Soil moisture shapes diversity and network structure of insect communities associated with *Cylindropuntia imbricata* (Cactaceae)

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Abstract

We evaluated the diversity and ecological network structure of insects associated with *Cylindropuntia imbricata*, a common cactus distributed throughout the Mexican high plateau (southern Chihuahuan desert). We performed a field assay where we randomly selected adult individuals of *C. imbricata* to analyze the effect of induced water stress on cacti. Our data revealed that insect diversity was higher as soil moisture increased; however, time of day highly influenced species composition. The results exhibited that ecological networks do not support stable interactions when cacti were watered. Probably, watering destabilized the nested pattern of the networks because is in attractive but short-lived resource for insects (hot moments). Time-subnetworks showed that watered cacti were nested only during the first hours of the day. Presumably, insect species responded to "hot moments" determined by induced soil moisture. The highest insect species composition and species interactions occurred at noon, demonstrating a threshold to avoid overheating and therefore, a temporal segregation of species during the day. Further research is needed to improve knowledge on environmental determinants such as water, as a critical issue to predict the impacts of climate change on species diversity and their trophic interactions, particularly in deserts where rains are scarce.

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Introduction

In deserts, rainfall is extremely variable in space and time, and droughts are extended (Granados et al. 2012). Thus, water is an important factor that limits plant growth in these environments (Pérez-Sánchez et al. 2015; González-Salvatierra and Flores 2019). In addition, water availability mediated by seasonality is one of the most important drivers of the vast biodiversity inhabiting desert environments (McCluney and Sabo 2009; McCluney et al. 2012; Rosano-Hinojosa et al. 2019). Particularly, Mexican deserts are dominated by the Cactaceae family, having near 850 species with 80% of endemism (Bravo-Hollis 1978; González-Medrano 2012). Success of cacti to colonize deserts is due to the characteristics developed in response to the extreme aridity (Hernández-Hernández et al. 2014). Moreover, cactus species establish multiple interactions because they represent an important source to provide food, water and shelter for many species inhabiting deserts (e.g., Wolf and Rio 2003; Flores-Torres and Montaña 2015; Rosano-Hinojosa et al. 2019).

Species interactions are integral to the stability of ecological communities and are the main driver for

biodiversity architecture (Bascompte et al. 2003). The study of interactions from the framework of the ecological network analysis is a critical tool to understand the main patters of species distribution due to the emergent network properties (Charbonneau et al. 2013). Moreover, the responses of species to extreme environmental fluctuations are key to understanding the evolution of these networks (Bascompte et al. 2003; Lance et al. 2017) and their roles in stabilizing ecological communities (Lance et al. 2017; Rosano-Hinojosa et al. 2019). Ecological networks integrate knowledge to provide insights into ecological communities by revealing the structure of complex multitrophic interactions (Charbonneau et al. 2013; Holland et al. 2013).

Some ecological networks exhibit a nested pattern in which there is a group of generalist organisms with a wide number of interactions (core species), whereas there is other set of species with few connections that interact with generalists (periphery species); as more nested a system is the more organized it is (Dáttilo et al. 2014). Abiotic factors modulate nestedness; for instance, Rico-Gray et al. (2012) documented that the nested pattern of ecological networks between ants and plants increase due to mean monthly temperature. Dáttilo et al. (2014) studied the structure of both diurnal and nocturnal ant distributions revealing that both networks showed a nested pattern; moreover, they found that core species varied between the day and night. Lance et al. (2017) showed that a decrease in the mean annual precipitation led to a loss of species interactions in drylands. Rosano-Hinojosa et al. (2019) observed that the cactus-beetle networks have a nested structure at both dry and rainy seasons, with an increase in nestedness during the rainy season; moreover, at the intra-population level they also found a nested structure in the interactions of beetles inhabiting decayed cacti from semi-arid environments in Mexico.

Abiotic factors play a critical role to determine the interaction network structure between plants and their associated entomofauna (Rico-Gray et al. 2012). For instance, water stress by drought influences the chemistry of plants and affect growth (Ward et al. 2019). Huberty and Denno (2004) proposed the "pulsed stress hypothesis", whereby bouts of plant stress and the recovery of plant turgor let sap-feeders to benefit from stress-induced increases in plant nitrogen. Furthermore, "hot moments" hypothesis are defined as short periods with fluctuations of abiotic factors such as variation in light periods, precipitation, temperature, soil moisture, among others, that can cause a disproportional high reaction rate such as pulses of flower, fruit, or nectar production (McClain et al. 2003; Ness 2020). In addition to "hot moments", the circadian rhythm of insects also determines their temporal segregation throughout the day due to a threshold to evade overheating; thus, species avoid niche overlapping (Krittika and Yadav 2020).

