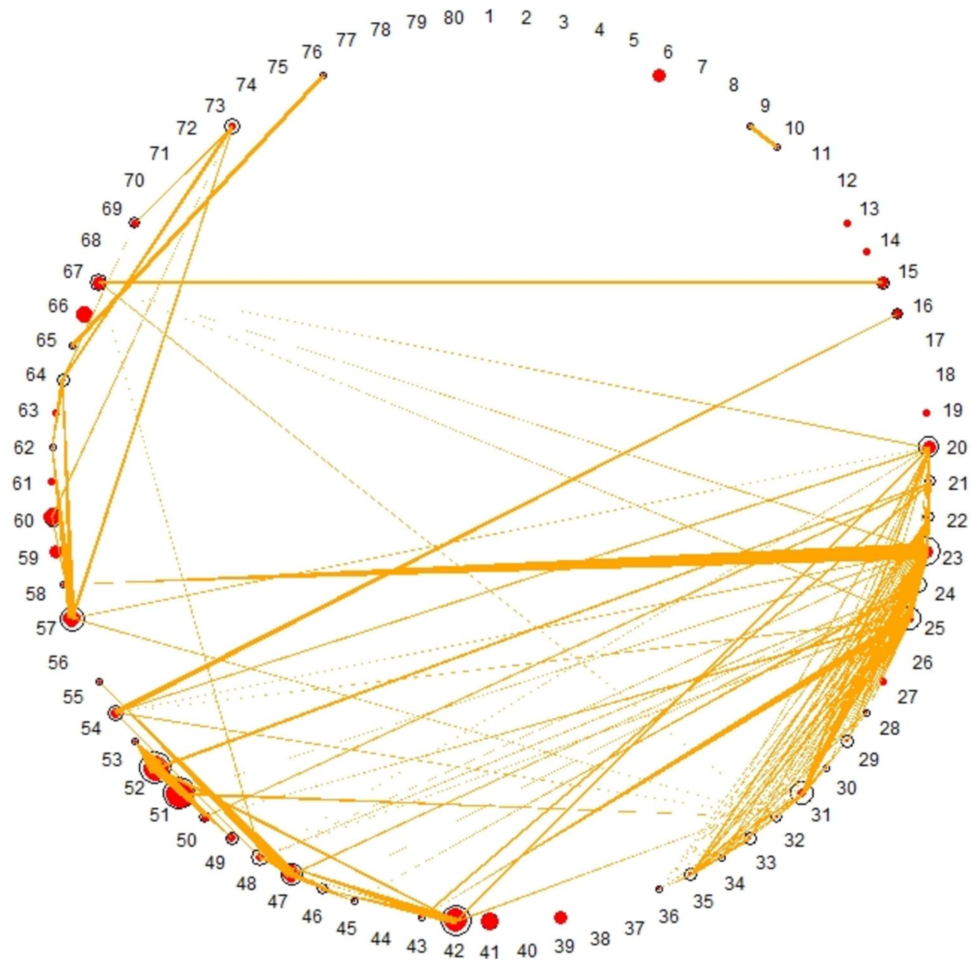

Fig. 6 Parasitoid overlap graph showing the potential for apparent competition between all herbivores of date palm and intercrops in Oman (Web B). The numbers represent herbivore species as given in Supplementary Table 7; herbivore 57 is the lesser date moth

Aonidiella orientalis and *Cadra cautella* fed on 8 species, *Brevicoryne brassicae, Rhopalosiphum padi* and *Spodoptera littoralis* fed on 7 species and *Spodoptera exempta*, *Aleurodicus disperses* and *Myzus persicae* fed on 6 species. Fifty-two of the 112 species of herbivores shared two or more host plant species and the herbivore load for plants was 4.43. The connectance of the plant–herbivore trophic web was 0.040, and the proportion of the herbivore overlap between the constituent plant species was 0.224 (Table 2, Fig. 7 and Supplementary Table 15, Supplementary Fig. 4).

