

Original paper

Antagonistic interaction networks in a native and an exotic legume species in Colombian tropical dry forest

Redes de interacción antagonística en una especie de leguminos nativa y una exótica en el bosque seco tropical colombiano

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ABSTRACT. Plant-animal interactions play a fundamental role in ecosystem functioning and structure. Seed-associated insect communities are expected to be very specific for each plant species due to the large amount of physical and chemical barriers plants impose on the herbivores. In addition, leguminous species, the dominant plant group in the tropical dry forest (TDF), offer a large quantity of resources for insect specialization, structuring specialist communities of herbivorous and parasitoids. However, the introduction of exotic species to TDF may alter the insect associated communities by diminishing diversity and simplifying interactions. By using ecological network analysis, we compared the diversity and structure of the insects associated with seeds and parasitoids of the native leguminous species *Pseudosamanea guachapele* (Kunth) Harms and the exotic and invasive leguminous *Leucaena leucocephala* (Lam.) de Wit. We also evaluated differences in seed chemistry between these species in order to determine to what extent this could help to explain differences in associated insect communities. The study was carried out in a tropical dry forest remnant in the department of Tolima, Colombia. We found seven species of herbivores and eight species of parasitoid



insects. The insect interaction networks from both species of plants had low connectance, nestedness, generality, and vulnerability. *Leucaena leucocephala* had the greatest diversity of herbivores and parasitoid insects compared to *P. guachapele*, perhaps because *Leucaena leucocephala* produces seeds all year around, while *P. guachapele* has marked seasonality, producing fruits only during one or two months of the year. We identified a total of 26 compounds in the seeds of the two hosts. Seeds of *P. guachapele* have twice the number of compounds than those of *Leucaena leucocephala*. Among the main differences between the composition of the host plant seeds are the fatty acids that offer different sources of cholesterol for insect development. It may help to explain the presence of species of seed feeders associated with each plant. It is important to notice that the networks described here may change across time and landscapes, making it interesting to continue analyzing the variation in richness and structure of such networks in order to define the extent to which the interactions found in this study remain constant.

Key words: ecological networks; bruchids; parasitoids; alien invasive species; legumes

RESUMEN. Las interacciones entre plantas y animales desempeñan un papel fundamental en el funcionamiento y la estructura de los ecosistemas. Se espera que las comunidades de insectos asociados a semillas sean muy específicas para cada especie de planta debido a la gran cantidad de barreras físicas y químicas que las semillas imponen a los herbívoros. Además, las especies leguminosas, el taxón vegetal dominante en el bosque seco tropical, ofrecen una gran cantidad de recursos para la especialización de insectos, estructurando comunidades especializadas de herbívoros. Sin embargo, la introducción de especies exóticas en este ecosistema puede reducir la diversidad y simplificar las interacciones. Mediante el análisis de redes ecológicas, comparamos la diversidad y estructura de los insectos asociados a las semillas y sus parasitoides entre la especie de leguminosa nativa *Pseudosamanea guachapele* y la leguminosa exótica e invasora *Leucaena leucocephala*. También evaluamos las diferencias en la composición química de semillas con el fin de determinar en qué medida ésta podría ayudar a explicar las diferencias en las comunidades de insectos asociadas. El estudio se llevó a cabo en un bosque seco tropical en el departamento de Tolima, Colombia. Encontramos siete especies de escarabajos y ocho especies de parasitoides. Las redes de interacción de insectos de ambas especies de plantas tenían baja conectividad, anidamiento, generalidad y vulnerabilidad. *Leucaena leucocephala* tuvo la mayor diversidad de escarabajos y parasitoides en comparación con *P. guachapele*, tal vez porque *L. leucocephala* produce semillas durante todo el año, mientras que *P. guachapele* tiene una estacionalidad marcada produciendo frutos sólo durante uno o dos meses del año. Identificamos un total de 26 compuestos en las semillas de los dos huéspedes. Las semillas de *P. guachapele*, tienen el doble de compuestos que las de *L. leucocephala*. Entre las principales diferencias entre la composición de las semillas de la planta hospedera se encuentran la composición de ácidos grasos, que ofrecen diferentes fuentes de colesterol para el desarrollo de insectos. Esto puede ayudar a explicar la presencia de especies de consumidores de semillas asociadas a cada planta. Es importante resaltar que las redes descritas aquí pueden cambiar a través del tiempo y los paisajes, haciendo interesante seguir analizando la variación en la riqueza y estructura de dichas redes con el fin de definir hasta qué punto las interacciones encontradas en este estudio se mantienen constantes.

Palabras clave: redes ecológicas; bruquidos; parasitoides; especies invasoras; leguminosas

INTRODUCTION

Changes in the abundance and richness of species may affect the type and intensity of animal-plant interactions and may have cascading effects on the functioning of ecosystems (Ings *et al.*, 2009; Barbour *et al.*, 2016). Among the diversity of interactions, seed consumption by insects is the largest cause of plant mortality (Nurse *et al.*, 2003; Nakagawa *et al.*, 2005). Seed consumers reduce the quality and quantity of seeds produced by plants (Louda *et al.*, 1990; Johnson *et al.*, 2004). Nevertheless, in some cases when beetles do not affect the embryo, they may increase the viability of the seeds through mechanical scarification. These insects develop in the seeds leaving holes that facilitate the entry of water (Fox *et al.*, 2010; Sanabria-Silva & Amarillo-Suárez, 2017). The seeds impose a strong evolutionary barrier for many insects because they are hard, have very little water content, have diverse chemical composition, as well as a great suite of secondary compounds (Amarillo-Suárez *et al.*, 2017). In this way, seed-associated insect communities are expected to be very specific for each plant species.