We studied *Cylindropuntia imbricata* (Cactaceae), a cactus species widely distributed across the Mexican high plateau. Studies aiming to understand the diversity and interaction network structure of the insect-associated of this cactus are still scarce (e.g., Ávila-Argáez et al. 2019). The aim of this study was to evaluate the influence of water irrigation on the community of insects associated with *C. imbricata* at two ecological levels: the diversity patterns and the structure of the ecological network of interactions at intra-population level. We considered all insects as associated with *C. imbricata* because the lack of taxonomic knowledge and thus, behavioral knowledge of species is scarce. We evaluated the possible changes in the diversity, composition, and structure of the ecological network of associated insects when cacti were irrigated and without irrigation; at two different hours of the day (8:00–9:00 h and 11:00–12:00 h) because this factor could influence the temperature range to which insects are active in deserts. It is because temperature in deserts is characterized by extreme hot days and cold nights and due to this, it could be a delay in species distribution until diurnal temperature is higher at noon (Holm and Edney 1973; Granados et al. 2012). The combination of treatments and time was assessed.

We hypothesized that insect diversity associated with *C. imbricata* is influenced by soil water availability. We expected an increase in species diversity because *C. imbricata* could represent an ephemeral humid microhabitat for insects. However, we also expected that regardless of soil moisture treatments, insect species composition be more affected by the time of the day to avoid the hottest hours, following Luna et al. (2018). Moreover, we also expected that network structure will be nested through watered cacti as well as time-subnetworks because the increase in soil moisture could be more attractive as site of perch for some insects; therefore, we suppose to find a particular set of core species (generalists) associated with watered condition.

Materials and methods

Study area

Fieldwork was conducted in San Juanico el Chico (22°14′07″ N, 100°59′48.3″ W, 1871 m.a.s.l.), located to the northeast of the San Luis Potosi city, Mexico, at the Southern Chihuahuan Desert. Climate of the area is semi-arid, mean annual temperature is 16.8 °C and mean annual precipitation is 372.9 mm (Medina-García et al. 2005). More than 80% of rainfalls occur in June–September (summer) (Medina-García et al. 2005) and this defines the growing season for plants. Vegetation is secondary desert scrub with a density higher than 35 individuals of *C. imbricata* per hectare (Ávila-Argáez et al. 2019). For *C. imbricata*, the period

of most active branch growth is short (from the last week of June to August) with growth rates of branches as high as 15 mm day-1 during July, when flowering also occurs (Kunst 1990). Our experiment was carried out when cacti were actively secreting EF nectar, after the flowering season (see Ávila-Argáez et al. 2019).

Water irrigation and field observations

Prior to developing our study, permission to access privately owned land was obtained from the landowner. The field assays were conducted in the dry season during 20 weeks from August to December 2012. We randomly selected 40 adult individuals of *C. imbricata* (1.0–1.5 m tall) and, to avoid overlap of samples we took care to maintain minimum distance of 5 m between neighboring plants. To analyze the effect of water stress on plants, we performed an experiment with watered and non-watered plants. We selected 20 individuals which were subjected to irrigation and the other 20 had no irrigation. The drip system delivered 1.5 L of water weekly at 7:00 o'clock using plastic bottles perforated following Ávila-Argáez et al. (2019). Observations of insects associated with cacti were conducted each hour for a period of a minute each between 8:00–9:00 h (hereafter referred as H1) and between 11:00–12:00 h (hereafter referred to H2), every 2 weeks during the 20 weeks of the experiment (a total of 400 min of observation per plant). All observations were carried out 24 h after watering. Insects were considered as associated with cacti if they were posing during near a minute, regardless the behavior activity. Specimens were counted and captured with an oral aspirator. They were placed in Falcon (14 ml) tubes with 70% ethyl alcohol for taxonomic identification. Insects were identified by using a taxonomical guide (Borror and White 1970).

Data analysis

We checked the accuracy of the inventory by using the sample coverage ($\hat{C}n$) estimator suggested by Chao and Jost (2012), which is a less biased estimator of sample completeness. Sample coverage has values from 0 (minimal completeness) to 100% (maximum completeness). We evaluated the effect of watering (DI *vs.* NI) and the hour of the day (H1 *vs.* H2) in the diversity of the insect visitor community associated with *C. imbricata* with the Hill numbers qD (Jost 2006) of order $q=0$ and $q=1$ by using the iNEXT package (Chao et al. 2016). In this sense, $q=0$ is the species richness value and is not sensitive to abundances; $q=1$ uses the exponential of Shannon's entropy to estimate effective species, which weights each species by its frequency in the sample without favoring either common or rare species. For further information about equations, see Jost (2006). For comparisons of diversities, the 95% CI was used, and differences

were determined following the recommendations of Cumming et al. (2007), where an absence of overlap between CI values indicates a significant difference.

