

Research Article

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# Interaction networks between solitary hymenopterans and their natural enemies in different restoration areas

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**Abstract**

The diversity of species and their interactions have been positively related with environmental complexity. Therefore, highly anthropized environments have their integrity under serious threat. These effects may last for years compromising the dynamics of natural communities, such as antagonistic and mutualistic interactions, including host-natural enemy interactions. To investigate these effects, trap nest methodology was used to assess the diversity of solitary bees, wasps and their natural enemies in three fragmented environments with different degree of anthropic perturbation, composed of a *Eucalyptus* plantation (considered here as higher perturbation), a Cerrado area (medium perturbation) and a Riparian forest (lesser perturbation). Then, host-natural enemies associations were analysed to verify the size, specialization degree and modularity of interaction network. The gradient from highest to lowest degree of anthropic perturbation was evidenced in the species diversity index, the size of the interaction network and the specialization indexes of the host-natural enemy network. The environment with *Eucalyptus* plantation showed higher values of diversity of natural enemies, greater number of species in the interaction network, lesser degree of specialization in the interaction and lesser modularity, than Cerrado and Riparian forest environments, respectively. The low degree of nestedness and lack of significance of this index to all sampled areas are indicative of a specialized pattern of networks. The results corroborate the notion that human impact may affect interaction networks, this being an important tool for checking the degree of anthropic alteration.

**Introduction**

The conservation status of an ecosystem depends mainly on its integrity (Caniani et al., 2016). Environmental integrity and its functional ecological processes are under serious threat from habitat fragmentation and other anthropogenic impacts (Haddad et al., 2015; Caniani et al., 2016). The current scenario is a landscape composed of fragments with varying degrees of human intervention, including remnants of the original vegetation and crop fields (Madeira et al. 2016). Human intervention may change communities structure and composition, affect the identity and strength of interactions between species (Tylianakis et al. 2006), limit the dispersion of animals that depend on the original habitat and confine them to fragmented remnants of natural vegetation (Giubbina et al., 2018) potentially resulting in changes in interaction network structure (Tylianakis et al. 2006).

Arthropods are the ones most affected by environmental fragmentation, especially those that act as natural enemies in food webs (Grab et al., 2018). Solitary bees and wasps are essential components of arthropod communities and are good models for environmental impact studies (Tscharrntke et al., 1998). These insects provide ecological services by acting as pollinators or natural enemies, directly responsible for crop pollination and biological control herbivores (Batra, 1984; O'Neill, 2001; Hoehn et al., 2008). The action of natural enemies is essential in maintaining ecosystem balance through an intense regulatory effect on the abundance of herbivorous insects (Sanders et al., 2018; Vidal and Murphy, 2018). The study of the effects of natural enemies as regulators allows us to understand the dynamics involved in multitrophic networks (Robinson et al., 2017), plant-pollinator and host-natural enemy interactions (Penczykowski et al., 2016). The understanding of these dynamics may grant access to the status of an ecosystem, by the assessment of interaction networks structure (Pocock et al., 2016).

Host-natural enemy interactions have their importance for the assessment of ecological networks structure, as organisms with parasitic habits act as connectors of trophic webs (Lafferty et al., 2006). Interaction networks allow us to find relevant information such as interconnected species diversity, the way the interactions between species are structured and the stability of these interactions (Pocock et al., 2016). The metrics commonly analysed in interaction network studies are nestedness (sensu Joppa et al. 2010), modularity (sensu Tylianakis et al., 2010) and

specialization degree (sensu Blüthgen *et al.* 2006). These metrics relate to network structure and, therefore, to which species are most vulnerable to eventual impacts that may occur (Bascompte *et al.*, 2006). The degree of specialization or generalization an interaction network reflects the number of connections that a node has (i.e., host and natural enemies species, in this work) and/or the ability of the connected species to establish the interaction (Pocock *et al.*, 2016).