Legumes are the dominant plant taxon in the tropical dry forest, offering a large amount of resources for insect specialization (Pizano & García, 2014). Hymenopteran parasitoids represent about 50% of the structure of the trophic networks in nature (Lasalle & Gauld, 1991). These interactions may be affected by several anthropogenic factors (Armbrecht, 1995; Didham *et al.*, 1998; Hendrickx *et al.*, 2007; González *et al.*, 2015). Exotic species have a negative effect on the structure of interactions by, for example, increasing competition for resources with the native species (Didham *et al.*, 2007), deviating natural generalist enemies of herbivores from native to exotic species that in turn increase herbivore abundance in the native species (Montero-Castaño & Vila, 2012). The introduction of exotic species can also affect the abundance of herbivores and therefore the abundance of their predators (Tallamy, 2004). Species that are generalists prefer to attack species (Parker & Hay, 2005), in consequence affecting the interaction networks (Sanabria-Silva & Amarillo-Suárez, 2017). In this study we compared the herbivores-parasitoid antagonist networks associated with two legume species the native *Pseudosmanaea guachapele* (Kunth) Harms, and the exotic and invasive *Leucaena leucocephala* (Lam.) de Wit, one of the 100 most invasive species in the world (Lowe *et al.*, 2004) and in Colombia (Baptiste *et al.*, 2010). The study took place in an area of tropical dry forest in Tolima, Colombia. We also compared the chemical composition of seeds in these two leguminous plants in order to establish possible relationships in the chemistry of the seeds and the community of insects associated with each species of legume.

MATERIALS AND METHODS

Study organisms. *Pseudosamanea guachapele*, Fabaceae is a Colombian native species that reaches 25 meters in height and one meter in trunk diameter. Its canopy is broad and has the shape of an umbrella. The tree produces white, hard seeds about ten mm long and five mm wide (Geilfus, 1989), and this species of tree is found in warm, temperate regions. In Colombia, the species is distributed in the Magdalena and Cauca River Valleys, the Atlantic coast, and in the watersheds of the Orinoco and Catatumbo rivers between sea level and 1,500 masl (Mahecha-Vega *et al.*, 2012). This tree species has been found in ecosystems of tropical dry forest, tropical wet forest, and pre-montane wet forest. Usually, the tree's wood is used as firewood. This species

is also used to provide shade for crops such as cocoa, coffee and for livestock; and it is ideal for restoration of mature forests (CorAntioquia, 2008).

Leucaena leucocephala, Fabaceae is native to Central América and is considered an exotic invasive species in Colombia. The species is considered one of the 100 most harmful exotic invasive species worldwide (Lowe *et al.*, 2004). It reaches 15 m in height and about 80 cm in diameter and develops brown seeds of 8 mm long by 5 mm wide (Mahecha-Vega *et al.*, 2012). In Colombia the tree is located in warm and temperate areas from sea level to 1,300 meters in ecosystems such as tropical dry forest and tropical humid forest. It is broadly used in soil recovery and control of erosion and is also used as a living fence (Mahecha-Vega *et al.*, 2012).

Data collection, experimental design and analyses. Sampling was carried out in the department of Tolima, Colombia during April 2015 the beginning of the dry season when we found the largest number of seeds available for the native *P. guachapele*. *Leucaena leucocephala* produce seeds all year around (senior author, personal observation for more than ten years). We collected seeds from *L. leucocephala* at 4° 15' N, 74° 44' W and from *P. guachapele* at 4° 15' N, 74° 37' W. From each tree species we collected mature seed pods (ten trees of *P. guachapele* and 20 trees of *L. leucocephala*) according to seed availability and from branches located at the four cardinal directions. The number of bags with seeds collected from each tree varied between one and five. Mature seed pods from each tree were preserved in hermetic plastic bags with a capacity of 3.7 L. All seeds were transported and processed at the Evolutionary Ecology and Conservation Laboratory at Pontificia Universidad Javeriana, Bogotá, Colombia.

Once in the laboratory, all ripe seed pods were opened. Seeds were set up in labeled hermetic plastic containers in a growth chamber at 28°C and 70% RH. Containers were inspected every 24 h for organisms emerging from the seeds; and once emerged, they were preserved in 97% alcohol. Insects were identified to the lowest possible taxonomic level using the keys and books of Borror & White (1970), Udayagiri and Wadhi (1982), Jhonson (1990), Fernández and Sharkey (2006), Manfio and Ribeiro-Costa (2016), and with the help of parasitoid wasp taxonomist Dr. Carlos Sarmiento from Universidad Nacional de Colombia and Curculionidae taxonomist Dr. Robert Anderson from Canadian Museum of Nature.

To study the antagonistic interaction between herbivores insects and parasitoids in the exotic and native legume plants, we performed separate analyses for each host plant. We built two unweighted networks and calculated the following parameters for each one: (1) nestedness, a parameter that indicated whether a community was composed by subsets of generalist species interacting with each other, and specialist species interacting only with generalist species (Corzo *et al.*, 2011). Values of nestedness ranged from a 100% to 0%; 100% was a perfectly nested network in which subsets of specialists interacted with generalists (Fortuna *et al.*, 2010; Bascompte & Jordano, 2014); (2) connectance, defined as the proportion of interactions found in the network in relation to maximum potential interactions (Dunne *et al.*, 2002; Delmas *et al.*, 2019); (3) generality, which determined the average number of links of herbivorous per parasitoid (Blüthgen *et al.*, 2008); and (4) vulnerability, which estimated the average number of links of parasitoids per herbivore

(Blühten *et al.*, 2008). Networks were analyzed and plotted with the R program (R Development Core Team, 2013), bipartite package (Dormann *et al.*, 2014).

We built one herbivore-parasitoid network for each legume plant. Regarding the type of herbivores that feed on the seeds (seed feeder), no direct interaction could be established between parasitoid species and a particular species of seed feeder. This was because more than one species of seed feeder emerged from the seeds. Thus, we generated record-based relationships by consulting literature on the associations between these trophic guilds (Hetz & Jhonson, 1988; Hagstrum & Subramanyam, 2009; Wood *et al.*, 2016; Delgado-Machuca *et al.*, 2019; Morales-Silva *et al.*, 2019; Pérez-Benavides *et al.*, 2019).

Last, we analyzed the chemical composition of the seeds in order to determine the differences between species. The analysis of seeds was done according to the procedures described in detail by Amarillo *et al.* (2017). We used dry, clean seeds of *P. guachapele* and *L. leucocephala* with no evidence of insects developing in them. Differences in the composition of seeds were evaluated following the analyses proposed by Borges *et al.* (2008). We compared the abundance and type of chemical compounds between the two legume species with a Mann Whitney test. This analysis was performed with R software (R Development Core Team, 2013).

