



Plant-solitary bee networks have stable cores but variable peripheries under differing agricultural management: Bioindicator nodes unveiled

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ABSTRACT

The identification of important nodes structuring pollination networks represents a key contribution to biodiversity conservation and pollination functioning. Understanding how species and their importance covary with management is essential if we aim to predict anthropic effects on the environment. In this study we used 96 bee trap nests to sample plant (pollen)-solitary bee interaction networks in 18 pairs of olive groves employing differing management techniques (intensive vs. organic). We applied a novel dual analytical approach consisting of identifying important nodes from two different perspectives: nodes that strongly determine the topological structure of the network and nodes that sustain rare or infrequent interactions. We employed this analytical approach to identify important nodes for the conservation of these networks and to study how different agricultural management practices modify the importance of the nodes. Specifically, *Osmia caerulea* appeared in the core of the network of organic farms and acts as a good bioindicator of agricultural management types. As well, *O. bicornis* participated in important singular interactions but only on organic farms and so can be considered as a good bioindicator of ecosystem recovery. Our results highlight the species that should be prioritized for conservation or restoration and reveal a core-periphery structure in networks, in which, despite most structuring species remaining constant across management types, certain important singular interactions differ. We demonstrate that the switch from intensive to organic farming on olive farms can restore the structure of these plant-solitary bee networks, mainly through the recovery of certain species and rare or infrequent interactions.

1. Introduction

During the past decade, the analysis of pollination networks has become a powerful applied tool for understanding pollination functioning and studying ecological systems from a mechanistic perspective (Tylianakis and Morris, 2017). It is now clear that interaction networks provide more insights than traditional methods that focus only on abundance or species richness and/or biodiversity. For instance, Magrach et al. (2018) show how plant-pollinator networks in semi-natural areas surrounding extensive flowering crops are relatively resistant to massive flowering pulses. Similarly, Martínez-Núñez et al. (2019) report that intensive management in agroecosystems can simplify and homogenize the diversity of plant-pollinator interactions at farm scale without affecting species richness.

The identification of keystone nodes for network robustness is a promising application of interaction network analysis that may help the

management and restoration of ecological networks (Pocock et al., 2012). Hegland et al. (2010) report that key nodes can be detected with relatively little effort, thereby ensuring that they can be implemented appropriately. However, there are still very few studies using this approach. For instance, Dallas and Cornelius (2015) simulated node extinctions to identify hosts that were key in the stability of host-parasite networks. Fantinato et al. (2018) showed how plant-pollinator networks and the contribution of plant species to network resistance varied along a sea-inland gradient, while Traveset et al. (2017) used stochastic co-extinction models to detect keystone pollinators. Furthermore, several authors have explored how the importance or the role of some species varies in accordance with conditions (e.g. native and alien ranges) and conclude that species' roles in networks tend to be stable (Emer et al., 2016; Stouffer et al., 2012). However, it is still unknown to what extent different agricultural management techniques shape wild plant-pollinator assemblages and drive variations in species

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importance, especially from the perspective of species identity/role rather than from a network structure standpoint.

In this study we focused on olive groves because they represent the most extensive and socioeconomically relevant permanent culture in Europe. Although good management in agroecosystems is vital for maintaining pollination services (Kennedy et al., 2013), olive groves have become ever more intensively farmed in recent years (Infante-Amate et al., 2016). In olive groves, the role of pollinator insects has been neglected, largely because olive trees are wind-pollinated. This lack of interest is shown by the lack of work focusing on pollinators in olive groves (but see Kennedy et al., 2013; Scalercio et al., 2007). Nonetheless, pollinators are fundamental for the wild plant species growing in olive groves that typically provide important ecosystem services (e.g. soil retention and fertilization). Pollinators are also relevant to yields in the insect-pollinated agroecosystems that coexist alongside olive groves (e.g. almond groves).

In this study, we used 96 bee trap nests to sample pollen-solitary bee networks in 18 pairs of olive groves under different management regimes (intensive vs. organic farms with ground cover; see *Study area* for specifications) spanning the whole distribution of olive cultivation in Andalusia (S Spain). We have previously shown that plant-solitary bee networks are simpler, less stable and spatially more homogeneous under intensive agricultural practices and landscape simplification (Martínez-Núñez et al., 2019). Here, we compare community composition and network structure and identify the most important plant and bee taxa for the stability of these networks subject to different management regimes. We also explore how node importance varies with management in order to provide answers to both applied and theoretical questions. Our initial hypotheses were: (i) agricultural management affects plant-pollinator community composition (node composition) due to shifts in floral resource availability; (ii) by means of interaction network analyses, it is possible to detect important plant/pollinator taxa for which conservation should be prioritized to maintain network stability and pollination functioning in olive groves; and (iii) the importance of species and the overall structure of these networks remain constant as conditions change (in this case, different management techniques), as has been suggested by studies in non-agricultural environments (Emer et al., 2016; Stouffer et al., 2012).