Host-natural enemy interaction networks tend to be specialized and modular (Bellay *et al.*, 2015; Bellay *et al.*, 2018). Some studies with natural environments show evidence for these patterns. For example, interaction networks between marine fishes and their metazoan parasites present high degrees of specialization of the host-parasite interactions and consequently, higher degrees of modularity (Bellay *et al.*, 2011). Studies in altered environments, however, present different patterns, finding networks with more generalized patterns (Matos *et al.*, 2012; Stangler *et al.*, 2015). Studies with solitary bees and wasps had also presented evidence for specialized patterns (Lima *et al.*, 2018; Rocha-Filho *et al.*, 2019). These networks, when occurring in natural environments, are composed by fewer species and modules (Vázquez *et al.*, 2005).

In addition to the analysis of interaction networks, the diversity indexes are commonly used to verify environmental quality. Areas with few species tend to have lower diversity indexes (i.e., Shannon index) (Lima *et al.*, 2018). On the other hand, areas with generalist species support a higher number of species and consequently higher diversity index values as evidenced in mutualistic networks (Encinas-Viso *et al.*, 2012). Meanwhile, simplified areas (i.e., monocultures) have less species and low diversity indexes (Tylianakis *et al.*, 2006). Therefore, the structure of the network depends on the interaction type and environmental complexity, among other factors (Bellay *et al.*, 2018).

Here we analysed host-natural enemies interaction network in a community of solitary bees and wasps in a fragmented landscape composed of a *Eucalyptus* plantation (considered here as higher anthropic perturbation), a Cerrado area (medium perturbation) and a Riparian forest (lesser perturbation). Once disturbed areas such as monoculture areas usually have a lower environmental complexity (i.e., a measure anthropic impact level), it was expected that networks associated with simplified areas (e.g., *Eucalyptus* plantation) would reflect the degree of human interference, showing lower diversity and lower degrees of network specialization, as generalist species are generally more resistant to environmental change. On the other hand, natural environments (e.g., Cerrado and Riparian forest areas) tend to maintain the integrity of interactions, in this case, highly specialized host-natural enemy interactions. Hence, we aimed to address whether there is a difference in species composition and diversity of natural enemies' species between areas with different levels of human impact and whether such impact results in networks with different structures in a solitary hymenopteran community.

### Study site

Fieldwork was conducted in an area under restoration located in Sao Carlos, SP, where three fragments could be found: (i) a fragment of Cerrado (−21.972904, −47.881649); (ii) a fragment with *Eucalyptus* plantation (−21.969998, −47.875637); and (iii) a fragment of Riparian forest along the Espiraído stream (−21.980915, −47.873918). The Cerrado and Riparian forest areas are fragments of secondary vegetation that had been through restoration process for some decades. We selected three sites, each of

them inside one of each fragment, with one kilometre apart from each other, where we placed trap nests, assuming a gradient of impact level: (i) a Cerrado fragment (−21.972904, −47.881649), with a record of conservation measures; (ii) a riparian forest (−21.980915, −47.873918), a small fragment with a stream and surrounding dense vegetation; (iii) an abandoned *Eucalyptus* plantation (−21.969998, −47.875637), where some Cerrado plants begin to grow. The climate of the region varies from tropical wet and dry to humid subtropical according to Köppen's system, and the vegetation consists predominantly of Cerrado, semi-deciduous and riparian forests, with regeneration areas (Soares *et al.* 2003). Data on mean monthly temperature and rainfall were obtained from the São Carlos Station (OMM code: 86845, 'Instituto Nacional de Meteorologia' – <http://www.inmet.gov.br/portal/>).

### Methods

In each site, we set trap nests for hymenopterans that nest in pre-existing cavities (Westerfelt *et al.*, 2015). Each trap consisted of four trunks of similar size, arranged on a 1.5m wide wooden platform. Each trunk had 34 holes of a given diameter (4, 6, 8 or 10 mm), totalling 136 cavities in each site (Fig 1). The trap nests were made of black cardboard (MacIvor, 2017). Pieces of about 10 cm long were wrapped into tubes of 4, 6, 8 and 10 mm in diameter and inserted into holes drilled in trunks. The nests were examined biweekly, from October 2017 to October 2018. The occupied nests were removed and replaced with new cardboard tubes of the same diameter.

