Solitary bees (Hymenoptera, Apoidea) as connectors in pollination networks: the case of *Rhodanthidium*

Daniel ROMERO¹, Concepción ORNOSA¹, Pablo VARGAS², Jens M. OLESEN³

¹Department of Biodiversity, Ecology and Evolution; Faculty of Biological Sciences, University Complutense of Madrid, José Antonio Nováis Street, 12, Ciudad Universitaria, 28040, Madrid, Spain

²Real Jardín Botánico, CSIC, Madrid, Spain

³Department of Bioscience, Aarhus University, Aarhus, Denmark

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Abstract – Bees (Apoidea) are the main pollinator group in Mediterranean ecosystems, having a dominant role as connectors of modules (groups of species tightly linked in pollination networks), but little is known about the role of particular species. Here, we analyse data from four Iberian networks, and we pay special attention to the role played by the solitary snail-shell bee *Rhodanthidium sticticum* (Fabricius, 1787) in shaping network modularity. Our results show that *R. sticticum* is a pollination generalist that acts as an important connector of modules, strongly influencing the topology of its networks. We also examined 51 networks from all over the world to determine the modular role of other Anthidiini species. Anthidiini were present in 14 of these networks and another *Rhodanthidium* species, but also two *Anthidium* species, played a role as connectors in their respective networks.

connector / pollination network / *Rhodanthidium* / solitary bees

1. INTRODUCTION

Within an ecological space, plant-flower visitor mutualistic interactions combine into pollination networks (Delmas et al. 2019, Herrera 2019). Pollination network studies may encompass all pollinator species within a given study area and period ('total pollination networks') or slice out certain groups of special interest, e.g. birds (Rodríguez-Rodríguez and Valido 2008, Traveset et al. 2015).

Here, we focus upon the bees. Their network role, as a group, has recently been addressed in

Mello et al. (2013), Tucker and Rehan (2016), Gresty et al. (2018) and Jauker et al. (2019). Thus, by now, we know that bees are commonplace in pollination networks and that they connect different modules, i.e. tightly linked network groups (Olesen et al. 2007), but the ecological role of particular species for network topology remains uncertain. This information could be very valuable for the development of network conservation plans, in particular those which focus upon ecosystem functionality.

In general, there is plenty of knowledge on the relationship between phenotypic traits and topological roles, as species morphology frequently modulates network structure by both facilitating and hindering possible interactions (Olesen et al. 2010, Ibáñez 2012). That is the case for birds' bills size and flower size (Biddick and Burns 2018), bees' proboscides length and flowers' spur length (Blanco-Pastor et al. 2015) and oil flowers and long-legged bees (Pauw et al. 2017).

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Corresponding author: D. Romero, danielromero@ucm.es

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However, not so much is known about the importance to networks of taxa with special biology, such as solitary and territorial bees or bees with specific nesting requirements. The ecological role of particular species in networks has only recently been addressed (Olesen et al. 2018) and it is unknown for most published networks and the species involved. The latter step is important because it bridges the gap between ecological network theory and the ecology of individual species.

As an example, we here analyse in detail the ecology and network roles played by *Rhodanthidium sticticum* (Fabricius, 1787) (Figure 1), a solitary bee distributed across the western Mediterranean (Ornosa et al. 2008). It belongs to the tribe Anthidiini, which is widespread in the world in terms of its genera. Its species are solitary and territorial (Michener 2007). However, the more detailed ecology is poorly studied, e.g. nesting, territorial behaviour and pollination ecology (Torres et al. 2001, Torné-Noguera et al. 2014). *Rhodanthidium sticticum* appears to be one of the most abundant species and a major pollinator in some Mediterranean plant communities (Torné-Noguera et al. 2014), being essential for some threatened and endemic species (Blanco-Pastor et al. 2015, Vargas et al. 2017). It is active during the entire flowering season (from the beginning of March to the end of June). Low pollen specialisation has been recorded for *R. sticticum*, and thus it is considered polylectic, i.e. it collects pollen from many unrelated plant families, at least in parts of its range (Torné-Noguera et al. 2014).

