


Hybrid networks reveal contrasting effects of agricultural intensification on antagonistic and mutualistic motifs

Carlos Martínez-Núñez^{1,2}  | Pedro J. Rey^{1,2}

¹Dept. Biología Animal, Biología Vegetal y Ecología, Universidad de Jaén, Jaén, Spain

²Instituto Interuniversitario del Sistema Tierra de Andalucía, Universidad de Jaén, Jaén, Spain

Correspondence

Carlos Martínez-Núñez
Email: cmnunez@ujaen.es

Funding information

European Commission, Grant/Award Number: LIFE14 NAT/ ES/001094; Ministerio de Economía y Competitividad, Grant/Award Number: BES-2016-078736, CGL2015-68963-C2 and PID2019-108332GB-I00

Handling Editor: Bo Dalsgaard

Abstract

1. Anthropogenic-driven perturbations such as agricultural intensification can affect simultaneously and distinctly several species groups and ecosystem functions. Unveiling these concurrent effects on interdependent species groups connected by different types of ecological interactions is a key challenge for ecologists. To this endeavour, hybrid ecological networks arise as a promising tool.
2. In this study, we used bee trap nests to sample hybrid networks that combined mutualistic and antagonistic interactions to explore agricultural intensification effects on the representation of network motifs (i.e. subnetworks showing different interaction types between a small number of species). Also, we assessed the variability of network motif's frequencies on farms under similar management regimes and the dissimilarity between farms under different ones. For this, we implemented a novel approach, calculating network functional spaces based on probability density estimates of network motif's frequencies, using network motifs as traits.
3. Results showed that environmentally friendly practices maximize the representation of mutualistic (cavity nesting bees–plants) and predation (wasps–prey and bees/wasps–antagonists) motifs. In contrast, intensive agriculture favoured generalist and intraguild predation interactions. Lastly, the frequency of motifs representing antagonistic interactions was more inconsistent and unpredictable across sites than mutualistic motifs, especially on intensified farms.
4. Our novel approach, dissecting hybrid networks into their motifs and analysing the functional space defined by these, reported detailed and contrasting effects of agricultural intensification on network motifs that represent the mutualistic and antagonistic interactions in this system.

KEYWORDS

motifs, mutualism, network, pollination, predation, TPD

1 | INTRODUCTION

Understanding how anthropogenic perturbations simultaneously affect different types of interactions and ecological processes is a key challenge in ecology (Li et al., 2020; Pellissier et al., 2018; Tylianakis & Morris, 2017). However, most literature until now has

focused on food webs, or bipartite networks (e.g. plant–frugivorous, plant–pollinators) that consider exclusively one type of relationship such as mutualistic (+/+) or antagonistic (+/-) interactions. Although still incipient, the use of multilayer networks (i.e. networks of interconnected networks), that incorporate different types of interactions (often called 'multiplex' or 'hybrid' networks) (Morrison

et al., 2020), arises as a promising alternative that represents better the complexity of nature and can help to shed light on some previously unexplored matters (García-Callejas et al., 2018a; Hutchinson et al., 2019; Pilosof et al., 2017). For instance, some authors have employed these networks to assess how tree diversity affects plant-hemipteran-ant interactions (Fornoff et al., 2019), to theoretically test how different interaction types influence network structure and stability (García-Callejas et al., 2018b; Hale et al., 2020; Sauve et al., 2014), or to study the effects of agricultural intensification on the robustness of plant-pollinator-herbivore networks (Morrison et al., 2020). Some of these examples illustrate how human-driven disturbances can disrupt species interactions and change the structure of interaction networks (Valiente-Banuet et al., 2014), which can ultimately affect the ecosystem functions (Yen et al., 2016). However, linking network structural characteristics to real-world properties is a difficult endeavour (Thompson et al., 2012), since there is often confusion about the ecological meaning or conservation consequences of particular network structural properties (Dormann et al., 2017). Some authors have recently highlighted that different network structures might promote stability or not depending on the type of the interactions involved (Sauve et al., 2014). Hence, more straightforward and functional approaches might be useful to advance our knowledge in this field. In this sense, network motifs (i.e. subgraphs that compose networks and show the frequency of a certain type of interaction) (Milo et al., 2002; Stone et al., 2019) can provide mechanistic and functional understanding of network properties (Klase & Johnson, 2017) and ecological processes (Simmons et al., 2020). For instance, Gilling et al. (2019) recently showed that plant diversity increased apparent competition and exploitative competition motifs in food webs while reduced omnivory-related motifs. Also, Jácome-Flores et al. (2020) reported that some interaction motifs were associated with seed dispersal effectiveness in individual-based networks. Therefore, the network motif profile offers a network fingerprint that can be very useful to compare network properties, and study the impact of environmental perturbations on ecosystem functions.

To our knowledge, there is no empirical study tackling the effects of agricultural intensification, which is a worldwide main driver of biodiversity and ecosystem function loss, on a coupled system with pollination and predation interactions at the same time (but see Morrison & Dirzo, 2020 for a structural analysis on a plant-pollinator-herbivore system). In addition, the effects of agricultural intensification on mutualistic networks have barely been studied and even less is known about these effects on food webs (but see Gagic et al., 2011; or Lohaus et al., 2013). Regarding mutualistic interactions, Martínez-Núñez, Manzaneda, and Rey (2019) reported that plant-solitary bee networks are more robust, stable and heterogeneous on farms under an organic management regime. Similarly, Power and Stout (2011) found that organic farms benefitted insect-flower pollination networks. Other studies, not focused on interaction networks but species diversity or abundance, have found similar patterns of deteriorated pollination functioning due to farming intensification (e.g. Kennedy et al., 2013; Nicholson et al., 2017).

In this study, we use bee trap nests on olive farms to build hybrid networks including mutualistic (bee-pollen) and antagonistic (natural enemies that use trap nests) layers. Using these hybrid networks, we explore the effects of agricultural intensification (conventional versus organic farming) on mutualistic-antagonistic interactions, and unveil simultaneous impacts on pollination and predation interaction frequencies in this complex bee trap nest system. We propose that the occurrence and frequency of different network motifs can be conceptualized as network traits, an analogous to species functional traits, which allows calculating functional spaces defined by motif frequencies in networks. Hence, we use a novel approach that consists of dissecting networks into their motifs and treating them as network traits. Then, we use motifs representing differing types of interactions to understand how these networks vary across agricultural management regimes (i.e. conventional versus organic practices). We further estimate the functional spaces for hybrid networks sampled under similar agricultural practices, to test the variability (i.e. reverse of consistency) of different interaction motifs across sites. Specifically, we address three main questions: (a) Does agricultural intensification affect the frequency of different hybrid network motifs? (b) What is the variability of the hybrid network's motifs across sites under each management regime? and (a) How dissimilar (overlapping) are functional spaces defined by hybrid network's motifs between and within management regimes? Because the studied organic olive farms have a higher abundance and richness of herb species, and do not use pesticides, we predict that plant-solitary bee mutualistic interactions will benefit from organic management through (a) a higher frequency of mutualistic motifs in these hybrid networks and (b) a lower variability across sites (i.e. smaller functional space across sites showing a higher functional consistency) for frequency of mutualistic motifs. Regarding the predation function, because the reduced herb cover and the use of pesticides decrease prey availability and habitat suitability for predators, and this function in this system relies on more stochastic events, we expect that (c) motifs representing different predation relationships will be less frequent on intensified farms and (d) overall, the frequency of motifs based on antagonistic interactions will be more variable/unpredictable (more unstable) across farms in conventional olive groves.