RESULTS

We collected a total of seven species of herbivores, all of them Coleoptera, and eight species of parasitoids, all of them Hymenoptera. Of this total, 85% of the herbivores and 100% of the parasitoid species were found in *L. leucocephala*, while 57% of the herbivorous and 87% of the parasitoid species were found in *P. guachapele* (Table 1). The seed feeding beetle *Merobruchus paquetae* (Kingsolver, 1980) was recently recorded emerging for the first time from seeds of the exotic legume *L. leucocephala* (Amarillo-Suárez & Camacho-Erazo, 2020). Two species of seed feeding beetles were exclusive to *P. guachapele*, and two were exclusive to *L. leucocephala*. Only one species of hymenopteran parasitoid was found in *L. leucocephala*. The remaining species of hymenopteran parasitoids were shared between the two networks (Table 1).

The interaction networks (Fig. 1) from both species had low connectance, nestedness, generality, and vulnerability. However, it is worth noting that the nestedness of the network in *L. leucocephala* was almost double than that in *P. guachapele* (Table 2).

We identified a total of 26 compounds in the seeds of the two hosts. The seeds of *P. guachapele* have twice as many compounds as those of *L. leucocephala* and the two species showed significant differences in chemical composition (Mann-Whitney U = 214.5, $p = 0.02$). Four steroid-type compounds, among which are campesterol, stigmasterol and gamma sitosterol (high concentration), were exclusive to *L. leucocephala*. Today those compounds are considered sources of cholesterol, which is essential to the growth and reproduction of insects (Behmer & Nes, 2003) and may additionally have an attractive effect on the bruchids found in the exotic species (Amarillo-Suarez & Camacho-Erazo, 2020). There were 16 compounds found in *P. guachapele*. The squalene, hexadecanoic acid, octadecanoic acid and some derivatives of the ester type compounds

found in the native species *P. guachapele* are mainly precursors of fatty acids and they are necessary in metabolism (Lozano-Grande et al., 2018) (Table 3).

Table 1. Arthropods associated with the seeds of two legume species: the native species *Pseudosamanea guachapele*, and the invasive species *Leucaena leucocephala* in an area of tropical dry forest in Colombia. The "x" represents the presence of the taxon in the seeds of the host plant.

Taxon	Trophic guild	Host	
		<i>L. leucocephala</i>	<i>P. guachapele</i>
Coleoptera			
Chrysomelidae			
<i>Merobruchus columbinus</i> (Sharp, 1885)	Seed feeder	x	x
<i>Acanthoscelides macrophthalmus</i> (Schaeffer, 1907)	Seed feeder	x	
<i>Merobruchus paquetae</i> (Kingsolver, 1980)	Seed feeder	x	
<i>Stator limbatus</i> (Horn, 1873)	Seed feeder		x
Curculionidae			
<i>Rhyssomatus</i> sp.	Seed feeder	x	x
Cucujidae			
Cucujidae sp.	Xylophagous	x	x
Cerambycidae			
Cerambycidae sp.	Xylophagous	x	
Hymenoptera			
Braconidae			
<i>Heterospilus</i> sp.	Parasitoid	x	x
<i>Stenocorse sudamericanus</i>	Parasitoid	x	x
Eulophidae			
<i>Horismenus</i> sp.	Parasitoid	x	x
Eurytomidae			
<i>Chryseida</i> sp.	Parasitoid	x	x
Eupelmidae			
<i>Eupelmus</i> sp.	Parasitoid	x	x
Ichneumonidae			
Ichneumonidae sp.	Parasitoid	x	
Bethylidae			
Bethylidae sp.	Parasitoid	x	x
Pteromalidae			
Pteromalidae sp.	Parasitoid	x	x

Table 2. Metrics of the ecological networks of arthropods associated with two legume hosts in an area of tropical dry forest in Colombia. Parasit. Parasitoid richness Herb. Herbivore richness, N. Nestedness, C. Connectance, V. Vulnerability, G. Generality.

	Parasit.	Herb.	N	C	V	G
<i>L. leucocephala</i>	8	6	34%	0,437	5,28	2,8
<i>P. guachapele</i>	7	4	18%	0,464	4,84	2,07

Table 3. Chemical compounds (%) found in the seeds of the two species *Pseudosamanea guachapele* and *Leucaena leucocephala*. RT, Retention Time.

Name of the Compound	RT	<i>P. guachapele</i>	<i>L. leucocephala</i>
Decane	3.46		0.21
Tetradecane	8.32	0.25	0.83
Hexadecane	10.73	0.31	1.02
Hexadecanoic Acid, Methyl Ester	14.21	0.23	0.15
Hexadecanoic Acid, Ethyl Ester	14.87	1.77	
9,12 Octadecadienoic Acid (Z,Z) -,Methyl Ester	15.83	0.78	0.16
9,12 Octadecadienoic Acid (Z,Z)	16.3		4.88
9,12 Octadecadienoic Acid (Z,Z) -,Ethyl Ester	16.45	33.17	
Octadecadienoic Acid	16.59	1.25	
Hexadienoic Acid Buthyl Ester	16.64	4.83	0.37
Isopropyl Linoleate	18.1	3.42	
Octadienoic Acid 2-Methylpropyl Ester	18.35	0.56	
Bacchotricuneatin C	18.44	0.29	
Tricosane	19.24	0.34	
2 -Methyl -Z,Z -3,13-Octadecadienol	19.6	0.15	
Hexacosane	20	0.24	
Nonadecane	20.47	0.13	
Heptacosane	20.75	1.34	
Squalene	21.71	0.36	
Nonacosane	22	1.18	
Nonadecane	22.38	1.27	
Beta Tocopherol	23.25	0.44	
Vitamin E	23.85	5.26	9.23
Campesterol	24.66		10.46
Stigmasterol	24.86		15.25
Gama Sitosterol	25.2	12.93	35.63