We compared differences in species composition by building a matrix with samples nested within plots/surveys and treatments (watering and non-watering) as well as the different hours of the day), then the abundance data were transformed with the square root to down-weight the influence of highly abundant taxa, and we constructed a Bray–Curtis similarity matrix. Next, we tested the significance of similarity values between treatments with a repeated measure PERMANOVA analysis after 999 permutations of residuals under the reduced model. In addition, we performed a metric multidimensional scaling (MDS) with the bootstrap procedure to show compositional differences. Analyzes and graphs were done in PRIMER v7 (Clarke and Gorley 2015).

We built qualitative networks using insect species associated with individuals of *C. imbricata*. For this, each network was defined by an adjacency matrix A, where aij = number of interactions from an individual cactus plant *j* by the insect species *i*, and zero otherwise (Bascompte et al. 2003). We used the *NODF* metric (Almeida-Neto et al. 2008) in ANINHADO software to measure the degree of nestedness for each network (Guimarães and Guimarães 2006) by using null model II (Bascompte et al. 2003). Qualitative nestedness vary from zero (no nestedness) to 100 (perfect nestedness) (Dáttilo et al. 2013b). We also estimated the modularity for each network by using the modularity index M (from 0, no subgroups, to 1, totally separated subgroups) based on Barber's algorithm obtained through simulating annealing (1000 randomizations performed) and by using Modular software (Marquitti et al. 2014). We plotted the networks' graphs and metrics were performed in R software (R Development Core Team 2015) with the "bipartite" package (Dormann et al. 2009).

To understand the importance of each insect species within the network, we performed the categorical core *vs.* periphery analysis that describes which species constitute the core (generalist species, those with the most interactions) or peripheral (those with fewer interactions) components of the network with the following equation (Dáttilo et al. 2013a):

$$Gc = \left(k_i - k_{\mathrm{mean}}\right)/\sigma_k$$

where k_i mean number of links for a given plant/insect species, k_{mean} mean number of links for all plant/insect species in the network, and σ_k is standard deviation of the number of links for plant/insect species. $Gc > 1$ are species with the larger number of interactions in relation to other species of the same trophic level and are therefore considered as species constituting the generalist core. $Gc < 1$ are species with

lower number of interactions in relation to other species of the same trophic level and are therefore considered as species constituting the periphery of networks.

Results

We registered 6,286 individuals belonging to six orders, 14 families and 18 species of visitor insects (Table 1). The ant *Liometopum apiculatum* Mayr, 1870 was the most abundant species representing 71% of the total visitants (Table 2) followed by ten insect species that were recorded with more than 100 individuals belonging to four orders and nine families: (1) Coleoptera [Buprestidae, *Acmaeodera pulchella* (Herbst 1801); Cleridae, *Cleridae* sp. 1; Curculionidae, *Dyslobus tanneri* Van Dyke, 1933], (2) Diptera [Tephritidae, *Campiglossa clathrata* (Loew, 1862), *Diptera* sp. 1], (3) Hemiptera [Aphididae, *Eriosoma lanigerum* (Hausmann, 1802), Nabidae, *Hemiptera* sp. 2, Thyreocoridae, *Hemiptera* sp. 1] and (4) Hymenoptera (Eulophidae, *Chrysocharis* sp. Förster, 1856; Formicidae, *Crematogaster opuntiae* Buren, 1968). We registered 3137 individuals and 18 species of insects associated with cacti exposed to irrigation, while 3149 individuals and 17 species of insects were recorded as visitors of non-watered cacti (Table 1).

Table 1 Diversity and network metric values of insects found associated with cacti with drip irrigation and no irrigation at the different hours of the day in San Juanico el Chico, San Luis Potosí, México

	DI	DI-H1	DI-H2	NI	NI-H1	NI-H2
S	18	18	18	17	17	17
No Ind	3137	1600	1537	3149	1669	1480
$\hat{C}n$	100	99	99	100	100	100
$q0$ ($\pm$IC)	1.47 ($\pm$0.03)	1.19 ($\pm$0.04)	1.71 ($\pm$0.04)	1.27 ($\pm$0.03)	1 ($\pm$0.04)	1.53 ($\pm$0.04)
$q1$ ($\pm$IC)	4.36 ($\pm$.13)	3.31 ($\pm$0.14)	5.55 ($\pm$0.21)	3.57 ($\pm$0.10)	2.72($\pm$0.10)	4.64($\pm$0.18)
NODF	76.25^{ns}	67.11*	76.5*	80.58*	62.21^{ns}	77.91*
Modularity	0.06^{ns}	0.14^{ns}	0.09^{ns}	0.07^{ns}	0.15^{ns}	0.11^{ns}