2 | MATERIALS AND METHODS

2.1 | Study sites and design

This work was conducted at the regional scale in Southern Spain, considering 18 paired olive farms sited in 9 localities (5°53'46" W to 2°64'87" W and 38°40'05" N to 36°78'36" N). Mean distances between farms and localities were high enough to ensure independence and replicability, respectively (mean >1 km between farms and >100 km between localities). In each locality, a pair of farms with contrasting management regimes was selected. One farm was managed under conventional practices while the other was managed organically. Conventional farms were characterized by a systematic

removal of the herbaceous cover (mostly using pre-emergence herbicides) and the use of synthetic fertilizers/insecticides. The studied organic farms did not use agrochemicals and also maintained herb cover across the whole farm during most of the year (controlling it by mowing or animal means). These contrasting agricultural practices drove differences in mean herb cover and herb richness, as shown by linear mixed models with locality as a random effect term: $t_{86} = 10.21, p = 0.000$; predicted mean $\pm 1SE$: 86 ± 0.05 on organic versus 49 ± 0.05 conventional farms; and $t_8 = 3.17, p = 0.013$; 72 ± 6.4 on organic versus 46 ± 6.4 on conventional farms, effect size 1.5 for cover and 1.3 for richness, respectively (see Martínez-Núñez, Manzaneda, & Rey, 2019 for more details).

This design allowed us to study differences attributable to contrasting agricultural management regimes while controlling for locality-associated confounding factors.

2.2 | Sampling and sample processing

Interaction networks were sampled using trap nests (also known as bee hotels), as a standardized passive good method to store and detect biotic relationships (Staab et al., 2018). This tool provides cavities to above-ground nesting bees and wasps, where they store the resources to feed their brood (pollen loads in the case of pollinating bees and insects in the case of wasps). These solitary bees are known to forage close to their nests. Their foraging ranges are most times lower than 200–300 m (Zurbuchen et al., 2010). In addition, some antagonists can attack these cavities to feed on the bees/wasps offspring or kleptoparasite their nests (e.g. kleptoparasitic bees). Therefore, this technique enables to detect not only mutualistic interactions between bees and the plants they forage but also antagonistic interactions between wasps and their prey, plus the bees/wasps and their antagonists (Martínez-Núñez, Manzaneda, & Rey, 2019).

In total, 96 trap nests were set up in March 2017. Each nest had 104 cavities, including different diameters and materials, to attract as many different species as possible (See Figure S1 for a picture of a trap nest and more details). Trap nests were revised monthly until November 2017, and the occupied material was collected. Sampling effort was adjusted to farm size, being four nests for small farms (<25 ha) and six for big farms (>50 ha). Conservatively assuming that insects in a radius of ca. 150 m around a nest can detect it and use it (Zurbuchen et al., 2010), sampling effort covered approximately 28 and 42 ha on small and big farms, respectively. In addition, because comparisons are paired at the locality scale, unbalance in the number of nests used in different localities is not a shortcoming. Also, cavity occupation was 22% (3%–33%), and cells were never saturated.

Samples were stored at environmental temperature. Emerging adults were identified to species level (or morphotypes for some antagonists). For each cavity containing bees, three samples of pollen were taken, dyed using fuchsin and inspected under a microscope (Figure S1). Pollen samples were identified to the species or morphospecies level, using expert knowledge and the reference collection of

the University of Jaén. Bees, wasps and antagonists were identified using a stereomicroscope (See Tables S1–S3, for a complete list of found species). Because bee females actively collect pollen and pack them to feed their brood, each cavity containing a bee and a plant (pollen) species was defined as an interaction between these two species (see Martínez-Núñez, Manzaneda, Lendínez, et al., 2019; Martínez-Núñez, Manzaneda, & Rey, 2019 for more details about the whole nesting process). Antagonistic relationships were also unveiled by linking predator and prey species found in the same cavity. For some predator species, only the predator was found inside the cavity (e.g. a wasp species) or the prey was unidentifiable. In these cases, a generic group of prey was inferred using information from literature (e.g. spiders) (see Table S3), adopting a conservative approach to avoid overestimating the number and diversity of antagonistic links. This constrained the antagonistic layer to some more general relationships (e.g. *Tripoxylon attenuatum* predaes on spiders). However, this was not a drawback because the overall taxonomic resolution was high (92% of nodes to species/morphospecies level), and network resolution was homogeneous across sites (e.g. *T. attenuatum* predaes on spiders in all networks where it appears), which makes networks comparable.

2.3 | Hybrid networks, motifs and completeness

Each hybrid network was composed by two merged networks, the mutualistic network, involving solitary bee–plant interactions, and the antagonistic network, involving bees, wasps and their prey/antagonists. The nodes representing bee species connected both networks, because they were mutualistic partners in one network, and prey in the other. Although these types of networks can be conceptually considered multilayer networks, the motifs already discriminate different types of interactions (i.e. bidirectional interaction for mutualistic relationships and unidirectional for antagonistic relationships). Hence, we could analyse environmental effects on two different types of networks/interaction types, using structurally single monolayer networks.

These hybrid networks were decomposed into all their subgraph components including only two and three species (Davis & Leinhardt, 1972), namely dyads and triads, respectively (i.e. motifs encompassing two/three nodes). Although some authors have used motifs involving four nodes (e.g. Solé & Valverde, 2006), our networks were not big enough to show variability in these motif profiles and interpreting them can be very difficult. Motif profiles show the frequency of different interactions of a kind (i.e. richness of interactions of a kind involving different nodes). We used the *triad_census* and *dyad_census* functions in the *igraph* R package (Csardi & Nepusz, 2006) to count the frequency of each different type of motif that appeared in each network (see Table 1 for a description of the motifs observed, their meaning and other details). Note that the frequency of a network motif represents the richness of interactions of a given type involving different nodes (i.e. it is not a weighted but a qualitative measure). The network motif profile is a network

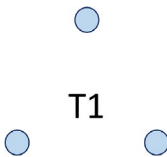
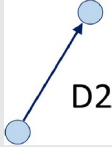
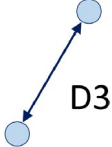
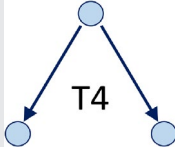
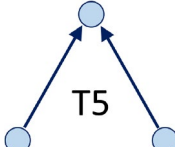
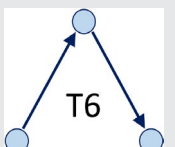
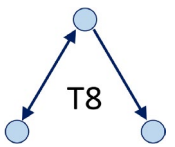
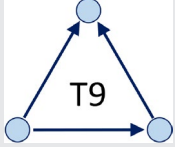
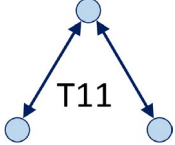
Motif	Interactions	Graphical representation	Ecological meaning
T1	A, B, C		Non-interacting species in the network. It is proportional to network size, link diversity and inversely correlated with connectance.
D2	A->B		Simple predation.
D3	A<->B		Mutualistic pollination interaction (or mutual predation; the latter not present in our data).
T4	A<-B->C		Exploitative Competition by two predators for the same prey.
T5	A->B<-C		Apparent competition. Double predation by a dominant or generalist predator.
T6	A->B->C		Transitive predation chain. Our data show the presence of a generalist top predator.
T8	A<->B->C		Pollination plus predation. The bee is predated. Represents complex relationships.
T9	A->B<-C, A->C		Omnivory/Intraguild predation. Transitive antagonistic relationships involving a dominant or generalist top predator.
T11	A<->B<->C		Plant-pollinator unspecific interaction.

TABLE 1 Motif types found in hybrid networks. Double-headed arrows correspond to mutualistic pollination interactions. Simple arrows correspond to antagonistic predation interactions. For convention, motif numbers correspond to the order in which they usually appear (see R function; note that Triad 7 and Triad 10 are absent in our networks). We substituted Triad 2 and Triad 3 by the antagonistic and mutualistic dyads, respectively, to avoid the floating node (third non-interacting node) to introduce noise in the measure

fingerprint, showing network characteristics in great detail. Because we can infer different network characteristics from each of these motif types (see Table 1; each one is related to a different ecosystem property such as degree of mutualism, apparent competition or intraguild predation), we used them as network traits that ultimately provide information about ecosystem properties. Hence, the

frequency of different motifs shows the intensity and diversity of a specific type of interaction (e.g. the asymmetric dyad 2 represents simple predation).