### Material examined

The collected nests were brought to the laboratory, stored in transparent glass tubes plugged with cotton and maintained under controlled temperature ( $28 \pm 2^\circ\text{C}$ ), (Gazola and Garofalo, 2009). The nests were observed daily, and emerged adults were collected and euthanized in absolute ethanol. All animals were deposited as vouchers in the Laboratory of Ecological Studies on Ethology and Evolution (LESTES) at the Federal University of São Carlos, Brazil. The material was identified with the aid of a magnifying stereomicroscope Leica MZ95 and consolidated identification keys for each group (Fernández and Sharkey, 2006), as well as expert help for some of the species collected.

### Data analysis

To address whether there is a difference in species composition and diversity between the sampled sites, we built a matrix with the abundance of each species of natural enemies for each area and used the Past 3.21 software (Hammer *et al.*, 2001) to calculate the Shannon-Winner index (H') (Poole, 1974) in a paired t-test to verify if there is a significant difference between index values among areas (Hutcheson, 1970). The host species were not included in these analyses because the diversity of natural enemies is determined by host diversity, which could generate collinearity of data and a false predictive power (Gazola and Garofalo, 2009; Lima *et al.*, 2018). Since species diversity affects coexistence and, consequently, trophic interactions among them (Kéfi *et al.* 2016; Ohlmann *et al.* 2019), in this study we consider the relevance of a diversity index to better compare the networks built.

To verify the structure of the interaction network host-natural enemies, we built three matrices of weighted adjacency containing the amount of host cells parasitized by each natural enemy, one

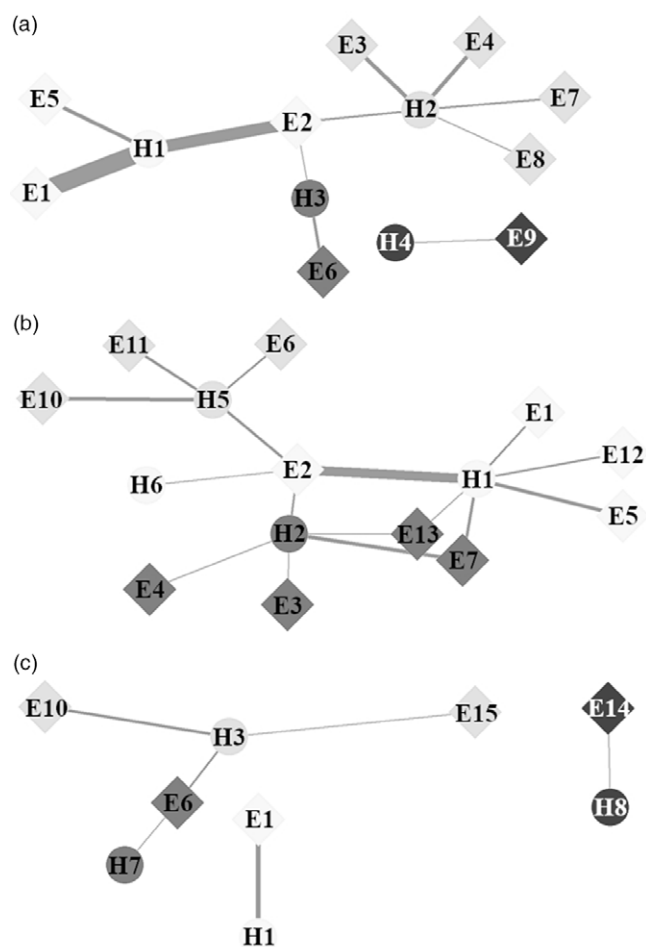
matrix for each study site. Hence, we calculated the degree of network specialization, the degree of nestedness and the modularity. The degree of network specialization ( $H_2'$  index) is a two-dimensional measurement ranging from 0 (extreme generalization) to 1 (extreme specialization) (*sensu* Blüthgen et al., 2006). We estimated the significance of this index using the Monte Carlo procedure with null model for 1,000 randomizations. These analyses were performed using the bipartite package (Dormann et al., 2008) of the R 3.5.1 software (R Core Team, 2018). To verify the presence of nestedness in the networks, we used the NODF index (*Nestedness metric based on Overlap and Decreasing Fill* – Almeida-Neto et al., 2008) using incidence matrices (presence and absence). This index ranges from 0 (no nestedness) to 100 (perfect nestedness). We estimated the significance of NODF index using the Monte Carlo procedure with 1,000 randomizations to the null model  $C_e$ , which keeps the total value of fixed lines during randomizations (see Guimarães and Guimarães, 2006). We used the software ANINHADO 3.0 (Guimarães and Guimarães, 2006) to address the NODF values and their significance. We calculated modularity of the networks using the ComputeModules from the bipartite package of the R 3.5.1 software, which uses a QuanBioMo (Q) algorithm for quantitative data matrices (*sensu* Dormann and Strauss, 2014). We tested the modularity through null models with 1,000 randomizations using R2d method, generating ZQ values equivalent to the z score of a normal distribution. ZQ values above 2.0 represent significant modularity (*sensu* Dormann and Strauss 2014). The modules formed in this analysis were represented in the network by using different shades in a greyscale.