S Species richness, *No Ind* number of individuals, *Ĉn* sample coverage estimator, *IC* Intervals of Confidence, *DI* drip irrigation, *NI* No irrigation, *H1* hour of the day between 8-9 h, *H2* hour of the day between 11-12 h, *ns* no significance

*$p < 0.005$

Table 2 Species and individuals of insects recorded visiting on *Cylindropuntia imbricata* (Cactaceae) individuals with and without watering in San Juanico el Chico, San Luis Potosí, Mexico

Order	Family	Species	Watering	Non-watering	Total
Coleoptera	Buprestidae	*Acmaeodera pulchella* (Herbst 1801)	88	73	161
		Acmaeodera rubronotata Laporte and Gory, 1835	50	38	88
	Cleridae	*Cleridae* sp. 1 Latreille, 1802	51	54	105
	Curculionidae	*Dyslobus tanneri* Van Dyke, 1933	66	48	114
Diptera	Chloropidae	*Ectecephala albistylum* Macquart, 1851	43	35	78
	Tephritidae	*Campiglossa clathrata* (Loew, 1862)	96	102	198
		Diptera sp. 1 Linnaeus, 1758	91	90	181
Hemiptera	Aphididae	*Eriosoma lanigerum* (Hausmann, 1802)	94	91	185
	Coreidae	*Narnia pallidicornis* Stål, 1870	50	40	90
	Nabidae	*Hemiptera* sp. 2 Linnaeus, 1758	60	51	111
	Pentatomidae	*Nezara viridula* Linnaeus, 1758	8	32	40
	Thyreocoridae	*Hemiptera* sp. 1 Linnaeus, 1758	62	54	116
Hymenoptera	Eulophidae	*Chrysocharis* sp. Förster, 1856	87	68	155
	Formicidae	*Crematogaster opuntiae* Buren, 1968	155	41	196
		Liometopum apiculatum Mayr, 1870	2117	2316	4433
		Pseudomyrmex pallidus (Smith, 1855)	4	0	4
Lepidoptera	Pieridae	*Hesperocharis* sp. Felder, 1862	4	4	8
Orthoptera	Acrididae	*Orthoptera* sp. 1 Latreille, 1793	11	12	23
Total			3137	3149	6286

Sample coverage estimator was < 99% of accuracy in all cases (Table 1). We found differences in the diversity of order $q = 0$ of cacti that were irrigated due to the ant *Pseudomyrmex pallidus* (Smith 1855) that was found only on those watered cacti (Table 1). However, we did not find significant differences for the rest of evaluated treatments because the number of species was the same in cacti with irrigation ($S = 18$) and with no irrigation ($S = 17$) (Table 1, Fig. 1). In contrast, we found significant differences in the diversity of order $q = 1$ for all the treatments evaluated because diversity was higher in cactus that were irrigated. Diversity was twice as high between H2 than between H1 regardless of water availability (Table 1, Fig. 1d, e).

Our findings showed that the main driver for species composition was given between the two hours of the day (*pseudo*-F = 4.99, *df* = 2, *p* = 0.001). In contrast, we did not find any effect of water availability on species composition (*pseudo*-F = 0.96, *df* = 1, *p* = 0.44) and even the interaction