There were 197 species of natural enemies (130 parasitoids and 67 predators) attacking the herbivores of date palm and its intercrops. Among the 130 species of parasitoids, 23 belonged to family Aphelinidae, 21 to the Encyrtidae, 20 to the Braconidae, 16 to the Eulophidae, 10 to the Trichogrammatidae, 7 to the Pteromalidae and 4 each to the Bethylidae, Chalcididae and Torymidae and 3 to the Ichneumonidae (Supplementary Table 14). Of the 67 species of predators, 49 belonged to Coleoptera, with 40 species in the family Coccinellidae and 9 in Cybocephalidae (Supplementary Table 14). The mean number of natural enemies per herbivore (natural enemy load) was 3.56, with higher parasitoid loads than predator loads (Table 2). The number of parasitoids and the number of predators attacking given herbivore species were positively correlated (Spearman's rank correlation: 0.451, $t = 4.04$, d.f. $= 87$, $P < 0.001$). The mean diet breadth of natural enemies was 1.93, with similar values when predators and parasitoids were considered separately (Table 2). The parasitoids that were natural enemies of many herbivore species include *Aphidius* sp. attacking 19 species, *Apanteles* sp. and *Ephedrus persicae* attacking 10 species, *Habrobracon hebetor* attacking 9 species, *Diaeretiella rapae* attacking 7 species, *Trichogramma* sp. attacking 6 species and *Aphytis* sp., *Telenomus* sp. and *Trichogramma evanescens* each attacking 5 species. The predators with multiple prey species include *Chrysoperla carnea* preying on 18 species, *Coccinella septempunctata* preying on 8, *Coccinella undecimpunctata* preying on 6 species, *Cheilomenes sexmaculata, Chilocorus bipustulatus, Cryptolaemus montrouzieri* and *Orius* sp. each preying on 5 herbivore species.

Of the recorded 197 natural enemies, 68 shared two or more herbivores as hosts or prey. The herbivore–natural enemy connectance was 0.017 and the proportion of the natural enemy overlap between the herbivore species was