We use additional metrics to verify species specialization inside interaction networks. From the three matrices, we calculated the degree of specialization ( $d'$  index) of the parasitoid species using the package bipartite of the R 3.5.1 program. The index  $d'$  is a measure of the normalized Kullback-Leibler distance measuring the specialization of a sort based on the frequency of the total number of network interactions. According to Blüthgen et al. (2006), this index ranges from 0 to 1, indicating extremely generalization and specialization, respectively. The strength of an interaction (i.e., the frequency that natural enemies parasitize hosts; prevalence of natural enemies) is indicated by graphic representations, where the force is indicated by the thickness of lines between taxa (Berlow et al., 2004).

## Results

In total, 1,586 individuals emerged from 234 trap nests collected. There was emergence of natural enemies in 80 of these nests, which were used in the present study. We sampled 15 species of natural enemies distributed among 12 families and five different insect orders, which were Coleoptera, Diptera, Neuroptera, Lepidoptera and Hymenoptera. We sampled natural enemies of Apidae, Chrysididae, Eulophidae, Gasteruptionidae, Ichneumonidae, Leucospidae, Megachilidae and Mutillidae. For each sampled area, four different host species have been identified. In all cases where there was parasitism, it was possible to determine the host and the number of affected cells. In the *Eucalyptus* site, we found 11 species of natural enemies in 44 trap nests, while we sampled nine species of natural enemies in 33 nests and five species of natural enemies in ten trap nests, in Cerrado and the Riparian forest, respectively (see Appendices Table 1).

The diversity indexes found were 2.07 for *Eucalyptus* plantation, 1.75 for the Cerrado fragment and 1.44 for the riparian forest,



**Figure 1.** Representation of interaction network obtained to (a) Cerrado fragment, (b) *Eucalyptus* plantation and (c) Riparian forest. The modules are represented by different shades in a greyscale. The thickness of edges represents quantity of interaction between the species. Natural enemies are represented by square nodes and hosts by circle nodes. For a list with the codes used in the networks, please see Appendices Table 2.

and there is difference only between the index values for *Eucalyptus* plantation and riparian forest sites (t-test,  $t = 2.83$ ,  $df = 27.168$ ;  $p = 0.01$ ). The values of diversity indexes between Cerrado and *Eucalyptus*, and Cerrado and Riparian forest were not different (t-test,  $t = -1.82$ ,  $df = 99.209$ ;  $p = 0.07$  and t-test,  $t = 1.38$ ,  $df = 26.513$ ;  $p = 0.18$ , respectively).

The three networks of interactions evaluated were modular and non-nested, showing high degrees of specialization ( $H_2'$ ) to Cerrado and Riparian forest (Table 1). We construct a graphic representation showing the strength of the interactions between the host and its natural enemy (Figure 1).