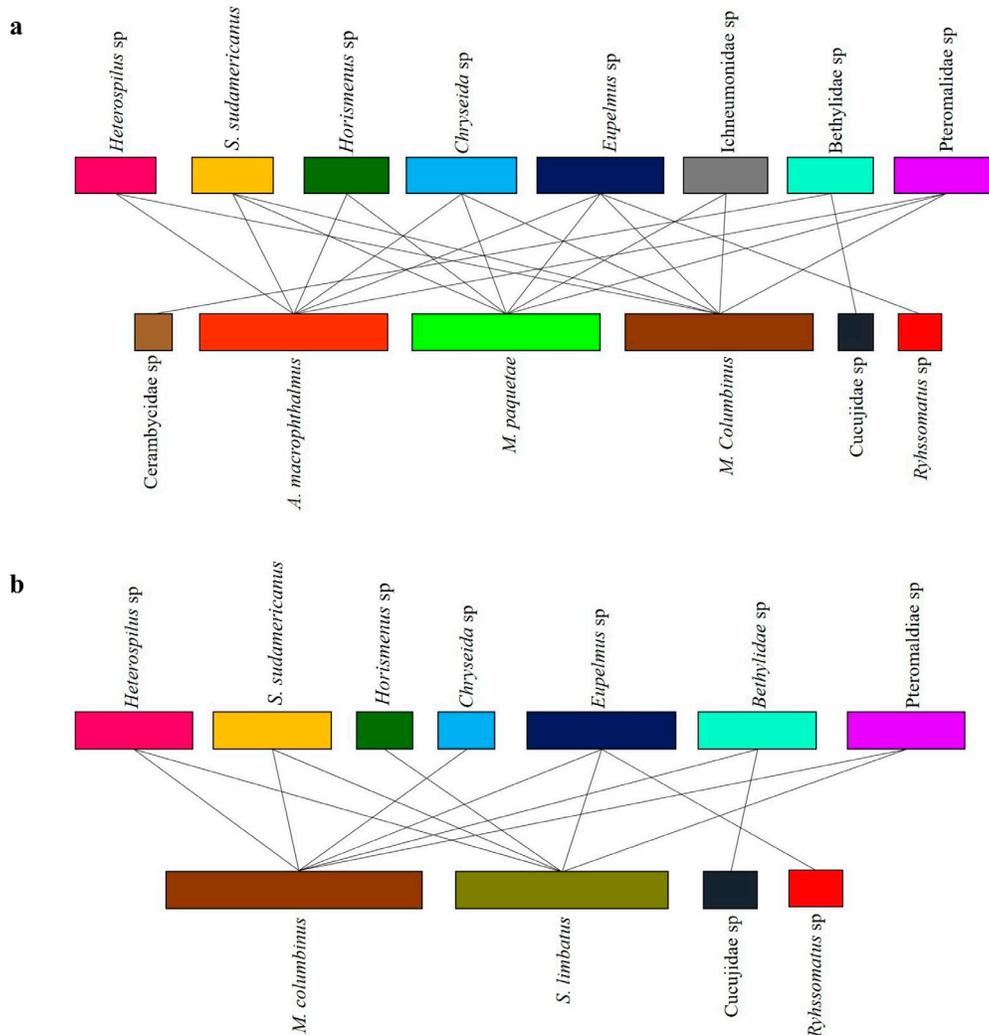


Figure 1. Antagonistic networks between herbivores and parasitoids associated with a) *L. leucocephala* and b) *P. guachapele*; each color represents a different species and the lines indicate the interaction between beetles and parasitoids.

DISCUSSION

This study compared the antagonist networks between seed-consumer beetles and parasitoids of a native and an exotic host species. Exotic species can cause negative effects on native species, such as increased competition and deviation of herbivorous and parasitoids from native species (Didham *et al.*, 2007). Parasitoid wasps exert top-down control over seed consumer communities (Cuevas-Reyes *et al.*, 2007). If these parasitoids move towards exotic plant species, the rate of seed consumer invasion in native plant species would increase; there will be no control over these communities and consequently there will be greater seed predation, thus generating a decrease in the reproductive capacity of native plant species (Maron & Crone, 2006; West, 2012).

Although, we found no significant differences in the diversity of herbivores ($X^2 = 0.5$; g. l. = 1; $p > 0.05$) and parasitoids ($X^2 = 0.13$; g. l. = 1; $p > 0.05$) between the two species of legumes, this

could be the case of the exotic species *L. leucocephala* that showed a greater diversity of herbivorous, and parasitoids compared to *P. guachapele*. Although we did not find a significant difference in the diversity of herbivores and parasitoids between the two species of legumes, the exotic species *L. leucocephala* showed higher diversity of herbivores and parasitoids compared to *P. guachapele*, perhaps because *L. leucocephala* produces seeds throughout the year (Grether *et al.*, 2006; Sharratt & Olckers, 2012) while *P. guachapele* is markedly seasonal and produces fruits only for one or two periods during the year (Senior author, personal observations for more than ten years). Seasonality affects the structure of the community of insects associated with legume seeds, since in one species it facilitates permanent access to the resources available, in this case, the seeds of the exotic species *L. leucocephala*. In the absence of *L. leucocephala*, seasonal fluctuations in richness and composition of arthropods associated with native legume seeds are expected to occur.

One assumes that more insects consuming *L. leucocephala* seeds would help to control the species expansion. However, previous studies on seed germination in this species show that in addition to the known harmful effects of seed-eating beetles, bruchids leave a hole at the time of adult emergence. The hole increases water retention by seeds; and in cases where the embryo is alive, the germination time decreases (Fox *et al.*, 2010; Sanabria-Silva & Amarillo-Suárez, 2017).