In a study of 18 Iberian plant species (Vargas et al. 2017), this bee species was the main pollinator of five snapdragons or *Antirrhinum* species (*A. barrelieri*, *A. charidemi*, *A. hispanicum*, *A. molle* and *A. microphyllum*) and a dominant pollinator of three other snapdragons (*A. australe*, *A. mollissimum* and *A. pulverulentum*), playing a key role to the survival of these species, of which some are threatened. Indeed, the pollination effectiveness of *R. sticticum* clearly favoured the reproductive success of these *Antirrhineae* species (Vargas et al. 2010). Consequently, *R. sticticum* could also be a selection factor in snapdragon evolution, as it is the case for the occluded corolla evolution of several species of the closely related *Linaria* (Blanco-Pastor

et al. 2015). *Rhodanthidium sticticum* may then play both an ecological and evolutionary role to *Antirrhinum* species, but its functional role in entire communities in which snapdragons are partners remains unknown, although we expect bees in general and *R. sticticum* in particular to be relevant connectors between network modules; we do so, because they visit a highly diverse group of plants. Eighty-five percent of all plant and pollinator species in pollination networks are of peripheral importance, i.e. they only interact with one or few other species (Olesen et al. 2007).

However, the last 15% are structurally important. They are either hubs, i.e. highly linked species within their own module, connectors linking different modules, or both. If any of these key species go extinct, modules and networks may disintegrate and trigger cascades of local extinction (Memmott et al. 2004, Kaiser-Bunbury et al. 2010). Thus, hubs and connectors should receive conservation priority. Our present hypothesis is that *R. sticticum* plays an essential structuring role in Mediterranean pollination networks in which *Antirrhinum* species are members. By essential role, we mean that it connects network modules and contributes to the structure and thus stability of the networks. Our objectives become (i) to analyse different plant communities where the interaction *Rhodanthidium*-*Antirrhinum* occurs; (ii) to determine the specific network role of *R. sticticum* in these communities; and (iii) to analyse the role of other Anthidiini species and, especially other *Rhodanthidium* species.

2. MATERIAL AND METHODS

2.1. Study sites and interaction sampling

Previously, we have observed the interaction between *Rhodanthidium* and *Antirrhinum* in eight communities in the Iberian Peninsula (Vargas et al. 2017); four of these were selected and field surveys were performed. By choosing these four locations, we obtained a range in level of visitation frequency performed by *R. sticticum* to different *Antirrhinum* species. The *Antirrhinum* species were *A. molle* (Huesca, Gabasa; 42.007153°, 0.416735°) and *A. microphyllum* (Guadalajara, Buendía; 40.394967°, –

Figure 1. Female (left and right) and male (centre) of *Rhodanthidium sticticum*.

2.791320°), both with *R. sticticum* as their main pollinator (> 50% of visits), *A. mollissimum* (Almería, Enix; 36.877929°, −2.609264°) with *R. sticticum* as its predominant pollinator (> 25% of visits), and *A. pulverulentum* (Zaragoza, Nuévalos; 41.213594°, −1.791900°) with *R. sticticum* as a secondary pollinator (< 25% of visits) (Vargas et al. 2017).

Plant-pollinator interactions were observed in May and June in 2017 and 2018, during the flowering peak of most plant species and diurnally from 10:00 to 17:00 h. Each locality was sampled during 5 days (20–25 h in total per locality). Sampling followed nonlinear transects covering vegetation patches of the different plant species within the area. The surveys were done by direct observation. An interaction was recorded when a visitor touched the flower reproductive parts, but not when it only landed on the flowers. Individuals of visitor species were captured and identified, and are deposited in the Entomology Collection of the Complutense University (UCME), Madrid. The identification of the different visitors was done with the help of identification keys and the comparison with specimens deposited in the UCME.