To ensure an adequate and non-biased sampling across treatments, we estimated network completeness, following Chacoff et al. (2012). Then, we used network interaction completeness as

a response variable, and ran a linear mixed model with management regime (conventional versus organic) as fixed factor, and locality as a random factor. The estimated sample completeness was $60\% \pm 19$ (mean \pm SD), similar to other network studies (e.g. 50% in Grass et al., 2018). The linear mixed model showed no differences in sampling completeness across management regimes ($\Delta\text{AIC} = 1.72$, $p = 0.59$, $R_m = 0.015$).

2.4 | Statistical analyses

First, we analysed differences in the frequency of several motif types across management regimes. We ran multilevel mixed Bayesian models, fitted through MCMC (Markov Chain Monte Carlo) in the *brms* R package (Bürkner, 2018). In these models, we introduced motif frequency (for each motif type separately) as response variable, management regime (conventional versus organic) as fixed term and locality ID as a random term. For the nine models (one for each motif type that appeared in our networks), we used uninformative diffuse priors (meaning that we do not have previous information about the response variables to bias the calculation of posterior probabilities) and model specifications that rendered stable outputs (4 chains and 50,000 iterations with the first 10,000 being burned). We also checked normality of the residuals by visual examination, convergence via $R^{\hat{}}$ (all equal to 1 or 1.01) and stability of results (by visual inspection of chains). We employed these Bayesian models because they perform better than frequentist methods for low-moderate sampling sizes ($N = 18$; $n = 9$ organic farms and $n = 9$ conventional farms). They are more straightforward to interpret and allow a probabilistic approach. In addition, inferences are conditional on the data, meaning that estimates are exact. Results were interpreted by calculating the probability of beta (slope) being positive/negative. To obtain more information about the magnitude of the effects from an intuitive perspective, we also estimated the probability of beta being a 30% higher/lower than the intercept. This threshold is arbitrary but provides intuitive additional information on differences between treatments.

Second, we applied a novel approach to assess the variability of the frequency of network motifs (or motif combinations) among networks that shared a given management type, and across different management regimes. We considered network motifs as network traits (analogous to species functional traits). The functional space defined by a certain motif (or group of motifs) across different networks provides information about the variability of ecological processes (e.g. apparent competition or predation) through networks. To calculate functional spaces defined by network motifs, we adapted the Trait Probability Density (TPD) approach to this endeavour (Carmona et al., 2019). The TPD method uses procedures based on kernel density estimations to calculate the probability of a trait (or multiple traits) for a group of individuals or species in a community. We introduced network motifs (i.e. network traits) instead of species traits, each network resembling

an individual/species, and each management regime type (conventional or organic) as a species/community. Using TPD, we estimated the motifs' functional space (i.e. frequency richness), functional evenness (i.e. frequency homogeneity) and functional divergence (i.e. distribution of frequency abundances within the functional space) for each management condition (conventional versus organic farms). Likewise, we estimated the functional dissimilarity (non-overlapping space) between network motifs' frequencies of conventional and organic farms. One of the main advantages of this extension of TPD approach is that it enables to test various traits (i.e. motifs) combined, offering calculations of higher-order properties (i.e. overall predation or mutualistic motifs). Then, we calculated functional metrics for each type of motif independently, and for two groups (antagonistic and mutualistic motifs). This method allows therefore the exploration of several variables related to the density and distribution of network motifs across sites, unveiling the variability of these properties within treatments and the dissimilarity between them.

Functional metrics were calculated using the R package *TPD* (Carmona et al., 2019). We considered 99% quantiles for probability density calculations, and used Principal Components instead of raw data, when we wanted to assess variations in more than four motif types (this method can deal with four dimensions as maximum). We did not use null models, because we are interested in absolute net differences (differences in motifs frequencies and function intensity) between management regimes, which can be importantly influenced by differences in abundance or diversity. Furthermore, sampling effort between pairs of farms was completely standardized and differences in interaction abundances reflect contrasts in communities and their interactions. Therefore, network size, connectance and other parameters that null models can control are legit contributors to the differences we aim to detect. In addition, null models do not take into account the feedback effects of these components (e.g. network size or connectance) on network structure (Dormann et al., 2017).

We used the package *GGPLOT2* (Wickham, 2016) to plot the results. All the analyses were run using R, version 3.6.1 (R Core Team, 2019).

3 | RESULTS

Hybrid networks were overall composed by 113 different nodes: 70 different plant (pollen) nodes, 13 pollinating bees and 30 predator nodes (wasps and cavity-nester antagonists). These nodes interacted 2,570 times, of which 2,185 were mutualistic and 385 antagonistic interactions (see Figures S2 and S3 for network visual representations). Seven different triads and two dyads were observed in these hybrid networks (including the three non-interacting nodes motif; T1). Table 1 describes each of these motifs and summarizes their ecological meaning. In total, we detected 35,257 triads (96,770, including T1) and 926 dyads (754 mutualistic and 172 antagonistic) (Figure 1).

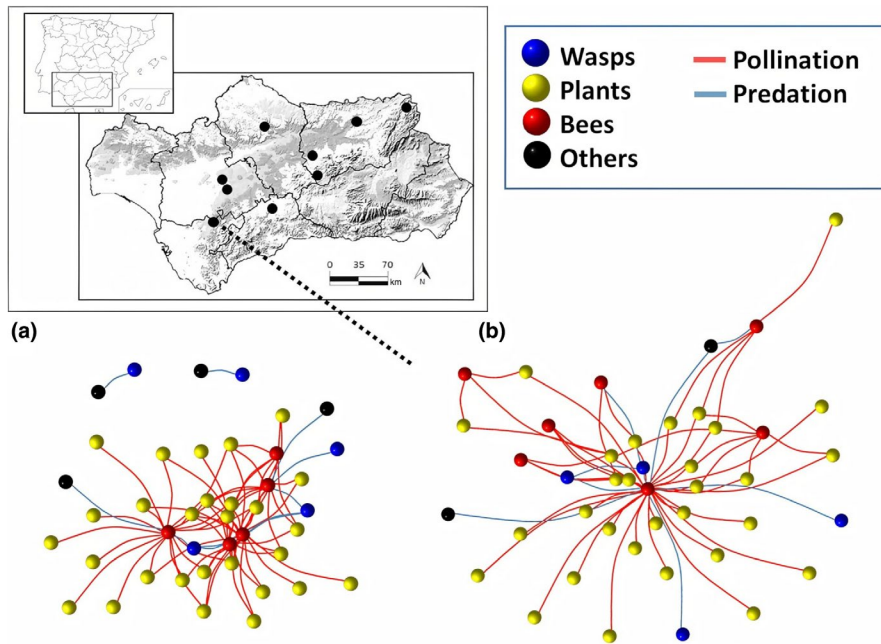


FIGURE 1 Map of Andalusia (Southern Spain), showing the location of study sites. In each location, a pair of farms with contrasting management regimes were sampled (organic versus conventional farming). Directed hybrid networks including mutualistic (pollination) and antagonistic (predation/parasitism) relationships are represented, and their functional properties compared. (a) Hybrid network on an organic olive farm. (b) Hybrid network on its paired conventional olive farm

TABLE 2 Results from Bayesian mixed models that show the estimated effect of management type (conventional or organic) on the frequency of different motifs (dyads and triads) in hybrid networks. The table displays the posterior estimate, standard error, 95% credible intervals, probability of beta being positive (i.e. higher in organic than in conventional). Note that the probability of the opposite is $1 - \text{Prob. } \beta > 0$ and $1 - \text{Prob. } \beta > 0.3$ for numbers with an asterisk (*). In bold, estimates with a high posterior probability of beta (slope from conventional to organic) being different from zero (i.e. motif more/less frequent on organic farms)