2. Material and methods

2.1. Study system

We conducted our study in olive groves in the Mediterranean biodiversity hotspot (Marchese, 2015). This strategic location confers great potential on olive groves as sites able to retain high levels of biodiversity (Rey et al., 2019; Potts et al., 2006). Notwithstanding this conservation potential, intensive management is habitual and organic farming, which is employed in only 5% of all olive groves in Andalusia, is still the exception (data from Regional Government, Junta de Andalucía).

2.2. Study area and design

We conducted the field samplings of this study in year 2017. We sampled 18 pairs of olive farms with different management regimes in nine localities throughout Andalusia (Southern Spain; see Table S1 and Fig. S1 for details, Supporting Information), the region of the world with the highest density of olive groves. Each pair consisted of a grove on an intensively managed farm and one on an organic farm. Intensive farms were characterized by the use of pesticides, synthetic fertilizers and the repeated removal of plant cover using herbicides or by ploughing. Organic farms, on the other hand, did not use synthetic fertilizers or pesticides and herb cover was only removed occasionally using less intrusive methods (mowing or grazing). As a consequence, these organic farms maintain herb ground cover for most of the year but

intensive farms do not. Distances between the farms in each locality and between localities were high (mean > 1 km and > 100 km, respectively), which ensured sampling independence for solitary bees. Olive groves vary in terms of size, climate, altitude or landscape complexity but efforts were made to ensure that these variables were as constant as possible in the pairs of groves in each location. The 18 farms cover a total surface area (convex polygon) of approximately 2000 ha (Table S1 and Fig. S1).

2.3. Sampling and sample processing

We focused our sampling on wild solitary bees that nest in cavities – e.g. hollow stems or holes in wood – above ground level. These species represent a significant bioindicator group of pollinators with high functional diversity and ubiquity that ensures the pollination of a high number of wild and cultivated plant species (Martínez-Núñez et al., 2020; Tschardt et al., 1998; Wood et al., 2017). Solitary bees, the plants they pollinate and their interactions can be sampled in an easy and standardized manner by using bee trap nests (Staab et al., 2018). Furthermore, as we have shown elsewhere, colonization rates of bee trap nests are correlated to pollinator visitation rates to neighbouring flowering patches on olive farms (Martínez-Núñez et al., 2020).

We sampled aboveground-nesting bees by setting four bee trap nests on small farms (< 25 ha) and six bee trap nests on large farms (> 50 ha). Bee trap nests were built using different materials with a variety of cavity sizes to host as much diversity as possible. Specifically, we used 40x ca. 9 mm bamboo, 20x ca. 12 mm reed internodes, 20x ca. 15 mm reed internodes, and 4x ca. 20 mm reed internodes, offering each trap nest 84 cavities that were never all occupied. Nest traps were placed in different microhabitats – i.e. crop areas (olive tree matrix) and non-crop areas (edges, patches of semi-natural habitat, etc.) – to obtain representative networks at farm scale. Assuming that bee traps sample a conservative buffer of 150 m radius around nests, a distance within the typical flight range of solitary bees from their nests (Zurbuchen et al., 2010), the sampling area provided by the nest traps covered an area of 18.8 ha (four nest traps) on small farms and 42.4 ha (six nest traps) on large farms. Rarefaction curves of solitary bee species richness on each farm showed that our sampling recorded species richness accurately (see Fig. S2). Moreover, because of the paired design, the imbalance in the number of bee trap nests between small and big farms at different sites did not represent any hindrance.

Trap nests were placed in the field in March –November 2017. Material from occupied traps was isolated and labelled. Pollinator larvae were reared to adult stage and were identified to species level. We also prepared three pollen samples per cavity from pollen packs. Pollen samples were dyed using fuchsin and identified under microscopes to the greatest possible resolution (most often species level). We defined an interaction as when pollen and a bee species co-occurred in the same cavity. Interactions were grouped at farm scale and, in all, 18 quantitative (weighted by interaction frequency) mutualistic networks were obtained.