The degree of species specialization ( $d'$  index) calculated for each natural enemy in each of the areas is shown in Table 2. The riparian forest had two species with maximum specialization degree ( $d' = 1.00$ ). The Cerrado fragment had four species with specialization degree higher than ( $d' = 0.5$ ), one of them with maximum degree. The *Eucalyptus* plantation had lower values of specialization degree, with the higher value found being ( $d' = 0.54$ ). The natural enemy *Chrysis* sp. (Hymenoptera: Chrysididae) has a higher degree of specialization in *Trypoxylon* sp2 (Hymenoptera: Crabronidae) in the area of Cerrado ( $d' = 0.75$ ). In *Eucalyptus* plantation area, the higher degree of specialization occurs

**Table 1.** Nestedness (NODF), modularity with interaction strengths (Q) with z-score values (zQ), number of modules (Mod), degree of network specialization ( $H_2'$ ) calculated to natural enemies in a fragment of Cerrado in restoration, a *Eucalyptus* plantation and a Riparian forest, sampled between October 2017 and October 2018, in São Carlos, SP, Brazil.

Metrics	<i>Eucalyptus</i> plantation	Cerrado area	Riparian forest
Specialization degree ( $H_2'$ )	0,47*	0,80*	1,00*
Nestedness (NODF)	16,09 <sup>NS</sup>	9,62 <sup>NS</sup>	15,51 <sup>NS</sup>
Number of modules	3	4	4
Modularity (Q)	0,40*	0,40*	0,53*
Z-score of modularity ( $Z_Q$ )	4,53	7,30	3,94

Meaning values to \*p<0,05 and <sup>NS</sup> to non-significant values.

**Table 2.** Specialization degrees ( $d'$ ) of natural enemies sampled at three spots in São Carlos, SP, Brazil, between October 2017 to October 2018. Values higher than ( $d' = 0.5$ ) are bolded.

Natural enemies	<i>Eucalyptus</i> plantation	Cerrado fragment	Riparian forest
<i>Anthrax</i> sp1	0.05	0.04	–
<i>Anthrax</i> sp2	0.14	–	–
<i>Anthrax</i> sp3	–	0.28	–
<i>Chrysis</i> sp.	0.36	<b>0.90</b>	0.42
<i>Coelioxoides</i> sp.	0.14	0.37	<b>1.00</b>
<i>Coelioxys</i> sp.	0.29	<b>0.53</b>	–
<i>Ephestia</i> sp.	0.27	0.39	–
Eulophidae	<b>0.54</b>	–	0.45
<i>Gasteruption</i> sp.	–	<b>1.00</b>	–
Ichneumonidae	–	–	<b>1.00</b>
<i>Leucospis</i> sp.	0.05	–	–
<i>Mesochora</i> sp.	0.29	<b>0.53</b>	–
<i>Nemognatha</i> sp.	0.28	0.12	–
<i>Plega</i> sp.	–	–	0.00
<i>Sphaerophthalma</i> sp.	0.47	–	–

between *Anthrax* sp1 (Diptera: Bombyliidae) and Anthidiini bees (Hymenoptera: Megachilidae) ( $d' = 1.00$ ). The interactions observed in the riparian forest, the maximum value of dependence ( $d' = 1.00$ ), was observed in the interactions between *Coelioxoides* sp. (Hymenoptera: Apidae) and *Tetrapedia diversipes* Klug (Hymenoptera: Apidae), *Chrysis* sp. (Hymenoptera: Chrysididae) and *Pseudodynerus* sp (Hymenoptera: Vespidae) and between Ichneumonidae and *Zethus* sp. (Hymenoptera: Vespidae).

## Discussion

Our results partially corroborate our initial hypothesis. We show the area with higher human interference, a *Eucalyptus* plantation, had higher values of diversity of natural enemies, greater number of species in the interaction network, lesser degree of specialization

in the interaction and lesser modularity, than Cerrado and Riparian forest environments, respectively. Thus, the gradient from highest to lowest degree of anthropic perturbation was evidenced in the species diversity index, the size of the interaction network and the specialization indexes of the host-natural enemy network. The low degree of nestedness and lack of significance of this index to all the three sampled areas is an indicative of a specialized pattern of these networks.