Fig. 1 Comparisons of the diversity values *q*D for insect communities between the treatments evaluated in San Luis Potosí, México. Shaded areas represent ± 95% CI. Diversity curves were built for comparisons between watering treatments and the hours of the day with the following combinations: **a** DI vs NI, **b** DI-H1 vs DI-H2, **c** NI-H1 vs NI-H2, **d** H1 (DI vs NI) and **e** H2 (DI vs NI). The letter combination has been previously defined in Table 1. Note the variation in the scale on the vertical axes
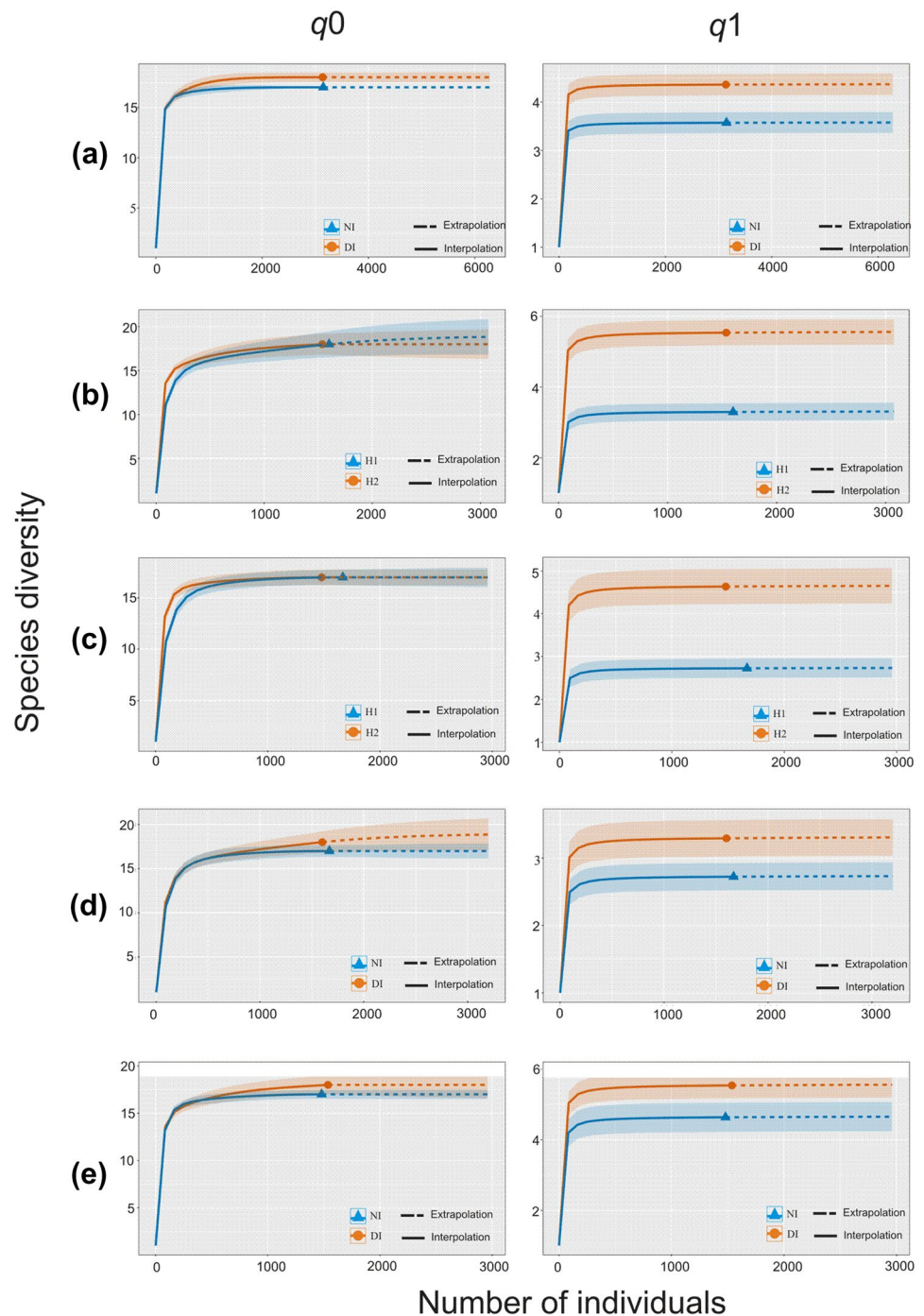
of water availability by hours (*pseudo*-F = 0.75, *df* = 2, *p* = 0.72). We represented these differences in an MDS plot (Fig. 2).

We found that only four qualitative networks showed a significant nested pattern (details in Table 1): the whole network of cacti that were not irrigated (NODF = 80.58, *p* = 0.001), the irrigated cacti network between 8–9 h (NODF = 67.11, *p* = 0.001) and networks between 11-12 h both with irrigated (NODF = 76.5, *p* = 0.001) and not irrigated cacti (NODF = 77.91, *p* = 0.001). None of the studied insect-cactus species networks presented a significant modular pattern (Table 1).

Liometopum apiculatum, *Campiglossa clathrata*, and *Eriosoma lanigerum* were species constituting the core of watered cacti at H1 (Fig. 3); *Hemiptera* sp. 1 as core species in cacti watered at H2 (Fig. 3) and *L. apiculatum* and *Diptera* sp. 1 as core species in cacti without watering at H2. Even though cacti with no irrigation showed a nested pattern, there were no core insect species associated (Fig. 3) which means that some cacti were more important as part of the core maintaining more interactions with few peripheral insects.