Acanthoscelides macrophthalmus (Schaeffer, 1907), a specialist bruchid of *L. leucocephala* with a distribution as extensive as its host plant, has been introduced in some places as a biological control agent of this leguminous plant (Sharratt & Olckers, 2012). However, evidence shows the efforts to control the exotic tree species are not sufficient (Tuda *et al.*, 2009). Thus, *L. leucocephala* remains among the 100 most invasive species worldwide (Lowe *et al.*, 2004) as well as in Colombia (Cardenas *et al.*, 2017). Breeding experiments conducted by Castro (2014) show that *A. macrophthalmus* cannot use the native legumes *P. guachapele*, *Senegalia riparia* (Kunth), *Parkinsonia aculeata* (L.) and *Acacia farnesiana* (L.) that are sympatric with *L. leucocephala* for its development. However, *L. leucocephala* has acquired new parasitoids of *A. macrophthalmus* such as *Stenocorse sudamericanus*. Recent phylogenetic studies show that there is more than one species of *Stenocorse*. *Stenocorse sudamericanus*, is only found in Colombia (Delgado-Machuca *et al.*, 2019; Zaldivar-Riverón *et al.*, 2019), and is a parasitoid of seed beetles that parasitizes native legume seeds such as *P. guachapele*, *S. riparia*, *Chloroleucon bogotense* Britton & Killip, and *A. farnesiana* (Amarillo-Suárez, 2010; Pizano & García, 2014; Sanabria-Silva & Amarillo-Suárez, 2017). Thus, the native parasitoid *Stenocorse sudamericanus* successfully managed to colonize an exotic species such as *L. leucocephala*.

With regard to interactional networks, the more diversity there is, there will be greater connection in the structure of the communities that promotes the persistence and resilience of networks (Sauve *et al.*, 2014). The intermediate values of connectance of our networks show that there is high stability in the communities of herbivores and parasitoids, since the dispersion of disturbances is limited (Kolchinsky *et al.*, 2015). However, it also means that a small proportion of possible links occurs (Dáttilo & Rico-Gray, 2018) generating simplified networks, given the low richness of interacting species (Table 2). In our case the dispersion of disturbances is limited due to the low species richness, thus generating simplified networks. We found that most parasitoid

species have more than one host insect, which explains the low levels of nestedness and suggests competition among the parasitoids that behave in both host plants as generalists. This could make the entire community more vulnerable, as supported by the values obtained in the vulnerability parameter of both networks (Dáttilo & Rico-Gray, 2018) (Table 3).

In addition, our networks are small and have low insect diversity because they are immersed in a remnant of tropical dry forest that has been used for livestock. Fragmentation generates cascading effects on the structure and stability of networks (Grass *et al.*, 2018). Thus, some network parameters are more sensitive to network size (Vanbergen *et al.*, 2017) since the vulnerability of having a small network with fewer herbivores per parasitoid. In our case we found the opposite, probably because the parasitoids we collected were generalist's species (Fernández & Sharkey, 2006). For metrics such as vulnerability and generality it is important to consider the size of the network since they are very sensitive to the absolute sampling effort; that is, the larger the network, the more that observations per species will decrease as the number of possible links or connectivity increases (Kenny & Loehle, 1991; Blüthgen *et al.*, 2008). In our case, we obtained low generality values, explained because we found fewer herbivores than parasitoids.

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Regarding the chemical composition of seeds, we found that the steroidal compounds campesterol, and stigmasterol are exclusive to *L. leucocephala*, and gamma sitosterol almost triplicates its concentration in *L. leucocephala*. These compounds are a source of cholesterol, an essential molecule for the development, growth, and reproduction of insects (Behmer & Nes, 2003). Cholesterol must be dealkylated in order to be used by insects in their metabolism (Behmer & Elias, 2000). *Pseudosamanea guachapele*, the native species, has other sources such as squalene and hexadecanoic acid, which makes the production of fatty acids for metabolism easier (Lozano-Grande *et al.*, 2018). Besides these large differences in chemical composition of seeds, it appears that it has effects on the specialist bruchids *A. macrophthalmus* and *M. paquetae* that only are found in seeds of *L. leucocephala* (Amarillo-Suarez & Camacho-Erazo, 2020), while the seed beetle *Stator limbatus* (Horn, 1873) only uses seeds of *P. guachapele* and other native legume plants in the same family (Amarillo-Suarez & Fox, 2006; Sanabria & Amarillo-Suarez, 2017).

Because ecological networks change across space (Bascompte & Jordano, 2014), across time (Olesen *et al.*, 2008; Carnicer *et al.*, 2009), and across host plants, as in this case, we expected that the networks we described here also change across space and time. Thus, it is necessary to continue the analysis of this variation at different spatial and temporal scales in order to measure the magnitude of these changes and to determine community effects at a broader scale. This will allow us to infer broader patterns of interactions and to develop management practices for exotic and native species in different landscapes and human altered ecosystems.

CONCLUSIONS

Invasive species such as *L. leucocephala* have managed to enter the pre-established ecological networks in the ecosystem, diverting parasitoids such as *Stenocorse sudamericanus*, native Colombian species that managed to successfully colonize an exotic species. In addition to this the ecological networks represented were immersed in a fragment of tropical dry forest which could cause the low richness and diversity that we found. Since the fragile tropical dry forest is home to the greatest diversity of legumes in the world (Gentry, 1995) and Colombia (Pizano & Garcia, 2014), it seemed necessary to continue studies that analyzed the several ways in which the exotic species *L. leucocephala* had become incorporated into ecological networks, like its interactions with pollinators, micorryzes, competition with other exotics, and native legumes, etc. This would allow the establishment of more responsible plans for the use and management of this legume, considered worldwide and nationally one of the 100 most harmful invasive species (Lowe *et al.*, 2004). Only in this way can responsibly plans for the use and management of this harmful legume be defined (Lowe *et al.*, 2004).