We contrasted management practices and the availability of floral resources for bees by estimating the richness and cover of herb species on every farm. From March to June, six (on small farms) and ten (on large farms) 1-m² squares were sampled in a fixed 50-m radius around plots spread throughout farms in both olive tree matrices and in non-crop areas. The percentage of herb cover was estimated visually by recording the surface area covered by herbs within an area whose corners were delimited by four olive trees. Ground herb cover and species richness (estimated at farm scale using the Chao's asymptotic estimator, Chao and Colwell, 2014) at farm scale were significantly higher on organic farms than on intensive farms (Linear Mixed Models with locality as random effect: $t_{86} = 10.21$, $p = 0.000$; predicted mean \pm 1SE: 86 ± 0.05 on organic vs. 49 ± 0.05 conventional farms; and $t_8 = 3.17$, $p = 0.013$; 72 ± 6.4 on organic vs. 46 ± 6.4 on conventional farms, effect size 1.5 for cover and 1.3 for richness,

respectively).

2.4. Network completeness

Sampled networks can be sensitive to differences in sampling efforts or sampling success. Completeness was calculated by dividing the observed interaction richness by the estimated asymptotic interaction richness (Chacoff et al., 2012) using Chao's method (Chao and Colwell, 2014). As shown elsewhere (Martínez-Núñez et al., 2019), the completeness of these networks was relatively high $59 \pm 22\%$ (mean \pm SD) and did not vary between management types (Linear mixed models: $\Delta AIC_{null} = 1.64$, $P = 0.57$).

2.5. Statistical analyses

We compared the community composition (taking into account network nodes) of organic and intensive olive farms as a means of detecting network and species differences that bioindicate management quality. We calculated the Chao asymptotic estimator for node richness and estimated the percentage of shared nodes using Chao's method and the package *SpadeR* with the function *ChaoShare* (Chao et al., 2000). We also ran an analysis of similarities (ANOSIM) using the *vegan* package (Oksanen et al., 2011) with 5000 permutations to test for significant differences in node composition between management types.

We defined important nodes in two different ways: the first approach considered the nodes that strongly determined the topological structure of the network (Zhang, 2012), while the second considered nodes that sustain rare or infrequent interactions whose extinction could lead to a loss of unique/scarcely species or original ecosystem functions (Coux et al., 2016). If species importance or role is affected by management, this dual approach will shed light on management quality (in the first case) and the degree of community recovery (in the second).

First, we calculated three metrics for each topologically important node in each interaction network. Specifically, we used the package *bipartite* (Dormann et al., 2008) to obtain the degree (number of interacting neighbours), number of interactions and node strength (weighted sum of all interactions). These three metrics are closely related to the abundance and functional importance of a node in a network and to its contribution to the observed structure (Hegland et al., 2010). We ran generalized linear models (Poisson distribution, log link function) and checked the back-transformed predicted means of these three metrics for each management type to identify and compare the most structuring network nodes/species. We omit here the p-values and statistical significance tests to be able to focus on ranking the importance (beyond the probability of observing these differences) so that plots can be interpreted in a more comprehensive and straightforward way than with significance tests (Amrhein et al., 2019). Nonetheless, Tables S2–S5 in the Supporting Information provide the predicted means for all species, the Tukey post-hoc groups and the p-values obtained from the generalized linear models.

Second, for the contribution of each node to the rare or infrequent interactions, we simulated the extinction of each node and recalculated the resulting loss in closeness for the whole network (sum of the inverse distances between each pair of nodes in the network). We used null models (5000 simulations) to standardize the metric, controlling for the number of links and network size (Patefield algorithm) that could legitimately influence the results obtained using the previous approach. The value of each species in each network was standardized by calculating the z-score in relation to the mean obtained from simulations. When standardized, this metric provides information about the relative importance of each node per link unit, that is, which nodes have singular/key links whose extinction would involve greater losses of closeness (that is, in this bipartite network, losses of nodes) and therefore are not important for the structure but for the maintenance of singular species/functions in the network. This metric was calculated using the function *swan_closeness* from the package *NetSwan* (Serge Lhomme,

Table 1

Node richness and compositional differences on farms under different management regimes.

	Intensive farms	Organic farms
Number of interactions (aggregated)	1045	1145
Number of different interactions (richness)	156	235
Plant richness	52*	64*
Bee richness	11	11
Observed shared species (plants)	48	
Estimated shared species (plants)	49.2 \pm 2.3	
Observed shared species (bees)	9	
Estimated shared species (bees)	9 \pm 0.4	
Anosim. Differences in composition (pollen loads)	p-value = 0.260	
Anosim. Differences in composition (bees)	p-value = 0.285	

* In this study we grouped all *Echium* species to genus level.

2015). All statistical analyses were conducted in R V3.5.2 (R Core Team, 2018).