2.2. Network structural properties

For each locality, unweighted or qualitative, undirected networks were built using the bipartite package (Dormann et al. 2008) in RStudio 1.1.383 (RStudio Team 2016) to calculate the following network structural properties: number of visitor species (A); number of plant species (P); number of potential interactions ($A \times P$);

number of observed interactions (I); and connectance ($C = I/AP$). Other parameters were calculated, and are included in Appendix 4. Connectance is the ratio between the number of established and potential interactions (Martínez 1992, Delmas et al. 2019). Proportions of the four most frequent visitor orders (Coleoptera, Diptera, Hymenoptera and Lepidoptera, the main pollinator groups in temperate areas) by species and by the number of visits and proportion of bees found in the networks were also calculated. Nestedness analyses were performed using Aninhado 3.0 (Bangu) (Guimaraes and Guimaraes 2006, Almeida-Neto et al. 2008). Values for modularity level (M), number of modules, percentages of connectors, module hubs and ecologically relevant species were calculated after performing modularity analysis. Species are defined as ecologically relevant to the network when they have one of three ecological roles (connector, network hub or module hub), i.e. we did not analyse further the group of species categorised by the modularity analysis as peripheral.

2.3. Modularity and species' ecological roles

Modularity (M) is the tendency of a network to be organised into well-delimited groups, called modules (Olesen et al. 2007, Jordano et al. 2009, Dupont and Olesen 2012). In particular, when links are mostly inside modules, and connectedness between modules is low, modularity becomes high. Modularity analyses were performed with NcCarto (Guimerá and Amaral, 2005a, b). Statistical significance of M was assessed by comparing the obtained M with modularity values for

100 randomizations of each network (iteration factor 1, cooling factor 0.99 and final temperature 0).

In order to identify the ecologically relevant species in the networks, we analysed two species parameters (output values from the modularity analysis): z (how well connected a species is inside its own module) and c (how well connected a species is to species in other modules) (Guimerá and Amaral 2005a, Olesen et al. 2007). Olesen et al. (2007) sorted all species in a pollination network into four categories: peripherals, connectors, module hubs and network hubs. According to that classification, species with between-module values (z) ≥ 2.5 were categorised as module hubs, and species with within-module values (c) ≥ 0.62 were categorised as connectors. Species with both, (z) ≥ 2.5 and (c) ≥ 0.62 , were considered network hubs and the rest of species were categorised as peripherals.

Additionally, 51 pollination networks from Argentina, Australia, Azores, Canada, the Canary Islands, Chile, Denmark, Galapagos, Greece, Greenland, Jamaica, Japan, Mallorca, Mauritius, New Zealand, continental Spain, Sweden, the USA and Venezuela, obtained from the dataset included in Olesen et al. (2007), were analysed in order to locate other Anthidiini species and, more specifically, other *Rhodanthidium* species. Modularity analyses were performed to determine the role of the different Anthidiini species in the networks where this tribe was present, using the same parameters as in our Iberian study.

3. RESULTS

3.1. *Rhodanthidium*-*Antirrhinum* networks

Modularity (M) was significant in the four networks, although it was low in Nuévalos. Nestedness (NODF) was only significant in Nuévalos (Table 1). To compare other parameters, see Appendix 4.

In the four networks, Hymenoptera was the most species-rich visitor order (Figure 2) and a vast majority of them were bees. In Buendía and Énix, the proportion of Hymenoptera was 67%. In Énix 97% of hymenopterans were bees, whilst in Buendía, this proportion was 71%. In Gabasa, the

proportion of Hymenoptera was 69% (83% of these were bees). In Nuévalos, 77% were Hymenoptera (94% of these were bees).

Between 76 and 94% of the total number of visits (Figure 2b) were performed by Hymenopteran and 70% (Buendía), 82% (Énix), 76% (Gabasa) and 93% (Nuévalos) by bees.

3.2. Modularity

In the four networks, most connectors were pollinators, whereas all module hubs were plants. Pollinator connectors were Coleoptera and Hymenoptera, but none were Diptera or Lepidoptera (Figure 3; the role of all species is listed in Appendix 1). In all the networks, at least one-third of the connectors were bees; Gabasa is the locality with most bee species being connectors (75%) (Figure 3b). *Rhodanthidium sticticum* was a connector in three of the networks, and a network hub in Énix.