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LITERATURE CITED

- Amarillo-Suárez, A. R., Fox, C. W.** (2006) Population differences in host use by a seed beetle: Local adaptation, phenotypic plasticity and maternal effects. *Oecologia*, 2, 247–258.
<https://doi.org/10.1007/s00442-006-0516-y>
- Amarillo-Suárez, A. R.** (2010) Top-down, bottom-up, and horizontal mortality variation in a generalist seed beetle. *Revista Colombiana de Entomología*, 36, 269–276.
- Amarillo-Suárez, A. R., Camacho-Erazo, M.** (2020) First record of the seed beetle *Merobruchus paquetae* (Chrysomelidae, Bruchinae) in the exotic tree *Leucaena leucocephala*. *Caldasia*, 42, 336–338.
<https://doi.org/10.15446/caldasia.v42n2.80061>
- Amarillo-Suárez, A. R., Repizo, A., Robles, J., Díaz, J., Bustamante, S.** (2017) Ability of a Generalist Seed Beetle to Colonize an Exotic Host: Effects of Host Plant Origin and Oviposition Host. *Neotropical Entomology*, 46, 268–379.
<https://doi.org/10.1007/s13744-016-0476-9>
- Armbrecht, I.** (1995) Comparación de la mirmecofauna en fragmentos boscosos del valle geográfico del no Cauca, Colombia. *Boletín Museo de Entomología Universidad del Valle*, 3, 1–14.
- Baptiste, M. P., Castaño, N., Cárdenas López, D., Gutiérrez, F. D. P., Gil, D., Lasso, C. A.** (2010) *Análisis de riesgo y propuesta de categorización de especies introducidas para Colombia.*

- Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Colombia, 200 pp.
- Barbour, M. A., Fortuna, M. A., Bascompte, J., Nicholson, J. R., Julkunen-Tiitto, R., Jules, E. S., Crutsinger, G. M.** (2016) Genetic specificity of a plant–insect food web: Implications for linking genetic variation to network complexity. *Proceedings of the National Academy of Sciences*, 113, 2128–2133.
<https://doi.org/10.1073/pnas.1513633113>
- Bascompte, J., Jordano, P.** (2014) *Mutualistic Networks*. Princeton University Press, United States, 292 pp.
- Blüthgen, N., Fründ, J., Vázquez, D. P., Menzel, F.** (2008) What do interaction network metrics tell us about specialization and biological traits? *Ecology*, 89, 3387–3399.
<https://doi.org/10.1890/07-2121.1>
- Behmer, S. T., Elias, D. O.** (2000) Sterol metabolic constraints as a factor contributing to the maintenance of diet mixing in grasshoppers (Orthoptera: Acrididae). *Physiological and Biochemical Zoology*, 73, 219–230.
<https://doi.org/10.1086/316728>
- Behmer, S. T., Nes, W. D.** (2003) Insect sterol nutrition and physiology: a global overview. *Advances in Insect Physiology*, 31, 1–72.
[https://doi.org/10.1016/s0065-2806\(03\)31001-x](https://doi.org/10.1016/s0065-2806(03)31001-x)
- Borror, D. J., White, R. E.** (1970) *Field Guide to Insects*. Peterson Field Guide. United States, 404 pp.
- Borges, R. M., Bessière, J., Hossaert-McKey, M.** (2008) The chemical ecology of seed dispersal in monoecious and dioecious figs. *Functional Ecology*, 22, 484–493.
<https://doi.org/10.1111/j.1365-2435.2008.01383.x>
- Cardenas, L. D, Baptiste, M. P., Castaño, N.** (2017) *Plantas exóticas con alto potencial de invasión en Colombia*. Instituto de Investigaciones de Recursos Biológicos Alexander Von Humboldt. Colombia, 295 pp.
- Carnicer, J., Jordano, P., Melián, C. J.** (2009) The temporal dynamics of resource use by frugivorous birds: a network approach. *Ecology*, 90, 1958–1970.
<https://doi.org/10.1890/07-1939.1>
- Castro, V.** (2014) Potencial de colonización de la especie exótica *Acanthoscelides macrophthalmus* (Coleoptera: Chrysomelidae) a semillas de especies nativas de leguminosas [Tesis de pregrado]. Pontificia Universidad Javeriana.
- CorAntioquia** (2008) *Manejo de las semillas y la propagación de diez especies forestales del Bosque Seco Tropical*. Corporación Autónoma Regional del Centro de Antioquia. Colombia, 82 pp.
- Corzo, G., Levartoski de Araujo, A. I, de Almeida, A. M.** (2011) Connectivity and Nestedness in Bipartite Networks from Community Ecology. *Journal of Physics*, 285, 012009.
<https://doi.org/10.1088/1742-6596/285/1/012009>
- Cuevas-Reyes, P., Quesada, M., Hanson, P., Oyama, K.** (2007) Interactions Among Three Trophic Levels and Diversity of Parasitoids: A Case of Top-Down Processes in Mexican Tropical Dry Forest. *BioOne*, 36, 792–800.
[http://dx.doi.org/10.1603/0046-225X\(2007\)36\[792:IATTLA\]2.0.CO;2](http://dx.doi.org/10.1603/0046-225X(2007)36[792:IATTLA]2.0.CO;2)

- Dáttilo, W., Rico-Gray, V.** (2018) *Ecological Networks in the tropics. An integrative overview of species interactions from some of the most species-rich habitats on earth.* Springer International. Switzerland, 216 pp.
- Delgado-Machuca, N., Meza-Lázaro, R. N., Romero-Nápoles, J., Sarmiento-Monroy, C., Amarillo-Suárez, A. R., Bayona-Vásquez, N. J., Zaldivar-Riverón, A.** (2019) Genetic structure, species limits and evolution of the parasitoid wasp genus *Stenocorse* (Braconidae: Doryctinae) based on nuclear 3RAD and mitochondrial data. *Systematic Entomology*, 45, 33–47.
<https://doi.org/10.1111/syen.12373>
- Delmas, E., Besson, M., Brice, M. H., Burkle, L. A., Dalla-Riva, G. V., Fortin, M. J., Gravel, D., Guimarães Jr, P. R., Hembry, D. H., Newman, E. A., Olesen, J. M., Pires, M. M., Yeakel, J. D., Poisot, T.** (2019) Analyzing ecological networks of species interactions. *Biological Reviews*, 94, 16–36.
<https://doi.org/10.1101/112540>
- Didham, R. K., Lawton, J. H., Hammond, P. M., Eggleton, P.** (1998) Trophic structure stability and extinction dynamics of beetles (Coleoptera) in tropical forest fragments. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 353, 437–451.
<https://doi.org/10.1098/rstb.1998.0221>
- Didham, R. K., Tylianakis, J. M., Gemmill, N. J., Rand, T. A., Ewers, R. M.** (2007) Interactive effects of habitat modification and species invasion on native species decline. *Trends in Ecology & Evolution*, 22, 489–496.
<https://doi.org/10.1016/j.tree.2007.07.001>
- Dormann, C. F., Fründ, J., Gruber, B.** (2014) Package 'bipartite'. Visualizing bipartite networks and calculating some (ecological) indices (Version 2.04). R Foundation for Statistical Computing.
- Dunne, J. A., Williams, R. J., Martinez, N. D.** (2002) Food-web structure and network theory: The role of connectance and size. *Proceedings of the National Academy of Sciences*, 99, 12917–12922.
<https://doi.org/10.1073/pnas.192407699>
- Fernández, F., Sharkey, M. J.** (2006) *Introducción a los Hymenoptera de la region neotropical.* Universidad Nacional de Colombia, Colombia, 920 pp.
- Fortuna, M. A., Stouffer, D. B., Olesen, J. M., Jordano, P., Mouillot, D., Krasnov, R. P., Bascompte, J.** (2010) Nestedness versus modularity in ecological networks: two sides of the same coin? *Journal of Animal Ecology*, 79, 811–817.
<https://doi.org/10.1111/j.1365-2656.2010.01688.x>
- Fox, C. W., Bush, M. L., Messina, F. J.** (2010) Biotypes of the seed beetle *Callosobruchus maculatus* have differing effects on the germination and growth of their legume hosts. *Agricultural and Forest Entomology*, 12, 353–362.
<https://doi.org/10.1111/j.1461-9563.2010.00484.x>
- Geilfus, F.** (1989) *El árbol al servicio del agricultor: Manual de agroforestería para el desarrollo rural.* Catie, Santo domingo, República Dominicana, 678 pp.
- González, E., Salvo, A., Valladares, G.** (2015) Arthropods on plants in a fragmented Neotropical dry forest: A functional analysis of area loss and edge effects. *Insect Science*, 22, 129–138.
<https://doi.org/10.1111/1744-7917.12107>