Model	Fixed factors (beta/slope)	Estimate	Standard error	95% LCI	95% UCI	Prob. $\beta > 0$	Prob. $ \beta > 0.3^* $
Triad 1	Conventional (intercept)	4,301	1,433	1,415	7,098		
	Organic (slope; β)	2,177	1573	-999	5,334	0.92	0.70
Dyad 2 (predation)	Conventional (intercept)	7.26	1.61	4.03	10.48		
	Organic	2.38	2.00	-1.58	6.38	0.89	0.54
Dyad 3 (mutualism)	Conventional (intercept)	27.86	7.09	13.93	41.86		
	Organic	15.85	7.01	1.96	29.80	0.98	0.84
Triad 4	Conventional (intercept)	12.41	3.63	5.29	19.57		
	Organic	-5.01	4.63	-14.28	4.09	0.13	0.69*
Triad 5	Conventional (intercept)	3.82	2.01	-0.16	7.77		
	Organic	-0.56	2.26	-5.05	4.03	0.39	0.62
Triad 6	Conventional (intercept)	-2.21	1.54	-6.28	-0.16		
	Organic	-0.33	0.82	-1.99	1.25	0.35	0.49
Triad 8	Conventional (intercept)	88.89	21.40	46.26	131.69		
	Organic	0.59	26.05	-52.42	52.49	0.51	0.29
Triad 9	Conventional (intercept)	-0.67	11.25	-18.61	26.05		
	Organic	-13.08	16.87	-57.88	0.74	0.04	0.90*
Triad 11	Conventional (intercept)	218.42	77.76	61.48	369.56		
	Organic	117.30	84.20	-49.78	288.65	0.92	0.72

The mixed Bayesian models showed that hybrid networks on organic farms had a higher frequency of unconnected nodes (triad 1), with a probability of 0.92 (see Table 2 and Figure 2). This effect was relatively strong, since the probability of being a 30% more frequent compared to conventional farms was 0.70. The asymmetric

dyad (dyad 2; simple predation) was also more frequent on organic farms, with a 0.89 probability. An even stronger pattern was found for the dyad 3 (mutualistic pollination), that was higher (probability of 0.98) on organic farms, and a 30% higher with a 0.84 probability (see Table 2 and Figure 2). The triad 4 (competition between

FIGURE 2 Predicted mean motif frequency and 95% HPD interval (Highest Posterior Density) for each motif and management type, estimated via Bayesian mixed models

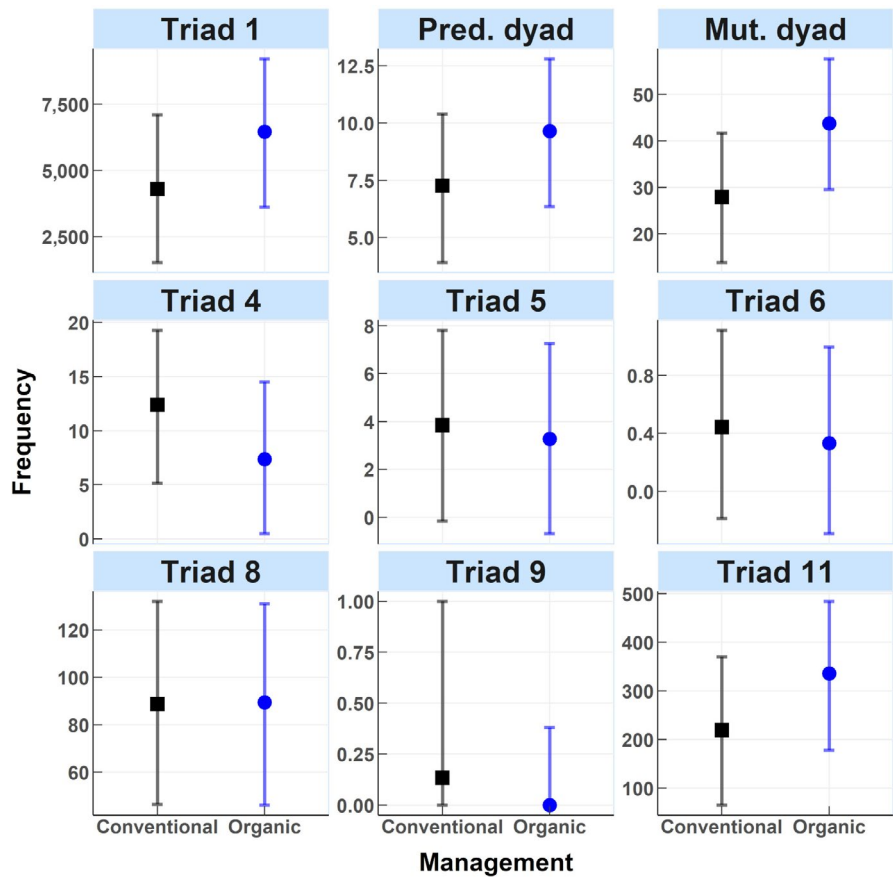


TABLE 3 Metrics of functional richness (FRich), evenness (FEve) and divergence (FDiv) for each motif or function (mutualistic/antagonistic triads) measured across sites. These numbers show the variability in triad frequency or function intensity between different networks sampled under the same agricultural regime, providing information about the stability/heterogeneity of the trait (function). Dissimilarity represents the non-overlapping spaces from 0 (not shared space) to 1 (full shared space) between conventional (C) and organic (O) farms. The mutualistic components are defined by dyad 3 and triad 11. Antagonistic components are defined by the motifs 2,4,5,6,8 and 9. The complex triads 6 and 9 were very infrequent; hence, we combined these two triads with the triad 8 that also informs about predation, to obtain a solid analysis

Model	Management	FRich	FEve	FDiv	Dissimilarity
Triad 1	Conventional	4.637	0.811	0.488	0.254
	Organic	4.806	0.769	0.601	
Dyad 2	C	6.471	0.745	0.506	0.612
	O	2.199	0.663	0.466	
Dyad 3	C	3.920	0.795	0.538	0.365
	O	4.340	0.791	0.629	
Triad 4	C	5.843	0.748	0.629	0.507
	O	1.867	0.754	0.469	
Triad 5	C	2.526	0.599	0.799	0.376
	O	2.427	0.809	0.614	
Triads 6, 8 and 9	C	17.579	0.478	0.745	0.744 ^a
	O	9.918	0.477	0.706	
Triad 11	C	4.000	0.786	0.522	0.253
	O	4.829	0.768	0.649	
Mutualistic components	C	4.264	0.625	0.558	0.442
	O	6.571	0.665	0.581	
Antagonistic components	C	58.610	0.439	0.709	0.858 ^a
	O	21.228	0.447	0.745	

^aNote that the more dimensions are included, the more dissimilarity is probable. For instance, dissimilarity for antagonistic components for only two dimensions (82% of variability explained) is 0.535.

predators) was more frequent on conventional farms, with a probability of 0.87. The frequency of triads 5, 6 and 8 did not show clear patterns across management types. However, the triad 9 (transitive antagonistic relationship) was lower on organic farms, with a high probability (0.96). The triad 11 (plant–pollinator not specialist interaction) was more frequent on organic farms (0.92) with a relatively strong effect (30% higher compared to conventional farms with a probability of 0.72).

Table 3 shows that the size of the functional space (i.e. Functional richness) occupied by the triad 1, dyad 3, triad 5 and triad 11 did not vary importantly across management types (ratios of 1.03, 1.11, 1.04 and 1.21 in functional space size, respectively). However, the functional space of the dyad 2 was almost threefold (ratio; 2.94) bigger in the array of networks belonging to conventional farms, compared to

the array of organic farms. The functional space of triad 4 was threefold bigger on conventional farms (ratio; 3.13) compared to organic farms. Similarly, the functional space defined by triads 6, 8 and 9 together was 1.77 times bigger in conventional olive groves (note that the complex triads 6 and 9 were very infrequent, hence we combined these two triads with the triad 8, which also informs about predation, to obtain a solid analysis). Functional evenness and divergence of network motifs did not show any remarkable pattern (see Table 3).