3.3. *Rhodanthidium sticticum* in the networks

In Énix and Nuévalos, *R. sticticum* was the visitor with links to most plant species (12 of 29 and nine of 16 species, respectively), followed by *A. mellifera* (nine of 29 and seven of 16, respectively). In Buendía, *R. sticticum* also visited the highest number of plant species (seven of 18 species) but, in this case, the next most linked species were two species of beetles (both visiting six of 18 species). *Apis mellifera* had fewer links (two of 18). In Gabasa, *R. sticticum* was more specialised with links to only three species of 22 (Appendix 1). In terms of total number of visits, *A. mellifera* was the species that performed the highest number of visits in Énix and Nuévalos, followed by *R. sticticum*. In Buendía, three bees, a wasp and a beetle were responsible of more visits than *R. sticticum*. In Gabasa, 21 pollinator species performed more visits to flowers than *R. sticticum* (Appendix 1).

Rhodanthidium sticticum shared modules with bee-pollinated plants and long-tongued bees. It appeared together with other connectors, but not with module hubs (for composition of the modules in the networks, see Appendix 2).

Table I. Network structural properties at four localities. No. of all visitor species (*A*); no. of plant species (*P*); no. of potential interactions (*A* × *P*); no. of interactions (*I*); connectance (*C*); no. of modules; percentage of connectors (% conn.), percentage of module hubs (% mod. hubs), nestedness (*NODF*). **P* < 0.05. In addition, there was also one network hub in Buendía (*Ruta angustifolia*) and Énix (*Rhodanthidium sticticum*) (not included in the table)

Dataset	A	P	A x P	I	C	M	No. of modules	% conn.	% mod. hubs	NODF
Buendía	65	18	1170	119	10.2	0.54*	7	12.0	2.4	5.95
Énix	33	29	957	91	7.5	0.52*	6	16.1	0.0	7.82
Gabasa	83	22	1826	123	6.7	0.66*	9	4.8	3.8	3.35
Nuévalos	23	16	368	56	15.2	0.46*	5	7.7	2.6	13.4*

3.4. Network role of Anthidiini

Worldwide, bees of the tribe Anthidiini were found in 14 of 51 networks (Tables II and III). Two *Rhodanthidium* species were present:

Rhodanthidium caturigense (one network) in Greece, in a Mediterranean shrubland (Table II) and *R. septemdentatum* (in three networks from Greece and Majorca, Spain, also in Mediterranean shrubland, Tables II and III). *Rhodanthidium septemdentatum* was a connector in two of the three networks (for the roles of all the species in the 14 networks, see Appendix 3). *Anthidium chilensis* and *A. latreillei* were also connectors

Figure 2. a Proportion of visitor species per insect order in Buendía, Énix, Gabasa and Nuévalos. Col., Coleoptera; Dip., Diptera; Hym., Hymenoptera; Lep., Lepidoptera. **b** Proportion of visits per insect order in Buendía, Énix, Gabasa and Nuévalos. Col., Coleoptera; Dip., Diptera; Hym., Hymenoptera; Lep., Lepidoptera.

Figure 3. a Percentage of connectors per insect order in Buendía, Énix, Gabasa and Nuévalos. Col., Coleoptera; Hym., Hymenoptera. **b** Percentage of bee species that are connectors out of the total number of connectors.

Table II. Role of Anthidiini in Spanish networks. Connectors are indicated with an asterisc (*); in bold, *Rhodanthidium* species. The species are named according to the identification in the corresponding reference

Species	Links	Locality	Province	Altitude (m)	Article
<i>Rhodanthidium septemdentatum</i>*	9	Son Bosc	Mallorca	0	Tur et al.
<i>Rhodanthidium septemdentatum</i>	3	Puig Major	Mallorca	1100	2013
<i>Anthidium manicatum</i> (Linnaeus, 1758)	1				
<i>Anthidium cingulatum</i> (Latreille, 1809)	1				
<i>Anthidiellum strigatum</i> (Panzer, 1805)	1	Doñana	Andalucía	10	Herrera, 1988
<i>Stelis signata</i>	1				
<i>Anthidium manicatum</i>	1	Cementerio de los Tajinastes, Teide N.P.	Tenerife	2050	Dupont et al. 2003
<i>Anthidium latreillei</i> (Lepeletier, 1841)*	3	Alcalá de Henares	Madrid	600	González, 2004
<i>Anthidium reticulatum</i> (Mocsáry, 1884)	3				
<i>Anthidium latreillei</i> var. <i>rubiginosum</i> (Lepeletier, 1841)	2				
<i>Anthidium cingulatum</i>	1				
<i>Anthidium schulthessi</i> (Friese, 1897)	1				
<i>Rhodanthidium sticticum</i>*	7	Buendía	Cuenca	645	This study
<i>Anthidiellum strigatum</i>	1				
<i>Rhodanthidium septemdentatum</i>	1				
<i>Rhodanthidium sticticum</i>*	12	Énix	Andalucía	795	
<i>Anthidiellum strigatum</i>	1				
<i>Rhodanthidium sticticum</i>*	3	Gabasa	Huesca	650	
<i>Anthidiellum strigatum</i>	3				
<i>Rhodanthidium septemdentatum</i>	1				
<i>Anthidium manicatum</i>	1				
<i>Rhodanthidium sticticum</i>*	9	Nuévalos	Zaragoza	705	
<i>Anthidium manicatum</i>	2				
<i>Rhodanthidium septemdentatum</i>	2				