Discussion

As we hypothesized, insect diversity and species composition, as well as the structure of the ecological network of species interactions, responded in different ways to both watering and non-watering cactus treatments. We did not find significant differences in species richness, but we observed that the ant species *P. pallidus* shifted when cacti

were watered. This ant species has preference for open and grassy habitats (Colby and Prowell 2006) and in our studied area it was found foraging on EFN (Ávila-Argáez et al. 2019); moreover, *P. pallidus* has been observed feeding on honeydew produced by some Hemiptera species as well as on nectar and extrafloral nectar of plants (Rico-Gray 1993). In addition, we found an increase in species diversity in watered cactus suggesting that with an increase in water availability, *C. imbricata* can offer a humid shelter for those insect species (e.g., herbivores, predators, visitors, etc.) that try to avoid the hottest hours of the day, as occurred in other cactus species (McCluney and Sabo 2009; McCluney et al. 2012; Ness 2020). Although our results showed that soil moisture increased insect species diversity associated with cacti, we found the highest diversity values at noon (H2), regardless of watering or no watering. We found that at H2 Formicidae was the most important family in terms of abundance. Particularly, we observed that *L. apiculatum* highlighted as the dominant species (more than 4000 individuals) associated with *C. imbricata*. The high number of ant individuals is presumably determined by an increase in nectar availability (see Ávila-Argáez et al. 2019). It is recognized that ants are highly associated with the EFN of some cactus species and this sugared trade-off can shape the ant foraging turnover throughout drylands (Mauseth et al. 2016).

We observed that species composition was not significantly determined by moisture, but time showed a clear short-term temporal species segregation. Although *L. apiculatum* is actively working 24 h a day, their main foraging activity is during the first hours of the day with decrease in activity at midday [see Lara-Juárez et al. (2015) and references therein]; nonetheless, in our study we found that this