3. Results

We identified 13 solitary bee species belonging to five different genera (*Anthidium*, *Heriades*, *Hoplitis*, *Megachile* and *Osmia*; Megachilidae) that occupied 831 cavities (11% of the total; range 4–20% per farm) and 80 nests (89% of the available total as six trap nests were lost or broken). Mean richness per farm was 4 ± 2 (mean \pm SD) in the range 2–8 species. Bees interacted 2185 times with plants and a total of 280 different interactions were registered. Bees transported pollen to their nests from many different plant species. A total of 68 pollen types were identified, belonging to 23 different families and 40 genera (see the full list of bees and pollen types in Tables S4 and S5, Supporting Information). The mean number of pollen types per farm was 20 ± 8 (mean \pm SD).

The analysis of compositional differences between network nodes under different management scenarios (Table 1) reveals that neither bee nor pollen node composition varied significantly with the type of agricultural management. Thus, organic and intensive farms shared 69% of bee species (ANOSIM; p-value = 0.260) and 71% of plant nodes (ANOSIM; p-value = 0.285). Intensive olive grove groves had 52 different plant nodes and 11 different bee nodes. Organic groves had 64 plant nodes and 11 bee nodes. The shared number of nodes was high (48 plants and 9 bees). Therefore, 20 plant nodes and four bee nodes were not shared (see Table S6, Supporting Information for specific species/nodes).

Fig. 1 shows the ten most important plant nodes for the topology of the networks under each management regime in terms of mean degree, mean number of interactions and mean strength (we do not show all nodes for convenience and simplicity). All ten of the most structuring plant nodes were common to both between organic and intensive olive groves: *Artemisia* sp., six unidentified species of Asteraceae, *Echium* sp., *Medicago* sp. and *Scorpiurus muricatus*. We highlight the fact that the Asteraceae species (especially Asteraceae sp1), the genera *Echium* (probably *E. vulgare*) and *Medicago* sp. played a particularly important role in these networks under both management types (Fig. 1). We assume that the observed important species of Asteraceae are probably among those showing the highest frequency of occurrence during the herb censuses performed in April–May, when a 95% trap nest colonization rate was observed. Some of the most important of these species are *Centaurea mellitensis*, *C. arvensis*, *Calendula arvensis*, *Glebionis coronaria*, *Hedypnois* sp., *Leontodon longirostris*, *Pallenis spinosa*, *Sonchus asper*, *S. oleraceus* and *Taraxacum officinale*.

Fig. 2 illustrates the most important bee species for the structure of these networks on both intensive and organic olive farms. The three metrics measuring the structural importance show consistent results. On intensive farms, *Osmia submicans* and *Hoplitis adunca* were