Dissimilarity (i.e. non-overlapping area/volume) between functional spaces of network arrays of conventional and organic olive groves was relatively low for the motifs: 1, 3, 5 and 11 (0.25, 0.37, 0.38 and 0.25, respectively). Dissimilarity was moderate for the triad 4 (0.507), relatively high for the dyad 2 (0.612) and high for the triads 6,8,9 together (0.744) (Table 3).

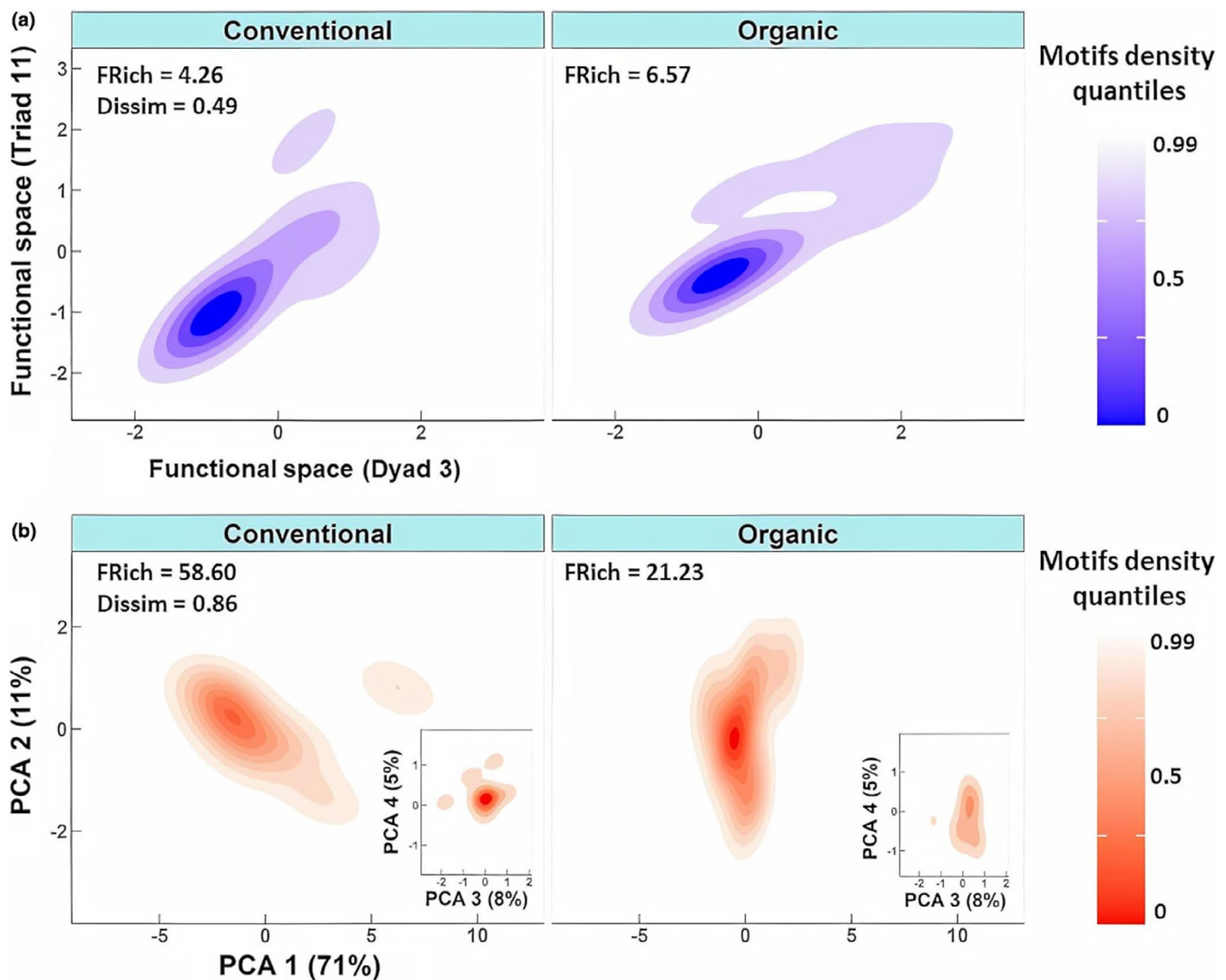


FIGURE 3 Probability of motif density distribution in the functional space defined by network motifs (case of the mutualistic components) or Principal Components of motif's variance (case of the antagonistic components) in hybrid networks sampled on conventional versus organic olive farms. FRich refers to the functional space occupied by the focal motifs considering all networks (on conventional or organic farms). Dissim reports the non-overlapping functional space between conventional and organic farms. In blue (a), mutualistic relationships defined by the dyad 3 and the triad 11. In red (b), antagonistic relationships defined by the motifs: 2, 4, 5, 6, 8 and 9. Note that FRich and Dissim in b correspond to the four dimensions (four first principal components) that are plotted in pairs due to dimensional visualization constrains

The analysis of combined mutualistic and antagonistic components showed that the variability of mutualistic motifs was 1.54 times higher on organic farms (FRich = 4.264 on conventional farms and FRich = 6.571 on organic farms). Interestingly, the antagonistic component (composed by the four principal components retaining information from motifs 2,4,5,6,8 and 9) showed a functional space 2.76 times bigger in conventional olive groves (FRich = 58.610 on conventional farms and FRich = 21.228 on organic farms). Similar to results for other motifs, functional evenness and divergence for mutualistic and antagonistic components did not vary importantly between management regimes. Functional space dissimilarity of mutualistic components on conventional and organic farms was moderate (0.442). In contrast, the functional space including all possible predation motifs showed a high dissimilarity between management types (0.858) (see Table 3 and Figure 3).

4 | DISCUSSION

To our knowledge, this is the first study to tackle the effects of agricultural intensification on hybrid networks incorporating both plant-pollinator and prey-predator interaction types. The novel analysis performed here, based on network motifs, let understand the simultaneous effects of these anthropic perturbations on the pollination and predation interactions. As a result, we observed interesting patterns that corroborated only partially our initial predictions. The first prediction was supported by data because we found more frequency of mutualistic motifs (mutualistic dyad D3 and T11) on organic farms. The second prediction was however not validated, since functional spaces for mutualistic motifs were relatively similar across management types. Prediction three was in part corroborated, because the frequency of predation motifs was maximized on organic farms. However, unexpectedly complex predation relationships, involving generalist top predators, increased on conventional farms. Lastly, the fourth hypothesis was also supported by the data, and the frequency of predation motifs was more variable across networks in conventional olive groves.

4.1 | Motifs frequency across management types

Different motifs showed distinct patterns in our system. The triad 1 (non-connected nodes) informed us that connectance was lower on organic farms, a pattern probably driven by networks size (more nodes in organic groves, and many forbidden links) (Banašek-Richter et al., 2004). Dyads 2 (simple predation interaction), 3 (simple pollination interaction) and triad 11 (not specialist pollination interaction) were also more frequent in organic groves. These results show that both simple pollination and predation interactions are more diverse in organic groves. Hence, both types of interactions are maximized by environmentally friendly farming practices. The maintenance of herb cover in these organic farms, plus the null use of pesticides, increases floral resources for

pollinators, prey availability for predators and habitat suitability for both resources and consumers (Hole et al., 2005; Martínez-Núñez et al., 2021). Concerning the mutualistic relationships, similar results were found through the structural analysis of plant-pollinator bipartite networks (Martínez-Núñez, Manzaneda, & Rey, 2019). The mechanism underlying this pattern seems to be an unsuccessful foraging by pollinators in disturbed habitats (Carman & Jenkins, 2016; Everaars et al., 2018) and the cumulative pernicious effects of pesticides (Biesmeijer et al., 2006; Kearns et al., 1998; Mullin, 2015).