Fig. 2 MDS ordination of treatments as defined by Bray–Curtis calculated from insect species abundance
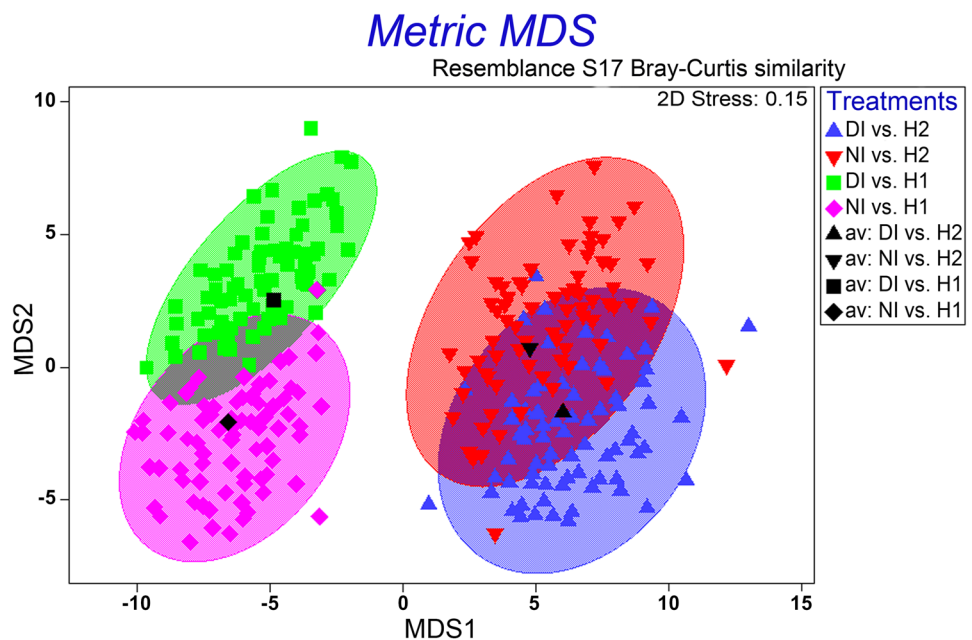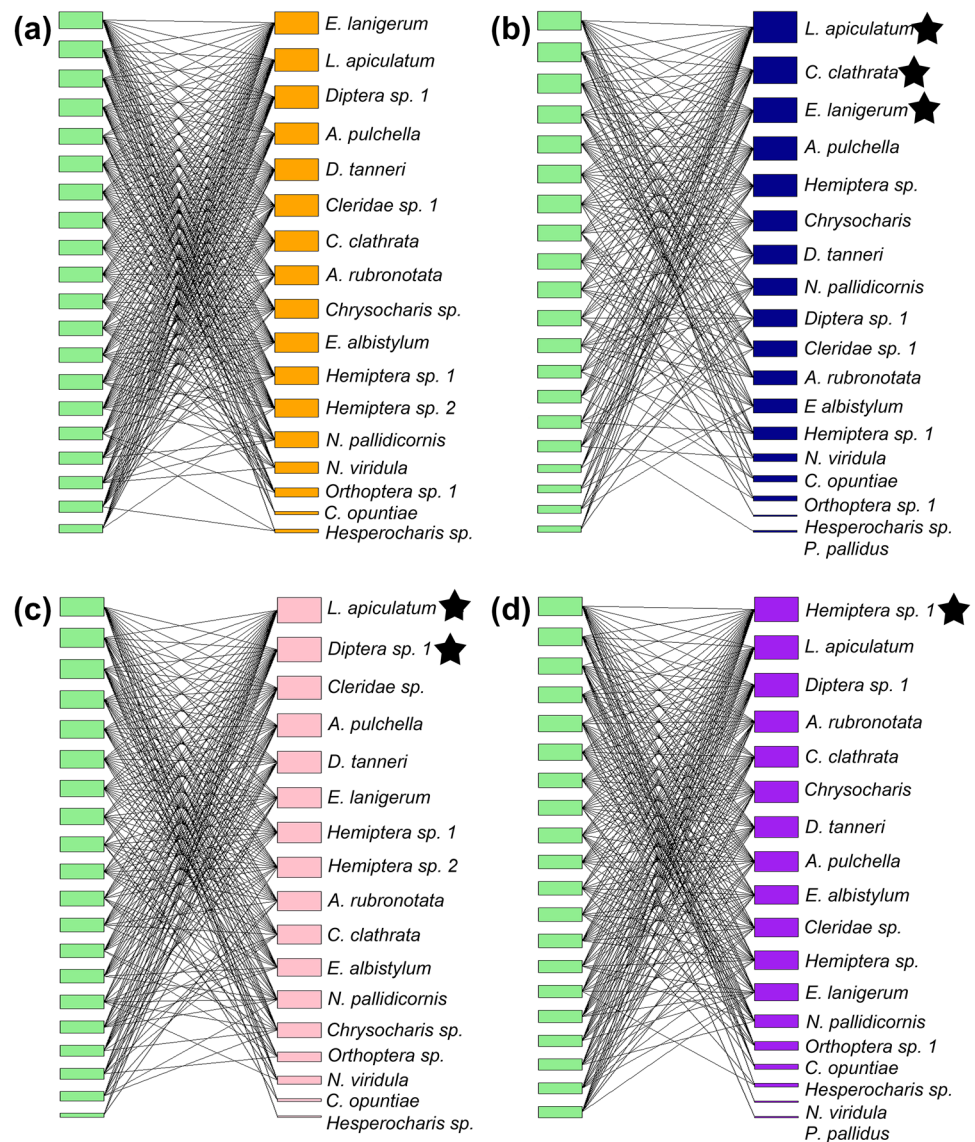
Fig. 3 Qualitative networks that showed a significant nested pattern **a** NI, **b** DI-H1, **c** NI-H2, **d** DI-H2. The star symbol represents those insect species that were part of the core through the network

species was the most dominant at 12 h. A possible explanation is that some competitive pressures may play an important role in temporal changes in the activity of ants, because some subordinated species shift from diurnal to nocturnal foraging to avoid behaviorally dominant species (Żmihorski and Ślipiński 2016; Dáttilo et al. 2014, 2015; Luna et al. 2018; Silva et al. 2019). For instance, we found that *C. opuntiae* was three times more abundant in watered cacti and both *L. apiculatum* and *C. opuntiae* have been recognized to have a mutualistic association with *C. imbricata*, but there is not competition for nectar resource between both (Miller 2007) as we also observed in our studied area.

Contrary to what we expected, our results revealed that the whole network of watered cacti did not show a nested pattern in contrast to non-irrigated cacti, which were nested. These results allow us to assume that the irrigation of cacti destabilizes the network interactions by breaking down its

nested structure. It is known that complex systems are characterized to be resilience (Gao et al. 2016). However, our results shed light that variations in the environmental abiotic factors such as an increase in humidity can be negatively affect a natural community adapted to drought as occurred in our study. This watered event can modify patterns of the phenology of plants and thus, the activity of insects is determining the nested pattern of the ecological networks (Corbet 1960; Rico-Gray et al. 2012; Descamps et al. 2018; Luna et al. 2018). However, when we have partitioned the network into time-subnetworks, we found that watered cacti showed a nested structure at H1. Insect activity in drylands along the day can be conditioned for changes in the environmental conditions that induces "hot moments" or short pulses in species activity (Ness 2020; McClain et al. 2003) as occurred in our study. Ávila-Argáez et al. (2019) suggested that watered *C. imbricata* individuals produced more

extrafloral nectar being an attractive resource for ant species, particularly. Besides, non-irrigated cacti at H1 did not show a nested pattern. Likely, insects found in this treatment is more specialize to these dry conditioning and generalist species avoid these conditions preferring to visit another surrounding plant. Future research could study the interactions of insects with plant species around cacti in understand how critical the plant is for the survival of insect species as a shelter.