Recent research has shown that networks involving hosts and parasites have high specialization indexes (Pereira-Peixoto *et al.* 2016; Araújo *et al.*, 2018; Lima *et al.*, 2018). This pattern is due to the nature of these interactions, which involves specific mutual adaptations because of coevolution between these organisms (Gómez *et al.*, 2015). Here, the specialist pattern was evidenced in all sampled areas. In this case, there was either a lack of nestedness or values of specialization that range from medium values (0.47 in the *Eucalyptus* plantation) to 1.0 in the riparian forest. The medium values of specialization of the network found for the *Eucalyptus* plantation can be related to the specialization degree of the species involved. Most of the diversity (10 out of 11 species) presented a tendency of generalization, with  $d'$  values under 0.5. Generalization favours interactions between species and contributes to a higher diversity (Vázquez *et al.* 2005), represented here by Shannon index, which was higher in the *Eucalyptus* plantation. Generalist species are less sensitive to land use (Holzschuh *et al.*, 2010) and thus are more likely to survive in less structured habitats (e.g., monocultures) (Pereira-Peixoto *et al.*, 2016). Therefore, higher values of species diversity of natural enemies found in the *Eucalyptus* plantation may reflect a generalization of the interactions established between the hosts and parasitoids and not necessarily anthropogenic impact.

On the other hand, the areas of Cerrado and riparian forest (i.e., lower anthropic impact) presented lower species diversity of natural enemies, but higher values of specialization of networks and species. Moreover, networks also exhibited more interaction modules. These areas may have higher structural complexity of the habitat – places with higher amount and diversity of niches. The complexity of an environment is positively correlated with the niche diversity (Mougi and Kondoh 2016), contributing to species diversity (Tylianakis *et al.*, 2006). Nevertheless, one must consider that environmental complexity must primarily favour the host when assessing host-parasite interactions, because parasitism depends on host diversity (Lagrange e Poulin, 2015).

In the Cerrado area, *Chrysis* (Hymenoptera: Chrysididae) and *Coelioxys* (Hymenoptera: Megachilidae) species presented higher specialization index ( $d'$ ) among hosts. Several authors showed that cleptoparasitoid *Coelioxoides* (Hymenoptera: Apidae) usually steal nests from related lineages, such as *Tetrapedia diversipes* Klug, 1810 (Hymenoptera: Apidae) (Araújo *et al.*, 2016; Rocha-Filho *et al.*, 2017; Lima *et al.*, 2018). In this study, flies of the genus *Anthrax* (Diptera: Bombyliidae) presented lower values of specialization, which agrees with the literature concerning this natural enemy (Krombein, 1967; Gazola and Garófalo, 2009; Mesquita and Augusto, 2011). *Tetrapedia diversipes* and *Centris analis* (Fabricius, 1804) (Hymenoptera: Apidae) bees registered the higher rates of parasitism. This was probably consequence of the higher abundance of nests built by these host species. These organisms are commonly found in higher abundance in studies with trap nests (Alves-dos-Santos, 2003; Buschini and Wolff, 2006; Gazola and Garófalo, 2009; Araújo *et al.*, 2016; Araújo *et al.*, 2018).

All these aspects demonstrate the complexity of host-parasite interactions and ecological interactions. Land use and

anthropogenic impact also affect diversity and abundance of trap nesting insects (Albrecht et al., 2007). These impacts may negatively influence trophic interactions (e.g., parasitism), even more intensely in fragmented and isolated fragments (Klein et al., 2006). To assess these interactions in the context of conservation demands a macrovision of ecological communities and a microvision of natural history of the species involved in the connections. In other words, the task of interpreting the results of network analyses with metrics is even more meticulous.

## Conclusion

In conclusion, this study showed the complexity of the ecological interactions in a fragmented landscape, through building and analysis of host-natural enemy interaction networks. The sampled area constitutes a region with fragments in recent process of restoration. This history can be determinant to the diversity of solitary wasps and bees sampled and the ways they explore resources, being generalists or specialists. Therefore, the history of land use and the fragmentation process must be accounted for in areas with distinct gradients of anthropogenic impacts to more precisely understand its effects.

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## Appendices

**Table 1.** Natural enemies and their hosts, sampled in trap nests collected between October 2017 and October 2018 in three areas of São Carlos, SP. NN is Number of Nests and NC is Number of Cells.