in their networks from Chile and Spain, respectively. Besides, *R. septemdentatum* was also a visitor in three of the *Antirrhinum* - *Rhodanthidium* networks (Gabasa, Buendía and Nuévalos), but not a connector.

In the Greek network, *R. septemdentatum* was a connector. Two bees and a fly had more links than *R. septemdentatum* (33 links).

In the Majorcan networks, *R. septemdentatum* behaved differently. In the network from Puig Major, it did not have an important ecological role in the network, i.e. it was a peripheral species. Two beetles, a fly and a bee had more links than *R. septemdentatum* (three links). In the network from Son Bosc, however, *R. septemdentatum*

was a connector. Three beetles, a fly, a bee and an ant had more links than *R. septemdentatum* (nine links).

4. DISCUSSION

The unique ecological and evolutionary role of *Rhodanthidium sticticum* is probably driven by its long tongue, which gives this bee access to nectar from numerous plants. This key trait defines its topological position in the studied pollination networks. By its ability to visit many different plant species, it becomes a connector between different modules. Most species act within their module, but connectors operate at a structurally higher

Table III. Role of Anthidiini in different networks outside Spain. Connectors are indicated with an asterisc (*); in bold, *Rhodanthidium* species. The species are named according to the identification in the corresponding reference

Species	Links	Locality	Country	Altitude (m)	Article
<i>Anthidium chubuti</i> (Cockerell, 1910)	3	Laguna Diamante	Argentina	3300	Medan et al. 2002
<i>Anthidium rubripes</i> (Friese, 1908)	1	Río Blanco		1900	
<i>Anthidium</i> sp. 1	13	Parque Cordillera Yerba Loca	Chile	3400	Arroyo et al. 1982
<i>Stenanthidium espinosai</i> (Ruiz, 1938)	2				
<i>Anthidium funereum</i> (Schletterer, 1890)	3	Parque Cordillera Yerba Loca		2900	
<i>Anthidium</i> sp. 1	2				
<i>Anthidium chilense</i> (Spinola, 1851)*	8	Parque Cordillera Yerba Loca		2400	
<i>Anthidium</i> sp. 1	6				
<i>Anthidium gayi</i> (Spinola, 1851)	5				
<i>Anthidium decaspilum</i> (Moure, 1957)	4				
<i>Anthidium adriani</i> (Ruiz, 1935)	1				
<i>Rhodanthidium septemdentatum</i> *	33	Diomedous Botanical Garden, Daphni	Greece	95	Petanidou and Ellis, 1993
<i>Anthidiellum strigatum</i>	18				
<i>Icteranidium grohmanni</i> (Spinola, 1838)	11				
<i>Anthidium florentinum</i> (Fabricius, 1775)	7				
<i>Anthidium elongatum</i> (Friese, 1897)	5				
<i>Rhodanthidium caturigense</i>	2				
<i>Anthidium taeniatum</i> (Latreille, 1809)	2				
<i>Anthidium manicatum</i>	1				
<i>Anthidium dalmaticum</i> (Mocsáry, 1884)	1				
<i>Anthidium undulatum</i> (Dours, 1873)	1				
<i>Eoanthidium insulare</i> (Morawitz, 1874)	1				
<i>Pseudoanthidium alpinum</i> (Morawitz, 1874)	1				
<i>Pseudoanthidium lituratum</i> (Panzer, 1801)	1				
<i>Stelis punctulatissima</i> (Kirby, 1802)	1				
<i>Pseudoanthidium cribratum</i> (Morawitz, 1875)	1				
<i>Mesanthidium carduele</i> (Morawitz, 1876)	1				
<i>Anthidium septemspinosa</i> (Lepeletier, 1841)	3	Campus of Kyoto University	Japan		Kakutani et al. 1990
<i>Anthidium tenuiflorae</i> (Cockerell, 1907)	1	Pikes Peak	USA	2590	Clements and Long, 1923