Type 4 triads (competition by two generalist predators) and 9 (intraguild predation) were more frequent in conventional groves. Two non-mutually exclusive mechanisms might explain this result. First, pesticides are not very harmful for generalist tolerant species such as the beetle *Trichodes apiarus*, the ectoparasitic wasp *Melittobia acasta* or *Megatoma* sp. (Dermeestidae) that can predate on many different cavity-nesting species, including other predators or bee/wasp antagonists (De Wael et al., 1995; Tscharrntke et al., 1998). Second, the detectability of trap nests and the probability of predation by generalist predators, likely, increase in simplified habitats. This is expected due to a reduced herb cover/richness and a higher proportion of bare soil. Hence, the presence of generalists and top predators favours the appearance of complex predation relationships, although, on the other hand, there is an overall reduction in simple predation interactions on conventional farms. Giling et al. (2019) also found that plant diversity can alter the frequency of different predation-related motifs in food webs; however, they found more tri-trophic predation relationships in more plant-diverse sites. Holzschuh et al. (2010) reported similar results to ours, by focusing on trap nest use. These authors found that generalist parasitoids were less sensitive to land use intensity than specialists.

Interestingly, the focal species of this study (species that use bee trap nests) belong to a relatively specialized guild. Further studies should unveil whether the observed patterns also hold for other multitrophic systems and less specialized species.

4.2 | Mutualistic and antagonistic interactions

The estimation of functional spaces through sites for each motif and for overall mutualistic/antagonistic interactions showed interesting and seldom reported results. The variability in the frequency of mutualistic motifs across localities was overall similar in conventional compared to organic farms. In addition, dissimilarity in motif frequencies was low, suggesting that the frequency of mutualistic motifs has a similar dispersion across sites regardless management type. Most plant and pollinator nodes are shared in these plant-pollinator (solitary bee-pollen) networks and central network nodes usually remain invariable across management types (Martínez-Núñez et al., 2020), which might explain these low differences in variability. Literature shows that temporal stability of pollination services increases with herb richness and closeness to natural habitats (Ebeling et al., 2008; Garibaldi et al., 2011). Our

results complement these reports by showing that the frequency of pollination motifs in which above-ground nesting bees are involved is relatively consistent/invariable across localities, provided a similar management regime.

Our fourth prediction anticipated that agricultural intensification would destabilize conventional farms, increasing the variability of frequency of the predation motifs across sites. This hypothesis was supported by data because some farms had very few predation motifs and others had a higher number (mainly driven by generalist predators). Therefore, the functional space defined by the frequency of motifs representing different predation-related links was bigger (i.e. more variable) across localities under conventional management practices. These results inform about the low consistency and predictability of predation motifs in intensified groves that might be driven by a lower diversity of interactions (Yeakel et al., 2020).

Interestingly, the dissimilarity of the predation functional spaces between management types was high, suggesting a high variability between farms in these types of interactions, as opposed to the similarity observed for the mutualistic ones. This outcome suggests a high stochasticity in these types of predation relationships, low functional insurance and a pull effect towards bee trap nests already parasitized. Hackett et al. (2019) reported that plants and pollinators were connecting hubs across landscapes while the presence of parasitoids and predators was more peripheral and context-dependent, findings that supports our results.

Studies analysing the differences on hybrid networks that include relationships of different sign (mutualistic versus antagonistic) can also help to shed light on a longstanding debate (May, 1972) about the stabilizing or destabilizing properties of different types of interactions. Although traditionally mutualistic interactions have been thought to introduce chaos in nature (Allesina & Tang, 2012), recent studies point in the opposite direction (Hale et al., 2020). Predominant type of interactions in ecosystems in a gradient of known stability can provide cues to this debate. This study was not aimed at elucidating the stabilizing or destabilizing properties of mutualistic/antagonistic interactions, but it can shed light on this matter too. Because we see that more stable systems (i.e. olive groves with persistent herbaceous cover and without recurrent pesticide application) have a higher frequency of mutualistic interactions, we argue that, at least in relatively high perturbed ecosystems such as agroecosystems, a high frequency of mutualistic interactions is not a limiting factor for stability.

5 | CONCLUSIONS

Our novel approach, dissecting hybrid networks on network motifs, reported detailed and varying effects of agricultural intensification on network motifs that represent mutualistic and predation interactions. While environmentally friendly management practices enhanced the frequency and consistency of pollination and simple/

specialized predation, intensive agriculture made generalist and complex predation interactions more frequent but highly variable across sites. This study showed that hybrid networks combined with new analytical approaches can help to understand how anthropogenic disturbances affect the occurrence of different types of interactions, and the consistency of network properties.

ACKNOWLEDGEMENTS

The authors would like to thank Gemma Calvo, Rubén Tarifa, Jorge Isla and Jose L. Molina for their help with fieldwork, as well as to the SEO-BirdLife volunteers, José Eugenio Gutiérrez, Carlos Ruiz, Antonio Manzaneda and Francisco Valera for the logistical support. Luis Ruiz Valenzuela trained us with pollen determination and facilitated access to the pollen collection of the UJA. We thank Sandra Lendínez for her laboratory work identifying the pollen samples. We especially appreciate Antonio Pérez help in fieldwork and bee identification. We are grateful too to the farm owners who granted us access to their properties. This work is part of the projects CGL2015-68963-C2 and PID2019-108332GB-I00 (MINECO/MICIIN, Gobierno de España and FEDER) and OLIVARES VIVOS (LIFE14 NAT/ ES/001094, European Commission). C.M.-N. was granted a predoctoral fellowship (BES-2016-078736). Authors have no conflict of interests.

AUTHORS' CONTRIBUTIONS

C.M.-N. and P.J.R. conceived and designed this study; C.M.-N. collected the data; P.J.R. supervised the data collection and provided the field/laboratory technicians to support field and laboratory work; C.M.-N. analysed the data and led the writing of the manuscript with feedback from P.J.R.

DATA AVAILABILITY STATEMENT

Data deposited in the Dryad Digital Repository <https://doi.org/10.5061/dryad.q2bvq83j8> (Martínez-Núñez & Rey, 2021).

ORCID

Carlos Martínez-Núñez  <https://orcid.org/0000-0001-7814-4985>

REFERENCES

- Allesina, S., & Tang, S. (2012). Stability criteria for complex ecosystems. *Nature*, 483(7388), 205–208. <https://doi.org/10.1038/nature10832>
- Banašek-Richter, C., Cattin, M. F., & Bersier, L. F. (2004). Sampling effects and the robustness of quantitative and qualitative food-web descriptors. *Journal of Theoretical Biology*, 226(1), 23–32. [https://doi.org/10.1016/S0022-5193\(03\)00305-9](https://doi.org/10.1016/S0022-5193(03)00305-9)
- Biesmeijer, J. C., Roberts, S. P. M., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T., & Kunin, W. E. (2006). Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science*, 313(5785), 351–354. <https://doi.org/10.1126/science.1127863>
- Bürkner, P.-C. (2018). Advanced Bayesian Multilevel Modeling with the R Package brms. *The R Journal*, 10(1), 395–411. <https://doi.org/10.32614/RJ-2018-017>
- Carman, K., & Jenkins, D. G. (2016). Comparing diversity to flower-bee interaction networks reveals unsuccessful foraging of native bees in disturbed habitats. *Biological Conservation*, 202, 110–118. <https://doi.org/10.1016/j.biocon.2016.08.030>