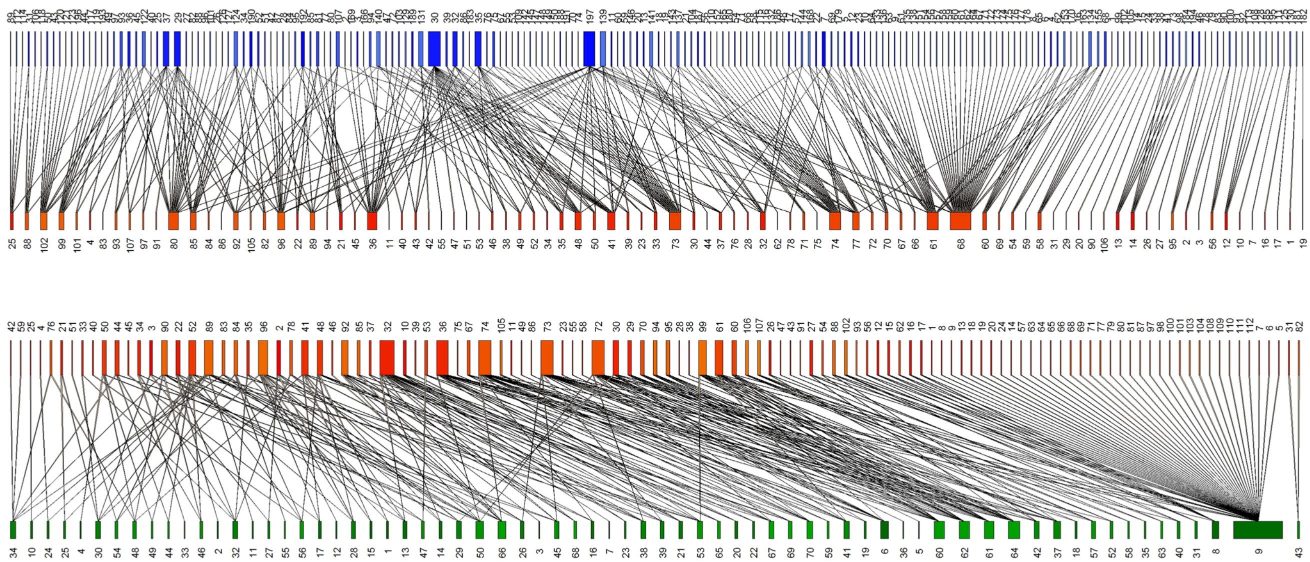

Fig. 7 Trophic interactions between plants, herbivores and natural enemies (parasitoids and predators) of date palm and intercrops across the Middle East: composite connectance web summarizing natural parasitism and predation (Web D). The upper panel represents interactions between herbivores (red) and their natural enemies (blue) and the lower panel represents interactions between plants (green) and their herbivores. Fewer species of herbivores (89) are shown in the upper panel than in the lower panel (112) because some reported species of herbivores had no recorded natural enemies in the Middle East. The lower panel represents 70 plant species including date palm, and the upper panel represents 197 species of natural enemies (1–130 are parasitoids and 131–197 are predators) attacking their herbivores. In each panel, species are ordered within rows in such a way as to produce the simplest trophic web possible, rather than according to their numerical labels: the order of herbivores thus differs between the panels. Supplementary Fig. 4 shows the same interactions as a single tri-trophic web, with all species ordered numerically. Species identities are given in Supplementary Tables 12, 13 and 14; date palm is plant species 9 (the widest bar) and herbivore 80 is the lesser date moth

0.080 (Table 2, Fig. 7 and Supplementary Table 16). The parasitoid and predator overlap values calculated separately were 0.052 and 0.035, respectively (Table 2). The potential for apparent competition between all herbivores within Web D (Fig. 8) appears to be the highest for all webs considered, as is the PAC value for LDM (Table 2).

The natural enemies of Lesser Date Moth

LDM has 10 species of natural enemies (8 parasitoids and 2 predators) when considering date palms only (without intercrops) and date palms with intercrops in Oman. Of these 10 species, 3 and 4 were shared with other herbivores in date palms only and date palms with intercrops plantations respectively (Table 2). The number of natural enemies increased to 15 (13 parasitoids and 2 predators) when considering the whole of Middle East. Out of these 15 species of natural enemies, 7 were shared with other herbivores in date palm only plantations and 9 in date palm plantations with intercrops considered (Table 2). The estimated potentials for apparent competition (PAC), due to shared natural enemies, between LDM and other herbivores were lower when considering date palms only compared to when considering date palms with intercrops (Table 2), both within Oman and across the Middle East. PAC values were also higher when records from all Middle Eastern countries were considered rather than Oman only (Table 2).

Discussion

Trophic webs are tools that aid understanding of agro-ecological interactions (Memmott and Godfray 1994; Peralta et al. 2014; Henri and van Veen 2016; Sanders et al. 2018) and help to answer specific ecological questions, such as the importance of intercrops and their associated insect fauna and of apparent competition (Frost et al. 2016; Shameer et al. 2018). These answers are in turn helpful in the formulation of integrated pest management strategies (Shameer et al. 2018; Malard et al. 2020).

We have constructed trophic webs for the date palm agro-ecosystem. The indirect method of assessing community structure, using prior literature records, that we employed in this study is time-consuming but nonetheless more rapid than direct empirical assessment. The method is, however, constrained to be qualitative rather than quantitative (Memmott and Godfray 1994; Sunderland et al. 2023) and results are likely to be broadly indicative of field reality across large geographical areas rather than reflecting accurately a trophic