Table III (continued)

Species	Links	Locality	Country	Altitude (m)	Article
<i>Anthidium</i> sp.	2	Llanos Altos Centrales	Venezuela	74	Ramirez and Brito, 1992
<i>Anthidiellum</i> sp.	1				

level, because they define the relationship between modules. Their presence synchronizes the ecology of the individual modules, because all kinds of information, such as disturbance events, are transmitted to other modules through the activities of the connectors (Olesen et al. 2018). Thus, the more connectors, the faster and more efficient information pass among modules.

4.1. *Rhodanthidium*-*Antirrhinum* networks

According to Olesen et al. (2007), almost 60% of all pollination networks are modular, but most are also nested. However, if network connectance gets high ($\geq 20\%$), modularity disappears, because it gets destroyed by the many links (Fortuna et al. 2010). Many connectors may also destroy modularity. The four networks of this study have a low connectance ($\leq 20\%$) and should thus be expected to be both modular and nested. This was not the case. Gabasa, Buendía and Énix were very modular, but not nested. On the other hand, Nuévalos had a low modularity, but was nested. However, species-poor networks (≤ 50 species) are often not modular (Olesen et al. 2007) or rephrased, they consist of only one module.

In our study, all *Antirrhinum* species were peripherals (see Appendix 1), i.e. they were either very specialized plants or rare species only attracting a few visitor species. Snapdragons have a corolla clearly marked by the development of a prominent palate (personate flower) that occludes the entrance of the corolla tube, which results in a floral filtering morphology to pollinators (Guzmán et al. 2015). If such peripheral species live in a nested network, they link to generalised flower visitors, i.e. to *Rhodanthidium*. Indeed, *Rhodanthidium sticticum* does not only visit *Antirrhinum* species, as it is a generalist (Vargas et al. 2010). It has been hypothesised that bees as a whole act as generalist pollinators within

specialised systems such as that of snapdragons and relatives (Guzmán et al. 2017). Other visitor species in the studied networks, like *Colletes albomaculatus* in Buendía, *Andrena boyerella* in Gabasa or *Hoplitis adunca* in Buendía and Gabasa, are among the highest-scoring visitors (Appendix 1), but visiting only one or two plant species, reinforcing the idea that specialists specialize on generalist, no matter if plant or pollinator.

4.2. *Rhodanthidium sticticum* in pollination networks

This is one of the first studies analysing functional roles of particular bee species, except for the Centridini oil bees that have also been studied in detail (Mello et al. 2013). *Rhodanthidium sticticum* was a connector in three of the four analysed networks, and a network hub in the last one. It is also the second most important visitor in terms of number of visits in two of the networks (Énix and Nuévalos), after *A. mellifera*, and the fourth in Buendía, not counting specialists like *Colletes albomaculatus*, *Heriades crenulatus* and *Hoplitis adunca* (see Appendix 1). Generalists like *R. sticticum* are keystone species for the networks (González et al. 2009) and, as shown here, *R. sticticum* is the visitor that interacts with more plants in three of the four networks. As a connector, it links different modules, being essential for the structure and operation of the community (Olesen et al. 2007). In these cases, *R. sticticum* is a generalist and a connector, but this is not always the case. A generalist could be, then, a peripheral, depending on the network structure and composition.