- Carmona, C. P., Bello, F., Mason, N. W. H., & Lepš, J. (2019). Trait probability density (TPD): Measuring functional diversity across scales based on <sc>TPD</sc> with R. *Ecology*, 100(12), e02876. <https://doi.org/10.1002/ecy.2876>
- Chacoff, N. P., Vázquez, D. P., Lomáscolo, S. B., Stevani, E. L., Dorado, J., & Padrón, B. (2012). Evaluating sampling completeness in a desert plant-pollinator network. *Journal of Animal Ecology*, 81(1), 190–200. <https://doi.org/10.1111/j.1365-2656.2011.01883.x>
- Csardi, G., & Nepusz, T. (2006). The igraph software package for complex network research. *InterJournal Complex Systems*, 1695, 1–9.
- Davis, J. A., & Leinhardt, S. (1972). The structure of positive interpersonal relations in small groups. In J. Berger (Ed.), *Sociological theories in progress* (Vol. 2, pp. 218–251). Houghton Mifflin.
- De Wael, L., De Greef, M., & Van Laere, O. (1995). Biology and control of *Melittobia Acasta*. *Bee World*, 76(2), 72–76. <https://doi.org/10.1080/0005772X.1995.11099244>
- Dormann, C. F., Fründ, J., & Schaefer, H. M. (2017). Identifying causes of patterns in ecological networks: Opportunities and limitations. *Annual Review of Ecology, Evolution, and Systematics*, 48, 559–584. <https://doi.org/10.1146/annurev-ecolsys-110316-022928>
- Ebeling, A., Klein, A. M., Schumacher, J., Weisser, W. W., & Tschardtke, T. (2008). How does plant richness affect pollinator richness and temporal stability of flower visits? *Oikos*, 117(12), 1808–1815. <https://doi.org/10.1111/j.1600-0706.2008.16819.x>
- Everaars, J., Settele, J., & Dormann, C. F. (2018). Fragmentation of nest and foraging habitat affects time budgets of solitary bees, their fitness and pollination services, depending on traits: Results from an individual-based model. *PLoS One*, 13(2), e0188269. <https://doi.org/10.1371/journal.pone.0188269>
- Fornoff, F., Klein, A.-M., Blüthgen, N., & Staab, M. (2019). Tree diversity increases robustness of multi-trophic interactions. *Proceedings of the Royal Society B: Biological Sciences*, 286(1898), 20182399. <https://doi.org/10.1098/rspb.2018.2399>
- Gagic, V., Tschardtke, T., Dormann, C. F., Gruber, B., Wilstermann, A., & Thies, C. (2011). Food web structure and biocontrol in a four-trophic level system across a landscape complexity gradient. *Proceedings of the Royal Society B: Biological Sciences*, 278(1720), 2946–2953. <https://doi.org/10.1098/rspb.2010.2645>
- García-Callejas, D., Molowny-Horas, R., & Araújo, M. B. (2018a). Multiple interactions networks: Towards more realistic descriptions of the web of life. *Oikos*, 127(1), 5–22. <https://doi.org/10.1111/oik.04428>
- García-Callejas, D., Molowny-Horas, R., & Araújo, M. B. (2018b). The effect of multiple biotic interaction types on species persistence. *Ecology*, 99(10), 2327–2337. <https://doi.org/10.1002/ecy.2465>
- Garibaldi, L. A., Steffan-Dewenter, I., Kremen, C., Morales, J. M., Bommarco, R., Cunningham, S. A., Carvalheiro, L. G., Chacoff, N. P., Dudenhöffer, J. H., Greenleaf, S. S., Holzschuh, A., Isaacs, R., Krewenka, K., Mandelik, Y., Mayfield, M. M., Morandin, L. A., Potts, S. G., Ricketts, T. H., Szentgyörgyi, H., ... Klein, A. M. (2011). Stability of pollination services decreases with isolation from natural areas despite honey bee visits. *Ecology Letters*, 14(10), 1062–1072. <https://doi.org/10.1111/j.1461-0248.2011.01669.x>
- Gilling, D. P., Ebeling, A., Eisenhauer, N., Meyer, S. T., Roscher, C., Rzanny, M., Voigt, W., Weisser, W. W., & Hines, J. (2019). Plant diversity alters the representation of motifs in food webs. *Nature Communications*, 10(1), 1–7. <https://doi.org/10.1038/s41467-019-08856-0>
- Grass, I., Jauker, B., Steffan-Dewenter, I., Tschardtke, T., & Jauker, F. (2018). Past and potential future effects of habitat fragmentation on structure and stability of plant-pollinator and host-parasitoid networks. *Nature Ecology & Evolution*, 2(9), 1408–1417. <https://doi.org/10.1038/s41559-018-0631-2>
- Hackett, T. D., Sauve, A. M. C., Davies, N., Montoya, D., Tylianakis, J. M., & Memmott, J. (2019). Reshaping our understanding of species' roles in landscape-scale networks. *Ecology Letters*, 22(9), 1367–1377. <https://doi.org/10.1111/ele.13292>
- Hale, K. R. S., Valdovinos, F. S., & Martínez, N. D. (2020). Mutualism increases diversity, stability, and function of multiplex networks that integrate pollinators into food webs. *Nature Communications*, 11(1), 2182. <https://doi.org/10.1038/s41467-020-15688-w>
- Hole, D. G., Perkins, A. J., Wilson, J. D., Alexander, I. H., Grice, P. V., & Evans, A. D. (2005). Does organic farming benefit biodiversity? *Biological Conservation*, 122(1), 113–130. <https://doi.org/10.1016/j.biocon.2004.07.018>
- Holzschuh, A., Steffan-Dewenter, I., & Tschardtke, T. (2010). How do landscape composition and configuration, organic farming and fallow strips affect the diversity of bees, wasps and their parasitoids? *Journal of Animal Ecology*, 79(2), 491–500. <https://doi.org/10.1111/j.1365-2656.2009.01642.x>
- Hutchinson, M. C., Bramer Mora, B., Pilosof, S., Barner, A. K., Kéfi, S., Thébault, E., & Stouffer, D. B. (2019). Seeing the forest for the trees: Putting multilayer networks to work for community ecology. *Functional Ecology*, 33(2), 206–217. <https://doi.org/10.1111/1365-2435.13237>
- Jácome-Flores, M. E., Jordano, P., Delibes, M., & Fedriani, J. M. (2020). Interaction motifs variability in a Mediterranean palm under environmental disturbances: The mutualism-antagonism continuum. *Oikos*, 129(3), 367–379. <https://doi.org/10.1111/oik.06688>
- Kearns, C. A., Inouye, D. W., & Waser, N. M. (1998). Endangered mutualisms: The conservation of plant-pollinator interactions. *Annual Review of Ecology and Systematics*, 29(1), 83–112. <https://doi.org/10.1146/annurev.ecolsys.29.1.83>
- Kennedy, C. M., Lonsdorf, E., Neel, M. C., Williams, N. M., Ricketts, T. H., Winfree, R., Bommarco, R., Brittain, C., Burley, A. L., Cariveau, D., Carvalheiro, L. G., Chacoff, N. P., Cunningham, S. A., Danforth, B. N., Dudenhöffer, J.-H., Elle, E., Gaines, H. R., Garibaldi, L. A., Gratton, C., ... Kremen, C. (2013). A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. *Ecology Letters*, 16(5), 584–599. <https://doi.org/10.1111/ele.12082>
- Klause, J., & Johnson, S. (2017). The origin of motif families in food webs. *Scientific Reports*, 7(1), 1–11. <https://doi.org/10.1038/s41598-017-15496-1>
- Li, H. D., Tang, L., Jia, C., Holyoak, M., Fründ, J., Huang, X., & Xiao, Z. (2020). The functional roles of species in metacommunities, as revealed by metanetwork analyses of bird-plant frugivory networks. *Ecology Letters*, 23(8), 1252–1262. <https://doi.org/10.1111/ele.13529>
- Lohaus, K., Vidal, S., & Thies, C. (2013). Farming practices change food web structures in cereal aphid-parasitoid-hyperparasitoid communities. *Oecologia*, 171(1), 249–259. <https://doi.org/10.1007/s00442-012-2387-8>
- Martínez-Núñez, C., Manzaneda, A. J., Lendínez, S., Pérez, A. J., Ruiz-Valenzuela, L., & Rey, P. J. (2019). Interacting effects of landscape and management on plant-solitary bee networks in olive orchards. *Functional Ecology*, 33(12), 2316–2326. <https://doi.org/10.1111/1365-2435.13465>
- Martínez-Núñez, C., Manzaneda, A. J., & Rey, P. J. (2019). Reviewing the use of bee trap nests for the study of interaction networks in agroecosystems: Insights from its use in olive farms. *Ecosistemas*, 28(3), 3–12. <https://doi.org/10.7818/ECOS.1766>
- Martínez-Núñez, C., Manzaneda, A. J., & Rey, P. J. (2020). Plant-solitary bee networks have stable cores but variable peripheries under differing agricultural management: Bioindicator nodes unveiled. *Ecological Indicators*, 115, 106422. <https://doi.org/10.1016/j.ecolind.2020.106422>
- Martínez-Núñez, C., & Rey, P. J. (2021). Data from: Hybrid networks reveal contrasting effects of agricultural intensification on antagonistic and mutualistic motifs. *Dryad, Digital Repository*, <https://doi.org/10.5061/dryad.q2bvq83j8>
- Martínez-Núñez, C., Rey, P. J., Salido, T., Manzaneda, A. J., Camacho, F. M., & Isla, J. (2021). Ant community potential for pest control in olive groves: Management and landscape effects. *Agriculture, Ecosystems & Environment*, 305, 107185. <https://doi.org/10.1016/j.agee.2020.107185>