- Grass, I., Jauker, B., Steffan-Dewenter, I., Tschardt, 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, 1408–1417.
<https://doi.org/10.1038/s41559-018-063>
- Grether, R., Martínez-Bernal, A., Luckow, M., Zárate, S.** (2006) *Fascículo 44. Mimosaceae tribu Mimoseae in: Flora del Valle de Tehuacán-Cuicatlán*, UNAM. Ciudad de México, México.
- Hagstrum, D. W., Subramanyam, B.** (2009) *Stored-product insect resource*. AACC International, United States, 509 pp.
- Hendrickx, F., Maelfait, J. P., Van Wingerden, W., Schweiger, O., Speelmans, M., Aviron, S., Augenstein, I., Billeter, R., Bailey, D., Bukacek, R., Françoise, B., diekötter, T., Dirksen, J., Herzog, F., Liira, J., Roubalova, M., Vandomme, V., Bugter, R.** (2007) How landscape structure, land-use intensity and habitat diversity affect components of total arthropod diversity in agricultural landscapes. *Journal of Applied Ecology*, 44, 340–351.
<https://doi.org/10.1111/j.1365-2664.2006.01270.x>
- Hetz, M., Johnson, C. D.** (1988) Hymenopterous parasites of some bruchid beetles of north and central America. *Journal of Stored Products Research*, 3, 131–144.
[https://doi.org/10.1016/0022-474X\(88\)90010-0](https://doi.org/10.1016/0022-474X(88)90010-0)
- Ings, T. C., Montoya, J. M., Blüthgen, N., Brown, L., Dormann, C. F., Edwards, F., Figueroa, D., Jacob, U., Jones, J. I., Lauridsen, R. B., Ledger, M. E., Lewis, H. M., Olesen, J. M., Veen, F. J., Warren, P. H., Woodward, G.** (2009) Ecological networks - Beyond food webs. *Journal Animal Ecology*, 78, 253–269.
<https://doi.org/10.1111/j.1365-2656.2008.01460.x>
- Jhonson, C. D.** (1990) Systematics of the seed beetle genus *Acanthoscelides* (Bruchidae) of Northern South America. *Transactions of the American Entomological Society*, 116, 297–618.
<https://www.jstor.org/stable/25078519>
- Jhonson, S., Collin, C., Wissman, H., Halvarsson, E., Agren, J.** (2004) Factors Contributing to Variation in Seed Production among Remnant Populations of the Endangered Daisy *Gerbera aurantiaca*. *Biotropica*, 36, 148–155.
<https://doi.org/10.1111/j.1744-7429.2004.tb00307.x>
- Kolchinsky, A., Gates, A. J., Rocha, L. M.** (2015) Modularity and the spread of perturbations in complex dynamical systems. *Physical Review*, 92, 060801.
<https://doi.org/10.1103/PhysRevE.92.060801>
- Kenny, D., Loehle, C.** (1991) Are Food Webs Randomly Connected? *Ecology*, 5, 1794–1799.
- LaSalle, J., Gauld, J. D.** (1991) Parasitic Hymenoptera and the biodiversity crisis. *Redia*, 4, 315–334.
- Louda, S. M., Potvin, M. A., Collinge, S. K.** (1990) Predispersal seed predation, postdispersal seed predation and competition in the recruitment of seedlings of a native thistle in sandhills prairie. *American Midland Naturalist*, 124, 105–113.
<https://doi.org/10.2307/2426083>
- Lowe, S., Browne, M., Boudjelas, S., De Poorter, M.** (2004) 100 de las Especies Exóticas Invasoras más dañinas del mundo. Una selección del Global Invasive Species Database. *Aliens*, 12, 1–12. Available at: <https://www.iucn.org/es/content/100-de-las-especies-exoticas-invasoras-mas-daninas-del-mundo-una-seleccion-del-global-invasive-species-database> (accessed on Jun 12, 2020).