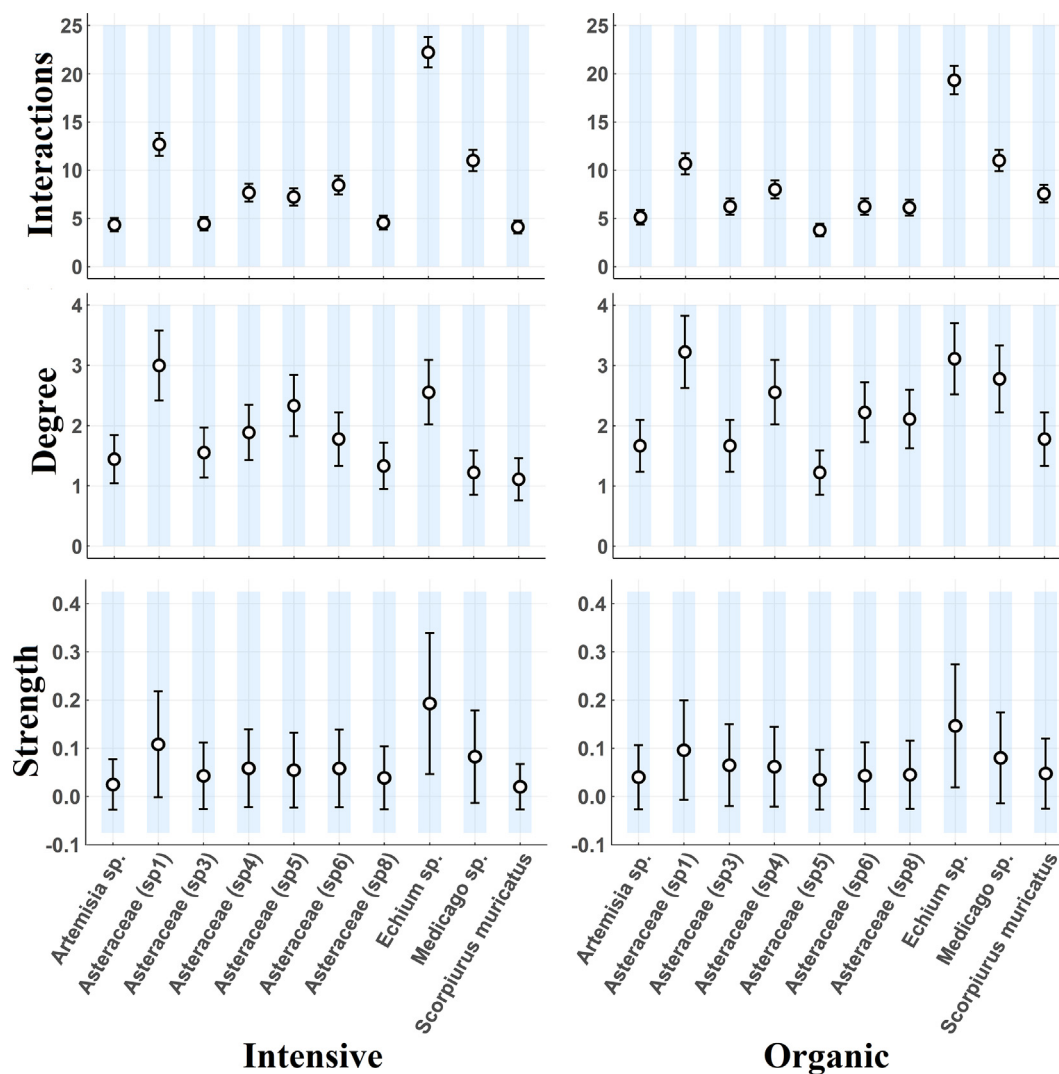


Fig. 1. Number of interactions, degree and node strength for each of the ten most important plant nodes on intensive and organic olive farms. Circles and error bars show back-transformed mean \pm SE. The strength plot for intensive farms omits two nodes (for simplicity) that should be within the 10 most important nodes: *Malva* sp. (0.038 ± 0.065) and *Astragalus hamosus* (0.078 ± 0.55) rather than *Artemisia* sp. and *S. muricatus*.

important, the former with a mean degree of 14.2 ± 1.4 (mean \pm SE), 63 ± 2.8 mean interactions and a mean strength of 0.55 ± 0.04 , and the latter 4.7 ± 1.4 , 25.4 ± 1.2 and 0.22 ± 0.04 , respectively. On organic farms, we detected three important species: the results for *O. submicans* coincided with those from intensive farms and was the most structuring species, with 12.5 ± 1.4 mean degree, 39.2 ± 7.1 mean number of interactions and 0.26 ± 0.04 mean strength. As on intensive farms, *H. adunca* was the second most important bee. However, interestingly, *O. caerulea* also plays an important part in the structure of these networks on organic farms, with values of 8.0 ± 1.4 , 25.5 ± 7.1 and 0.15 ± 0.04 for degree, number of interactions and strength, respectively.

The ten most important plant nodes for the maintenance of singular, rare or specialized interactions, were not found under both management regimes (Fig. 3). Only *Sinapis alba* and *Silene* sp. were the only nodes only found under both management regimes. The other 16 plant nodes (eight per management type) were important for maintaining specialized interactions only on farms with either intensive or organic management, not on both. Their importance also varied considerably depending on the locality (high standard error). We detected no clear patterns in management types regarding their importance for sustaining singular interactions for the ten most singular plant or bee nodes under each management type. However, there was an apparent trend for two

bee species, *Osmia bicornis* and *O. cyanoxantha*, to participate in particular interactions, mainly on organic farms. Although in the case of the latter species, there was some uncertainty because it only appeared in one locality.

The patterns described above suggest that these networks have in both intensive and organic management regimes a strong nested structure, with a core of more frequent interactions and a periphery of singular ones connected to the core. The visualization of networks and the calculation of their nestedness indices verify this expected structure (Fig. S3).

4. Discussion

Our results supported two of our three predictions. We did not find differences in node composition between management practices. However, we were able to identify the species that should be prioritized for conservation or restoration. Additionally, our results show that these networks have a stable core-periphery structure, where the most structuring species remain constant across management types albeit with the presence of important singular interactions.