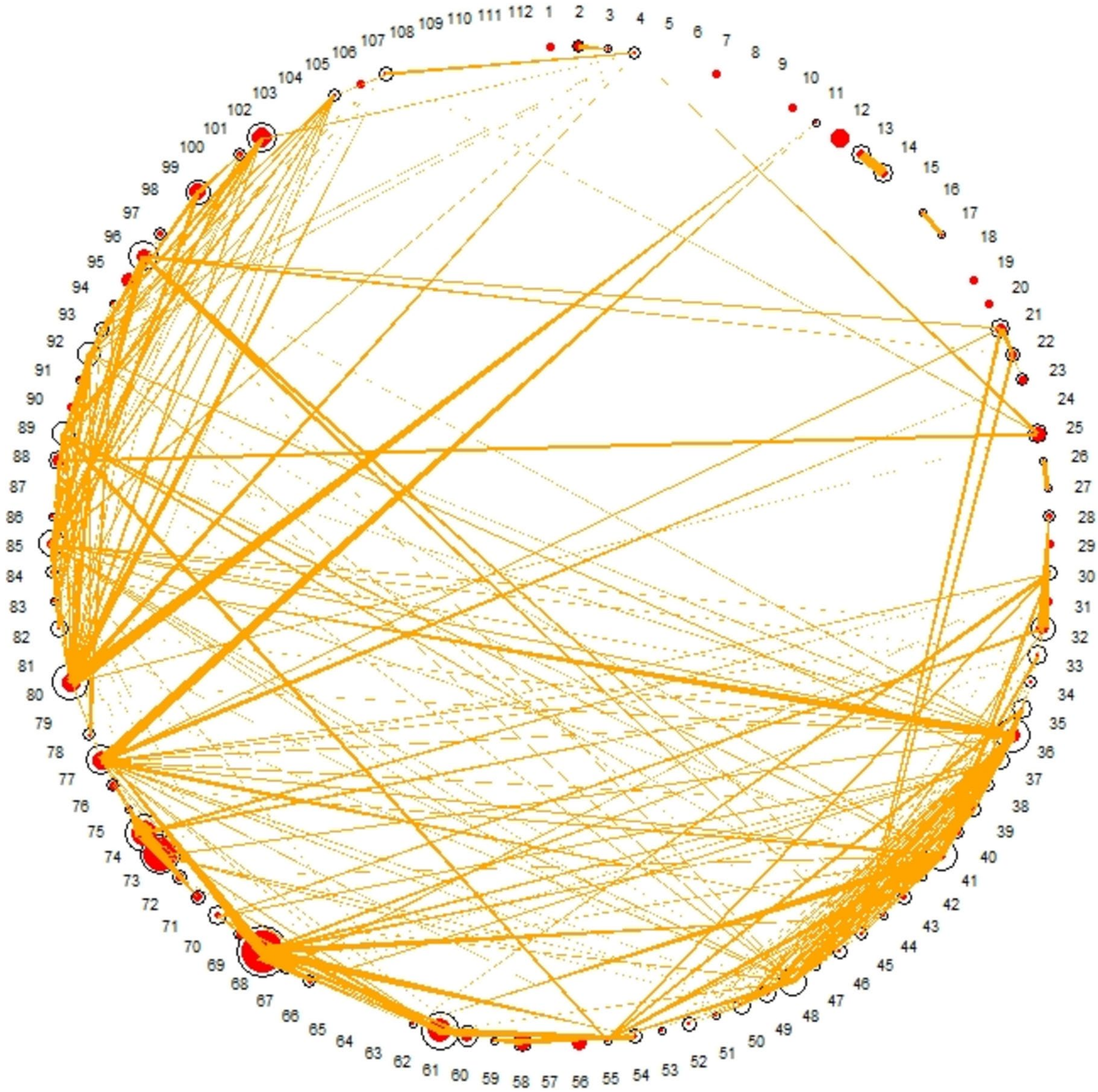

Fig. 8 Parasitoid overlap graph showing the potential for apparent competition between all herbivores of date palm and intercrops in the Middle East (Web D). The numbers represent herbivore species as given in Supplementary Table 12; herbivore 80 is the lesser date moth

situation in a given locality. We constructed webs using literature collected at two different geographical scales, within Oman and across the Middle East, to enable us to assess the likely sensitivity of community metric estimates to regional variation in literature records. We found that estimates of connectance (community complexity), plant–herbivore overlap, herbivore–natural enemy overlap and natural enemy diet breadth were little affected by the geographical scale considered, suggesting that literature-based trophic web construction may be efficiently based on subsets of wider sources of information. Visualizations of parasitoid overlap between all herbivores within the constructed webs were also similar at national and regional scales, but estimates of the potential for apparent competition between LDM and other herbivores were higher at the regional scale.