- Lozano-Grande, M. A., Gorinstein, S., Espitia-Rangel, E., Dávila-Ortiz, G., Martínez-Ayala, A. L.** (2018) Plant Sources, Extraction Methods, and Uses of Squalene. *International journal of agronomy*, 2018, 1829160.
<https://doi.org/10.1155/2018/1829160>
- Mahecha-Vega, G. E., Ovalle-Escobar, A., Camelo-Salamanca, D., Rozo-Fernández, A., Barrero-Barrero, D.** (2012) *Vegetación del territorio CAR, 450 especies de sus llanuras y montañas*. Corporación Autónoma Regional. Colombia, 893 pp.
- Manfio, D., Ribeiro-Costa, C. S.** (2016) A key to American genus *Merobruchus* Bridwell (Coleoptera: Chrysomelidae: Bruchinae) with descriptions of species and two new host plant records for the subfamily. *Zootaxa*, 4078, 284–319.
<https://doi.org/10.11646/zootaxa.4078.1.25>
- Maron, J. L., Crone, E.** (2006) Herbivory: effects on plant abundance, distribution and population growth. *Proceedings of the royal society B*, 273, 2575–2584.
<https://doi.org/10.1098/rspb.2006.3587>
- Montero-Castaño, A., Vila, M.** (2012) Impact of landscape alteration and invasions on pollinators: a meta-analysis. *Journal of Ecology*, 100, 884–893.
<https://doi.org/10.1111/j.1365-2745.2012.01968.x>
- Morales-Silva, T., Maia, L. F., Martins, A. L., Modesto-Zampieron, S. L.** (2019) Herbivore, parasitoid and hyperparasitoid insects associated with fruits and seeds of *Enterolobium contortisiliquum* (Vell.) Morong (Fabaceae). *Brazilian Journal of Biology*, 9, 369–376.
<https://doi.org/10.1590/1519-6984.170105>
- Nakagawa, T., Takeuchi, Y., Kenta, T., Nakashizuka, T.** (2005) Predispersal seed predation by insects vs. vertebrates in six dipterocarp species in Sarawak, Malaysia. *Biotropica*, 37, 389–396.
<https://doi.org/10.1111/j.1744-7429.2005.00051.x>
- Nurse, R. E, Booth, B. D., Swanton, C. J.** (2003) Predispersal seed predation of *Amaranthus retroflexus* and *Chenopodium album* growing in soyabean fields. *Weed Research*, 43, 260–268.
<https://doi.org/10.1046/j.1365-3180.2003.00342.x>
- Olesen, J. M., Bascompte, J., Elberling, H., Jordano, P.** (2008) Temporal dynamics in a pollination network. *Ecology*, 89, 1573–1582.
<https://doi.org/10.1890/07-0451.1>
- Parker, J. D., Hay, M. E.** (2005) Biotic resistance to plant invasions? Native herbivores prefer non-native plants. *Ecology letter*, 8, 959–967.
<https://doi.org/10.1111/j.1461-0248.2005.00799.x>
- Pérez-Benavides, A. L., Hernández-Baz, F., González, J. M., Zaldívar-Riverón, A.** (2019) Updated taxonomic checklist of Chalcidoidea (Hymenoptera) associated with Bruchinae (Coleoptera: Chrysomelidae). *Zootaxa*, 4638, 301–343.
<https://doi.org/10.11646/zootaxa.4638.3.1>
- Pizano, C., García, H.** (2014) *El bosque seco tropical en Colombia*. Instituto de Investigaciones de Recursos Biológicos Alexander Von Humboldt. Colombia, 354 pp.
- R Core Team** (2013) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Austria.

- Sanabria-Silva, A. M., Amarillo-Suárez, A. R.** (2017) Same but different: Diversity and complexity of an arthropod trophic network and comparative seed viability of an invasive and a native legume species. *Journal of Arid Environment*, 145, 10–17.
<https://doi.org/10.1016/j.jaridenv.2017.04.004>
- Sharratt, M. E. J., Olckers, T.** (2012) The biological control agent *Acanthoscelides macrophthalmus* (Chrysomelidae: Bruchinae) inflicts moderate levels of seed damage on its target, the invasive tree *Leucaena leucocephala* (Fabaceae), in the KwaZulu-Natal coastal region of South Africa. *African Entomology*, 20, 44–51.
<https://doi.org/10.4001/003.020.0106>
- Sauve, A. M. C., Fontaine, C., Thébault, E.** (2014) Structure–stability relationships in networks combining mutualistic and antagonistic interactions. *Oikos*, 123, 378–384.
<https://doi.org/10.1111/j.1600-0706.2013.00743.x>
- Tallamy, D. G.** (2004) Do alien plants reduce insect biomass? *Conservation biology*, 18, 1689–1692.
<https://doi.org/10.1111/j.1523-1739.2004.00512.x>
- Tuda, M., Wu, L., Tateishi, Y., Niyomdham, C., Buranapanichpan, S., Morimoto, K., Wang, C. P., Zhang, Y. C., Murugan, K., Chou, L. Y., Jhonson, C. D.** (2009) A novel host shift and invaded range of a seed predator, *Acanthoscelides macrophthalmus* (Coleoptera: Chrysomelidae: Bruchinae), of an invasive weed, *Leucaena leucocephala*. *Entomological Science*, 12, 1–8.
<https://doi.org/10.1111/j.1479-8298.2009.00297.x>
- Udayagiri, S., Wadhi, R.** (1982) A key to world bruchid Genera. *NBPGR Sci, Monogr*, 5, 1–19.
- Vanbergen, A. J., Woodcock, B. A., Heard, M. S., Chapman, D. S.** (2017) Network size, structure and mutualism dependence affect the propensity for plant–pollinator extinction cascades. *Functional Ecology*, 31, 1285–1293.
<https://doi.org/10.1111/1365-2435.12823>
- West, N. M.** (2012) *Herbivory affects patterns of plant reproductive effort and seed production (Major)*. The University of Nebraska.
- Wood, A., Haga, E. B., Costa, V. A., Rossi, M. N.** (2016) Geographic distribution, large-scale spatial structure and diversity of parasitoids of the seed-feeding beetle. *Bulletin of Entomological Research*, 107, 22–331.
<https://doi.org/10.1017/S0007485316000924>
- Zaldivar-Riverón, A., Jasso-Martínez, J., Delgado-Machuca, N., Sarmiento-Monroy, C., González-Joya, A., Del Bianco-Faria, L.** (2019) Taxonomic Revision of the New World Genus *Stenocorse* Marsh (Hymenoptera: Braconidae: Doryctinae). *Annales Zoologici*, 69, 617–639.
<https://doi.org/10.3161/00034541ANZ2019.69.3.011>