Contrarily to our first prediction, compositional differences show that most plant and bee species were present irrespective of the management regimes and, more importantly, that the most abundant and

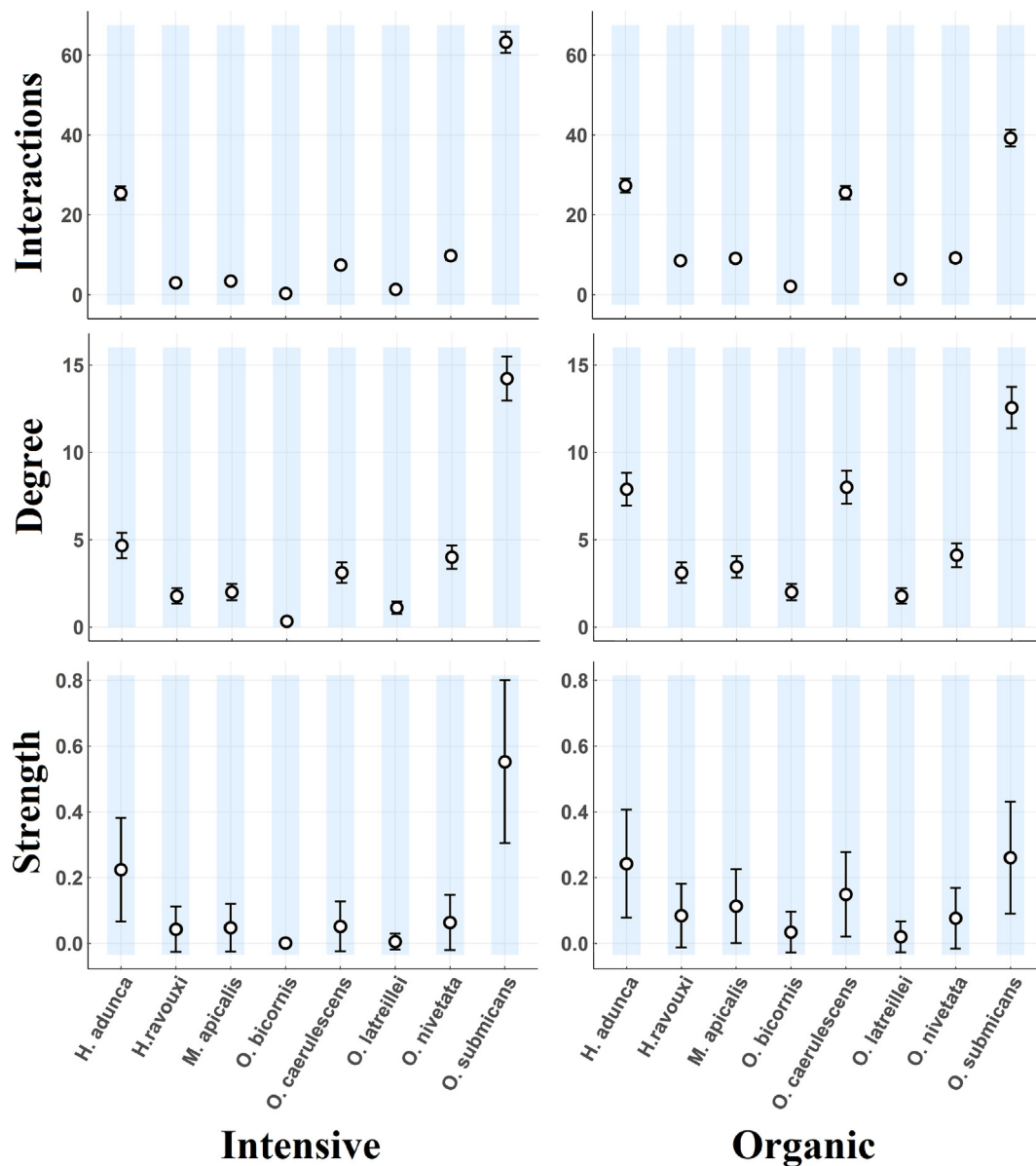


Fig. 2. Number of interactions, degree and node strength for each of the eight most frequent bee species on intensive and organic olive farms. Circles and error bars show back-transformed mean \pm SE. Absent species in these plots were very infrequent and their models/means were not robust.

relevant species (for network structure and pollination functioning) were common. However, ca. 20% of plant species visited by bees in organic groves do not occur in intensive groves, thereby suggesting that differences between networks under different management regimes are mediated by variations in the availability of floral resources (Martínez-Núñez et al., 2019). The contrast in floral resources between management types was clear for both herb species richness and abundance (herb cover), and probably drives differences in foraging success (Carman and Jenkins, 2016). This agrees with the fact that the abundance of interactions did not vary, although the richness of interactions did, being higher in organic groves (Table 1). Therefore, the induced variation in herb cover/richness due to cover management is key for providing foraging resources for pollinators, driving bottom-up effects in the networks and providing more niche opportunities for pollinators in organic groves. In terms of bee node composition, we found that 13 solitary bee species foraged on 68 different plant taxa (probably around 80 species since in some cases it was difficult to separate pollen types from the same genera or even families). This demonstrates the importance of aboveground cavity-nesting bees (and native pollinators in

a broader sense) for the conservation of wild plants in agroecosystems (Rollin et al., 2016). It also shows the high generality found in these networks that, as discussed below, confers on these communities a considerable robustness against perturbations (Astegiano et al., 2015).