We constructed trophic webs both including and excluding consideration of intercrop species to enable us to identify the likely effects of crop plant diversity on the structure of the insect community and to draw inference on how these might affect pest and natural enemy populations. In general, increased crop diversity increases the complexity of communities, and the density and type of alternative host plants can influence pest populations (van Veen et al. 2006; Zhang et al. 2017) by supporting them during periods when their primary host plants are seasonally unavailable (Clementine et al. 2005; Goodell 2009; Saeed et al. 2015) and also by supporting natural enemies that can suppress pests via indirect ecological interactions (e.g. Shameer et al. 2018). In date palm plantations, intercropping may be unpractised in some areas (e.g. Israel) and very common in others: in Oman date palm is intercropped with many field crops (e.g. wheat, barley, sorghum, maize, alfalfa), vegetables (e.g. onion, garlic, okra) and fruit trees (e.g. mango, guava, jujuba, pomegranate, grapes) (Siebert et al. 2007). Such intercropping is carried out without consequent reductions on date palm yield (Letourneau et al. 2011; Iverson et al. 2014), which provides extra produce and income for farmers (T.A. pers. obs.).

We found that when considering herbivores and their natural enemies, connectance estimates were not greatly affected by the inclusion or exclusion of intercrops. When intercrops were included, the estimate of plant–herbivore connectance was low but not dissimilar to equivalent estimates reported from a similar study of coconut palm agro-ecosystem structure (Shameer et al. 2018). Our estimates of plant–herbivore overlap (circa 0.2 when intercrops were considered) were relatively high (e.g. an order of magnitude higher than the equivalent value, 0.034, reported in Shameer et al. 2018), suggesting that herbivores in the date palm agro-ecosystem are typically not specialist on a given plant species. Estimates of herbivore–natural enemy overlap values were an order of magnitude greater when calculated from the communities considering intercrops and the same patterns were found considering predators and parasitoids separately. This implies that if intercrops are present in an agro-ecosystem, ignoring them when constructing herbivore–natural enemy trophic webs in a study that was focussed on a given crop could generate considerable interpretational errors. The lower estimates (*circa* 0.01), obtained when intercrops were not considered, imply that natural enemies are specialists and thus that the likelihood of indirect ecological interactions, such as diffuse apparent competition, to have an important regulatory effect on herbivore populations is low. The higher values (*circa* 0.05), which may be more accurate reflections of the natural degree of overlap given that they consider intercrop species that are typically present in the field, are not large (e.g. in comparison to the value of *circa* 0.5 reported in Shameer et al. 2018, considering coconut palm and intercrops), suggesting that diffuse apparent competition may be present but relatively weak. Nonetheless, these estimates indicate that the presence of intercrops is likely to increase the degree of apparent competition between herbivore species within the date palm agro-ecosystem and may contribute to pest population regulation. This is further supported by visual comparison of parasitoid overlap between all herbivores within webs that include or exclude herbivores: overlap is clearly greater in the more complex crop communities.

Our estimates of natural enemy diet breadth (the numbers of herbivore species attacked) were greater when considering more complex arrays of plants (which were also associated with greater numbers of herbivores and greater numbers of natural enemies) but the differences were not large. We also found that herbivore species with higher numbers of predators also had higher numbers of parasitoids. Further analyses will be required to establish whether the life-history characteristics, such as whether they feed in exposed or concealed and protected locations (e.g. on leaf surfaces or within plant stems, Hochberg and Hawkins 1992) is correlated with natural enemy load in the date palm agro-ecosystem.