Natural enemies	Hosts	Eucalyptus plantation		Cerrado area		Riparian forest		Total		
		NN	NC	NN	NC	NN	NC	NN	NC	
Coleoptera (Meloidae)	<i>Nemognatha</i> sp.	<i>Tetrapedia diversipes</i> Klug, 1810	4	4	4	4	0	0	8	8
Diptera (Bombyliidae)	<i>Anthrax</i> sp1	Anthidiini	1	1	0	0	0	0	1	1
		<i>Centris analis</i> (Fabricius, 1804)	2	2	2	2	0	0	4	4
		<i>T. diversipes</i>	8	10	11	13	0	0	19	23
		<i>Trypoxylon</i> sp1	3	3	0	0	0	0	3	3
		<i>Trypoxylon</i> sp2	0	0	1	1	0	0	1	1
		<i>Anthrax</i> sp2	<i>T. diversipes</i>	1	2	0	0	0	0	1
	<i>Anthrax</i> sp3	<i>C. analis</i>	0	0	1	1	0	0	1	1
Hymenoptera (Apidae)	<i>Coelioxoides</i> sp.	<i>T. diversipes</i>	2	2	15	19	4	5	21	26
	<i>Mesochora</i> sp.	<i>C. analis</i>	1	1	4	4	0	0	5	5
Hymenoptera (Chalcidoidea)*	Eulophidae	<i>Trypoxylon lactitarse</i> Saussure, 1867	1	4	0	0	0	0	1	4
		<i>Trypoxylon</i> sp2	0	0	0	0	2	3	2	3
Hymenoptera (Chrysididae)	<i>Chrysis</i> sp.	<i>Pseudodynerus</i> sp2	0	0	0	0	1	1	1	1
		<i>Trypoxylon</i> sp1	2	2	0	0	0	0	2	2
		<i>Trypoxylon</i> sp2	0	0	2	3	1	2	3	5
Hymenoptera (Gasteruptiidae)	<i>Gasteruption</i> sp.	<i>Pseudodynerus</i> sp1	0	0	1	1	0	0	1	1
Hymenoptera (Ichneumonoidea)	Ichneumonidae	<i>Zethus</i> sp.	0	0	0	0	1	1	1	1
Hymenoptera (Leucospidae)	<i>Leucospis</i> sp.	<i>C. analis</i>	1	1	0	0	0	0	1	1
		<i>T. diversipes</i>	1	1	0	0	0	0	1	1
Hymenoptera (Megachilidae)	<i>Coelioxys</i> sp.	<i>C. analis</i>	1	1	2	4	0	0	3	5
Hymenoptera (Mutillidae)	<i>Sphaerophthalma</i> sp.	<i>Trypoxylon</i> sp1	1	3	0	0	0	0	1	3
Lepidoptera (Pyralidae)*	<i>Ephestia</i> sp.	<i>C. analis</i>	2	4	1	2	0	0	3	6
		<i>T. diversipes</i>	2	3	0	0	0	0	2	3
Neuroptera (Mantispidae)	<i>Plega</i> sp.	<i>Trypoxylon</i> sp2	0	0	0	0	1	1	1	1
<b>TOTAL</b>			<b>33</b>	<b>44</b>	<b>44</b>	<b>54</b>	<b>10</b>	<b>13</b>	<b>87</b>	<b>111</b>

**Table 2.** List of codes to identify species in the network representations.

Natural Enemies	Codes	Hosts	Codes
<i>Coelioxoides</i> sp.	E1	<i>Tetrapedia diversipes</i>	H1
<i>Anthrax</i> sp1	E2	<i>Centris analis</i>	H2
<i>Coelioxys</i> sp.	E3	<i>Trypoxylon</i> sp2	H3
<i>Mesochaira</i> sp.	E4	<i>Pseudodynerus</i> sp1	H4
<i>Nemognatha</i> sp.	E5	<i>Trypoxylon lactitarse</i>	H5
<i>Chrysis</i> sp.	E6	Anthidiini	H6
<i>Ephestia</i> sp.	E7	<i>Pseudodynerus</i> sp2	H7
<i>Anthrax</i> sp3	E8	<i>Zethus</i> sp.	H8
<i>Gasteruption</i> sp.	E9		
Eulophidae	E10		
<i>Sphaerophthalma</i> sp.	E11		
<i>Anthrax</i> sp2	E12		
<i>Leucospis</i> sp.	E13		
Ichneumonidae	E14		
<i>Plega</i> sp.	E15		