Notwithstanding the above, we found that time-subnetworks at H2 showed a nested pattern regardless watered treatment. Our results showed that insects exploit the resources available in a bimodal way, in which some species are distributed at the early hours of the day associated with a threshold to avoid overheating; however, other insect species are adapted to be active at higher temperatures (Corbet 1960). In addition, there are a temporal segregation in insect activity associated with the exploitation of a particular resource or to avoid predators or niche overlapping (Żmihorski and Ślipiński 2016). This is evident if we observe the behavior of insect species into the networks which change their position according to the time of day by moving from the core to the periphery of the network and vice versa. Nevertheless, further research is needed to increase knowledge on the temporal segregation of insect species along the day in relation with their thermal tolerance ranges and competition.

Despite the ecological network without irrigation was significantly nested, we did not find any core species (seven insect species were > 0.9 of probability to be considered a core species). Insect community associated with cacti without irrigation seems to be a very connected network and it is probably that the number of the interactions of insect species are into the average of links per species. Likely, this can be because there was a single cactus producing high levels of nectar and thus, there were "core" cactus in supporting a group of peripheral insects that search for this resource. *Liometopum apiculatum* was the most abundant ant species that has been recognized as mutualistic of *C. imbricata* and, not surprisingly its role as core of the network for the protection it provides to this cactus (Miller 2007). Moreover, insect species changed their role from core to periphery into the network.

For instance, *C. clathrata* was found as core species in cacti where soil was watered at 8–9 h. This tephritid species feed on many different plants belonging to the genus *Haplopappus* and *Senecio* (Johnson et al. 2017) and probably its presence on *C. imbricata* was occasional due to the improved conditions of soil moisture after watered cacti, significantly increasing their abundance. Besides, *E. lanigerum* is an aphid associated with the apple orchard that found through the Mexican high plateau, including San Luis Potosí (Myartseva et al. 2014). Likely, this species is distributed infesting apples or secondary plants from local gardens through our study area in which this aphid was found as core during the morning in watered cacti; probably, *C. imbricata* could represent a secondary host plant of this aphid species owing to the proximity of the human settlements.

Cylindropuntia imbricata is a cactus species adapted to the extreme characteristic conditions from drylands. Seasonality in these environments lead the phenology of plants and can be considered as a "pulsed stress" on *C. imbricata*. Probably, this fact can explain that this cactus species is not able to support stable interactions when soil moisture is increased during the dry season. Insects prefer broadly those plants that are naturally stressed mainly by seasonality. We induced soil moisture causing the breakdown of the ecological network of cactus-herbivores interactions. In addition to the "stressed pulse" that affected cacti, it also affected ants because EFN were stimulated to produce more nectar with the increase of soil moisture; accordingly, ants were more active as a response to a "hot moment" determined by high nectar production as occurred in Ávila-Argáez et al. (2019). However, further research is needed to understand the response of other visiting insects associated with *C. imbricata*. Despite these induced patterns, insects were also affected by their circadian rhythm that help them avoid the most extreme temperatures, therefore, species distribution was different during the different hours of the day evaluated in this study.

In summary, species diversity was highest when soil moisture increased; however, species composition was mainly determined by the different time of day. Soil moisture is key for the interplay of the insect species associated with *C. imbricata*. The ecological network of cacti that were not irrigated seems to be naturally nested in accordance with the "pulsed stress hypothesis"; however, irrigation destabilized the nested pattern of the networks. It is more informative to do a partition into time-subnetworks to gather a broad overview of the insect dynamics in the community which are affected by hot moments mediated by soil moisture. Watered cacti influenced on a set of species such as an "island" of humidity and warmest site to stay and live. This is the first study on the influence of soil moisture on insect diversity and interactions in drylands, revealing that both are conditioned by water availability in different ways. Further research is needed to improve knowledge on environmental determinants such as water, as a critical issue to predict the impacts of climate change on species diversity and their trophic interactions, particularly in deserts where rains are scarce.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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