As predicted by our second hypothesis, the network analysis of interactions successfully identified the most important nodes for the stability and complexity of these networks. Interestingly, the ten most structurally important plant taxa were the same for both management regimes (intensive and organic). These taxa are characterized by their offering of nectar to pollinators, a trait that determines to a large extent the reproductive success of insect-pollinated plants and their floral traits (Parachnowitsch et al., 2019). These results suggest that plant-pollinator assemblages are based on preferential interactions (Olesen et al., 2008). Some authors, however, have argued against preferential interactions and defend opportunistic interaction (Ponisio et al., 2017) as the mechanism underlying plant-pollinator network structure. We suggest that the plant-pollinator network structure may be determined to a large extent by floral traits because the species most-foraged by solitary bees in olive groves are highly dependent on pollinators due to

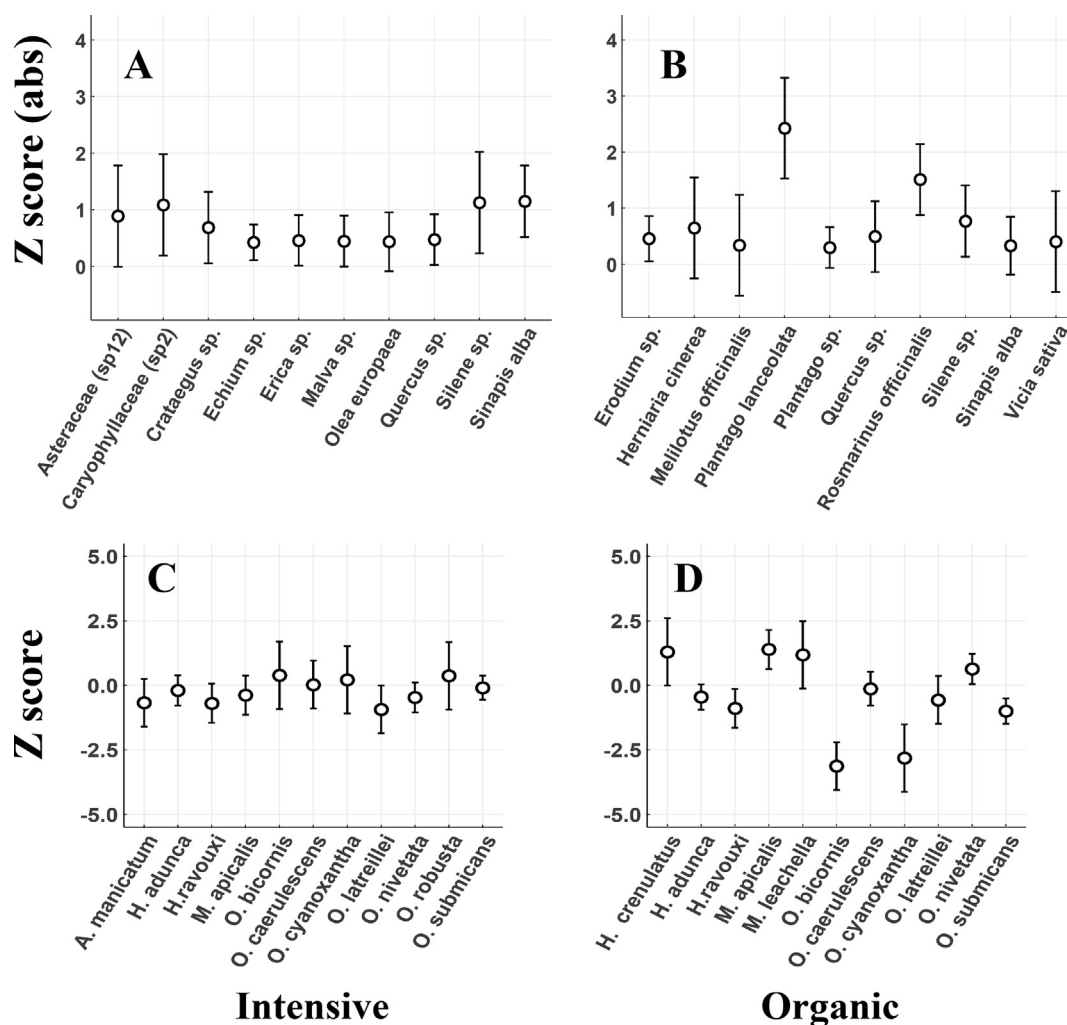


Fig. 3. Importance of plant and bee nodes for the maintenance of rare or infrequent interactions. This is shown as the standardized mean (z-score) of the loss in network closeness due to the targeted removal of a plant node (A; B) or a bee node (C; D), on farms with intensive (A; C) or organic (B; D) management regimes. The z-score refers to null networks where the links of each node are randomly connected to other nodes. Circles and error bars show the mean \pm SE. Note that plant panels (A and B) show non-negative ($|\text{abs}|$) values for the ten most important nodes (more negative z-scores). Panels representing bees (C and D) show all the species as relative values (more negative, more important than random).