We constructed trophic webs for date palm agro-ecosystems with a particular interest in how community structure might affect populations of the lesser date moth, LDM, a major pest. The only reported host plant for LDM in the literature from the Middle East was date palm and LDM was thus considered monophagous in this study; it is, however, reported to feed on *Derris trifoliata* (Fabaceae) in India (Gerson and Applebaum 2019). From the literature on Oman, we found records of 10 species of natural enemies and that the number of natural enemies that are shared with other herbivores is greater when considering intercrops (4) than when considering only date palms (3). Similarly, when the whole of the Middle East was considered, there were records of 15 species of natural enemies and the number of natural enemies that were shared with other herbivores was 7 in date palm only and 9 when intercrops were considered. Additional shared natural enemies in intercropped date palm plantations might be expected to affect LDM populations via apparent competition. The estimates of the potential for apparent competition between LDM and other herbivores that we obtained clearly suggest that it will be more intense when date palm is grown with intercrops. While the presence of apparent competition in agro-ecosystems may not always reduce pest damage (Jaworski et al. 2015), the presence of intercrop herbivores may help sustain natural enemy populations in the absence of key pests (Settle et al. 1996; Holt and Hochberg 2001; Clementine et al. 2005; Feng et al. 2017) and thus intercrops may influence the survival natural enemies of LDM by maintaining populations of alternative hosts when LDM larvae are seasonally absent.

Assertions from indirect studies can be evaluated by targeted empirical studies conducted in the field to provide direct estimates of the trophic structure of the community, although these may require considerably greater resources. At present, very few direct empirical studies of insect communities have been carried out for the date palm agro-ecosystem. However, Rahnama and Latifian (2013) reported that the practice of intercropping enhances the numbers of beneficial arthropods, reduces damage by pests, including the LDM, and hence increases date yield. The fact that our indirect approach and a direct study arrive at compatible conclusions suggests that literature-based trophic web construction can be a robust alternative, or addition, to empirical methodologies.

The information obtained in the present study will guide towards a more detailed understanding of the dynamics of the date palm agro-ecosystem. Further studies could usefully construct quantitative trophic webs to overcome the limitation that the connectance webs generated by our indirect methodology do not reflect the relative strengths of the trophic interactions within communities, potentially distorting the descriptive metrics obtained. However, neither qualitative nor quantitative webs provide information on why particular trophic interactions are present or absent. While there are numerous classes of potential explanations for given feeding associations, herbivore diet breadth is likely to be affected by the chemical composition of crop plants and natural enemy diet breadth is similarly likely to be influenced by the nutritional composition of herbivore species. Metabolomic analyses may assist in understanding the suitability of crops and intercrops as food for herbivores and of herbivores for parasitism and predation (Bukovinszky et al. 2008; Snart et al. 2015; Schuman et al. 2016) and hence reveal key factors that influence the structure of the arthropod communities observed.

Conclusions

The structure of the host plant and insect community is likely to influence the natural control of the LDM. This key pest has 10–15 species of natural enemies (from Omani and Middle Eastern records, respectively) and shares 3–9 of these with other herbivores. These herbivores may thus maintain populations of natural enemies of the LDM during periods when it is seasonally unavailable and, as such, are likely to contribute to, rather than detract from, its control. From this we would expect that pest problems will be less severe in date palm plantations that are intercropped than in those that are monocultures. These conclusions are drawn from an indirect approach employing pre-existing literature records of plant–herbivore–natural enemy associations, with information sourced at national and regional scales generating broadly similar conclusions. While this approach, taken across an entire agro-ecosystem, is likely to be indicative rather than exact in its estimation of the importance of ecological interactions, the expectation derived from the consideration of literature reports of trophic relationships matches an empirical report of the benefits of intercropping in a particular date palm agro-ecosystem (Rahnama and Latifian 2013).

Overall, current evidence suggests that literature-based trophic web construction can provide an efficient and robust alternative, or addition, to direct empirical methodologies. The approach has the advantages that is it relatively rapid and provides a broad indication of likely community structure across a given agro-ecosystem. This can suggest the value of given cropping and pest management strategies plus indicate further avenues for more direct research.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10340-023-01730-5.

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Author contributions KSS and TA contributed approximately equally. ICWH conceived the study in discussion with KSS and TA. KSS and TA searched the literature and constructed and analysed the trophic webs. All authors wrote and revised the manuscript.

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Declarations

Competing interests The authors declare no competing interests.

Conflict of interest The authors declare an absence of conflicts of interest.

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