The role of *R. sticticum* to the survival of species of Antirrhineae has already been assessed, but not at a community level. *Rhodanthidium sticticum* is a key species in the pollination of five

Antirrhinum species, including two endangered ones (Vargas et al. 2017). It is also a key species to the survival of four endangered and endemic *Linaria* taxa from the Iberian Peninsula (Blanco-Pastor et al. 2015). These species, besides being self-incompatible (Blanco-Pastor and Vargas 2013) and, therefore, in need of cross-pollination, have an occluded corolla. In spite of this, they achieve high fecundity and viability of their seeds due to the effectiveness of *R. sticticum* (Vargas et al. 2010).

Apparently, the majority of plant species pollinated by *R. sticticum* does not seem to be pollinator-limited with respect to number of pollinator species (with the exception of the *Linaria* and *Antirrhinum* species), but perhaps with respect to total pollinator abundance. On a local scale, *R. sticticum* is one of the most abundant species, even being the most abundant long-tongued bee in the entire bee community (Torné-Noguera et al. 2014). Thus, for the moment, its functional and topological role as a connector in Mediterranean communities appears to be stable.

4.3. Anthidiini and *Rhodanthidium* in other networks

Bees of the Anthidiini were part of 14 of the 51 studied networks in Olesen et al. (2007), all but one from temperate areas, and two *Anthidium* species (*A. chilensis* and *A. latreillei*) were connectors in their respective communities (Tables II and III). All other potential connector bee species belonging to different tribes of the Megachilidae or other families were not considered here (their roles are shown in Appendix 1 and 3, though). *R. septemdentatum* was a connector in two Mediterranean networks, one from continental Greece and one from the island of Majorca (Spain). However, if it co-occurred with *R. sticticum*, *R. septemdentatum* lost its ecological role (in Gabasa, Buendía and Nuévalos networks). The only available study of the abundances of *R. septemdentatum* and *R. sticticum* shows that the abundance of the first is eight

times lower than the abundance of *R. sticticum* (Torné-Noguera et al. 2014), which could explain how, when both species coexist in the same network, one outnumbers the other and displaces its ecological role.

The biology and, particularly, the behaviour of *R. sticticum* are very similar to those of many other Anthidiini (especially within the genera *Anthidium* and *Rhodanthidium*) in terms of flight ability, territoriality, sociality and flower visitation (Severinghaus et al. 1981, García-González and Ornos, 1999, Michener 2007). This makes the species a good representative of the group, allowing us to generalise from species to tribus. As it occurs with *A. latreillei* and *A. chilensis*, other *Anthidium* could be ecologically relevant in their networks, connecting different modules.

5. CONCLUSIONS

As a connector and a generalist, *Rhodanthidium sticticum* is the most ecologically important solitary bee for the studied plant communities. Due to its relevance for some snapdragons and other endangered Antirrhineae, *R. sticticum* should be taken into account in conservation plans for these plants. *Rhodanthidium septemdentatum* is also an ecologically valuable species in other Mediterranean networks, but apparently this is not the case, when it occurs together with *R. sticticum*. Species belonging to the *Anthidium* genus also have ecologically relevant roles in some temperate networks, thus making the Anthidiini tribe (especially the *Rhodanthidium* and *Anthidium* genera) noteworthy for future pollination network studies. Research in pollination networks should pay more attention to the role of these and other solitary bees, due to their importance for the structure of the network and the survival of plant species in the entire community. Thus, protecting particular species in the networks (connectors and hubs, plants and pollinators alike) might have high conservation value to entire ecosystems. Conservation plans at community level should, as a minimum, consider network-relevant species in order to protect the diversity of interactions and processes that keep a high functionality of their ecosystems.

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AUTHOR CONTRIBUTIONS

DR, CO, PV and JO conceived this research, participated in the collection and interpretation of data, performed analyses, wrote the paper and participated in the revisions. All authors read and approved the final manuscript. Funding information

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Des abeilles solitaires (Hyménoptères, Apoïdées) comme connecteurs dans les réseaux de pollinisation : le cas *Rhodanthidium*.

connecteur / réseau de pollinisation / *Rhodanthidium* / abeilles solitaires.

Solitäre Bienen (Hymenoptera, Apoidea) als Bindeglieder in Bestäubernnetzwerken: der Fall *Rhodanthidium*.

Bindeglied / Bestäubernnetzwerk / *Rhodanthidium* / solitäre Bienen.

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