- May, R. M. (1972). Will a large complex system be stable? *Nature*, 238(5364), 413–414. <https://doi.org/10.1038/238413a0>
- Milo, R., Shen-Orr, S., Itzkovitz, S., Kashtan, N., Chklovskii, D., & Alon, U. (2002). Network motifs: Simple building blocks of complex networks. *Science*, 298(5594), 824–827. <https://doi.org/10.1126/science.298.5594.824>
- Morrison, B. M. L., Brosi, B. J., & Dirzo, R. (2020). Agricultural intensification drives changes in hybrid network robustness by modifying network structure. *Ecology Letters*, 23(2), 359–369. <https://doi.org/10.1111/ele.13440>
- Morrison, B. M. L., & Dirzo, R. (2020). Distinct responses of antagonistic and mutualistic networks to agricultural intensification. *Ecology*, 101(10), e03116. <https://doi.org/10.1002/ecy.3116>
- Mullin, C. A. (2015). Effects of 'inactive' ingredients on bees. *Current Opinion in Insect Science*, 10, 194–200. <https://doi.org/10.1016/j.cois.2015.05.006>
- Nicholson, C. C., Koh, I., Richardson, L. L., Beauchemin, A., & Ricketts, T. H. (2017). Farm and landscape factors interact to affect the supply of pollination services. *Agriculture, Ecosystems & Environment*, 250, 113–122. <https://doi.org/10.1016/j.agee.2017.08.030>
- Pellissier, L., Albouy, C., Bascompte, J., Farwig, N., Graham, C., Loreau, M., Maglianesi, M. A., Melián, C. J., Pitteloud, C., Roslin, T., Rohr, R., Saavedra, S., Thuiller, W., Woodward, G., Zimmermann, N. E., & Gravel, D. (2018). Comparing species interaction networks along environmental gradients. *Biological Reviews*, 93(2), 785–800. <https://doi.org/10.1111/brv.12366>
- Piloso, S., Porter, M. A., Pascual, M., & Kéfi, S. (2017). The multilayer nature of ecological networks. *Nature Ecology & Evolution*, 1(4), 0101. <https://doi.org/10.1038/s41559-017-0101>
- Power, E. F., & Stout, J. C. (2011). Organic dairy farming: Impacts on insect-flower interaction networks and pollination. *Journal of Applied Ecology*, 48(3), 561–569. <https://doi.org/10.1111/j.1365-2664.2010.01949.x>
- R Core Team. (2019). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.
- Sauve, A. M. C., Fontaine, C., & Thébault, E. (2014). Structure-stability relationships in networks combining mutualistic and antagonistic interactions. *Oikos*, 123(3), 378–384. <https://doi.org/10.1111/j.1600-0706.2013.00743.x>
- Simmons, B. I., Beckerman, A. P., Hansen, K., Maruyama, P. K., Televantos, C., Vizentin-Bugoni, J., & Dalsgaard, B. (2020). Niche and neutral processes leave distinct structural imprints on indirect interactions in mutualistic networks. *Functional Ecology*, 35(3), 753–763. <https://doi.org/10.1111/1365-2435.13736>
- Solé, R. V., & Valverde, S. (2006). Are network motifs the spandrels of cellular complexity? *Trends in Ecology & Evolution*, 21(8), 419–422. <https://doi.org/10.1016/j.tree.2006.05.013>
- Staab, M., Pufal, G., Tschantke, T., & Klein, A.-M. (2018). Trap nests for bees and wasps to analyse trophic interactions in changing environments—A systematic overview and user guide. *Methods in Ecology and Evolution*, 9(11), 2226–2239. <https://doi.org/10.1111/2041-210X.13070>
- Stone, L., Simberloff, D., & Artzy-Randrup, Y. (2019). Network motifs and their origins. *PLOS Computational Biology*, 15(4), e1006749. <https://doi.org/10.1371/journal.pcbi.1006749>
- Thompson, R. M., Brose, U., Dunne, J. A., Hall, R. O., Hladyz, S., Kitching, R. L., Tylianakis, J. M. (2012). Food webs: Reconciling the structure and function of biodiversity. *Trends in Ecology and Evolution*, 27(12), 689–697. <https://doi.org/10.1016/j.tree.2012.08.005>
- Tschantke, T., Gathmann, A., & Steffan-Dewenter, I. (1998). Bioindication using trap-nesting bees and wasps and their natural enemies: Community structure and interactions. *Journal of Applied Ecology*, 35, 708–719. <https://doi.org/10.1046/j.1365-2664.1998.355343.x>
- Tylianakis, J. M., & Morris, R. J. (2017). Ecological networks across environmental gradients. *Annual Review of Ecology, Evolution, and Systematics*, 48(1), 25–48. <https://doi.org/10.1146/annurev-ecolsys-110316-022821>
- Valiente-Banuet, A., Aizen, M. A., Alcántara, J. M., Arroyo, J., Cocucci, A., Galetti, M., García, M. B., García, D., Gómez, J. M., Jordano, P., Medel, R., Navarro, L., Obeso, J. R., Oviedo, R., Ramírez, N., Rey, P. J., Traveset, A., Verdú, M., & Zamora, R. (2014). Beyond species loss: the extinction of ecological interactions in a changing world. *Functional Ecology*, 29(3), 299–307. <https://doi.org/10.1111/1365-2435.12356>
- Wickham, H. (2016). *ggplot2*. Springer International Publishing. <https://doi.org/10.1007/978-3-319-24277-4>
- Yeakel, J. D., Pires, M. M., de Aguiar, M. A. M., O'Donnell, J. L., Guimarães, P. R., Gravel, D., & Gross, T. (2020). Diverse interactions and ecosystem engineering can stabilize community assembly. *Nature Communications*, 11(1), <https://doi.org/10.1038/s41467-020-17164-x>
- Yen, J. D. L., Cabral, R. B., Cantor, M., Hatton, I., Kortsch, S., Patrício, J., & Yamamichi, M. (2016). Linking structure and function in food webs: Maximization of different ecological functions generates distinct food web structures. *Journal of Animal Ecology*, 85(2), 537–547. <https://doi.org/10.1111/1365-2656.12484>
- Zurbuchen, A., Landert, L., Klaiber, J., Müller, A., Hein, S., & Dorn, S. (2010). Maximum foraging ranges in solitary bees: Only few individuals have the capability to cover long foraging distances. *Biological Conservation*, 143(3), 669–676. <https://doi.org/10.1016/j.biocon.2009.12.003>

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Martínez-Núñez C, Rey PJ. Hybrid networks reveal contrasting effects of agricultural intensification on antagonistic and mutualistic motifs. *Funct Ecol*. 2021;35:1341–1352. <https://doi.org/10.1111/1365-2435.13800>