sporophytic incompatibility (de Nettancourt, 1997) and all provide nectar and/or pollen to their visitors. The degree, number of interactions and strength of bee nodes all reveal that *O. submicans* and *H. adunca* (especially the former) strongly dominate bee pollination in intensively managed farms and so are the cornerstone of the network structure. In organic olive groves, we found a better balance between bee nodes because topological importance was shared by several species (even though *O. submicans* and *H. adunca* still dominate). Specifically, *O. caerulea* occurs in these systems as an important species for network topology, which is not the case in intensive groves. Possibly, this difference between management practices is due to reduced competition and increased niche opportunities in organic groves, driven or mediated by a higher availability of foraging resources. This pattern suggests that network structure in organic groves is more resistant to disturbance and underlines the fact that *O. caerulea* is potentially a good bioindicator of management quality in Andalusian olive groves.

As predicted by our third hypothesis, plant-solitary bee networks are fairly stable across management types. An alternative interpretation, however, could be that these communities are already fairly disturbed and thus we might merely be comparing previously filtered or resistant communities. Nonetheless, the fact that we observed network spatial homogenization on intensive but not organic farms (Martínez-Núñez et al., 2019) gives more credibility to the first suggestion (i.e.

these networks are fairly stable across management types). Although the most important nodes from a structural standpoint were constant between management regimes, this was not the case for nodes involved in singular or rare links. The importance of plant nodes in the network structure – i.e. their degree, number of interactions and node strength – is inversely proportional to their vulnerability. Hence, highly specialized plants that only interact with very few bee species may still be relevant nodes from a structural rather than functional perspective. In this sense, our results show that the plant nodes with unique interactions (i.e. more important per interaction unit) differ between management regimes. This pattern has been observed in other scientific fields (Csermely et al., 2013; Peralta-Maraver et al., 2017). There are stable (i.e. constant, invariant) and frequent interactions that constitute the network core, while other peripheral interactions explain differences in networks (Mora et al., 2018). To our knowledge, we highlight here for the first time this pattern in interaction networks in farms employing differing agricultural management techniques. Thus, while core-structuring nodes remain constant between the two management types, unique links do vary, which, in the case of a severe perturbation (e.g. the removal of core plants), might push the communities with different peripheral species towards diverging points of stability. In particular, the propensity of a bee species, *Osmia bicornis* to participate in specialized interactions (mainly on organic farms) reveals its role in

pollination network recuperation thanks to the application of an agri-environmental scheme (i.e. these species are useful as bioindicators of recovery). *Osmia cyanoxantha*, might also be a bioindicator of system recovery, but it only appeared in one organic farm, hindering confident conclusions.

Our analysis of plant-solitary bee networks on olive farms suggest that (i) aboveground cavity-nesting solitary bees play a very active role in the conservation of many wild plants by contributing to their pollination; (ii) the species with the greatest importance for network structure were the same under both management regimes, namely, certain plants belonging to the Asteraceae family, as well as *Echium* sp., and *Medicago* sp., and the bees *O. submicans* and *H. adunca*. These species are thus of conservation priority for these communities; (iii) the previous consideration and the common core-periphery structure suggest that these networks are fairly stable across management types; (iv) the species with the most unique interactions, however, did vary across management regimes. Hence, we expect that there will be great efficiency in the restoration of these networks and pollination functioning when switching from intensive to organic management practices with ground cover. The main gain derived from any such switch in management will be the recuperation of rare or infrequent links, which seem to be driven by a greater availability and richness of foraging resources; and, finally, (v) *O. caerulea* could be a good bioindicator of management quality as it is more active/abundant on organic olive farms, while *O. bicornis* and *O. cyanoxantha* could indicate the degree of community and ecosystem recovery since they only participated in singular interactions on organic farms.

5. Author's contributions

CMN, AJM and PJR conceived the study and the main ideas, CMN analysed the data, CMN and PJR led the writing of the manuscript. All the authors contributed critically to the final version.

Data availability

The data and the code are available in Mendeley data: DOI: [10.17632/c2wyd8ry6t.1](https://doi.org/10.17632/c2wyd8ry6t.1).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2020.106422>.

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