

ORIGINAL ARTICLE

Diversity of trophic interactions between scorpions and insects

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Abstract Trophic interactions, the fundamental links in food webs, are an important modulator of biodiversity structuring and ecosystem functioning. However, interactions between scorpions and insects remain poorly understood despite their high biomass and diversity in natural ecosystems and more than 410 million years of evolutionary history. Here we summarize three trophic interaction types from 95 scorpion-insect species pairs in which both scorpions and insects were identified at least to the genus level. Predator-prey relationships were the most documented trophic interactions between scorpions and insects, involving 45 scorpion species from 9 families and 79 insect species from 11 orders. Prey-predator interactions were recorded between 11 species pairs of insects from four orders and scorpions from five families. Parasitoidism was documented between four dipterans (3 families) and five scorpions (3 families). The mega-diversity of insects and the high biomass of scorpion species in natural ecosystems imply that their complex trophic interactions await to be characterized.

Key words Food web, predation, parasitoidism, bipartite networks.

1 Introduction

Taxonomy provides the fundamental units for organizing and assessing biodiversity (Sandall *et al.*, 2023). Since Linnaean time, species has been the central unit in taxonomy and species diversity has been the predominant focus of taxonomic works (Padial *et al.*, 2010). However, numerous studies addressing theoretical and applied issues in ecology and biological conservation have acknowledged that we must go beyond documenting species diversity and take into account the diversity of species interactions (Dyer *et al.*, 2010). Now scientists are increasingly aware that species interactions play a crucial role in biodiversity stability and eco-evolutionary community dynamics (Valiente-Banuet *et al.*, 2014; Ratzke *et al.*, 2020; Åkesson *et al.*, 2021).

Trophic interactions, the feeding relationships among organisms, represent a fundamental ecological interaction type that links species with the nutrient flow and generates food webs that sustain ecosystems. It has been well demonstrated that trophic interactions actively rewire food webs and play an important role in community stability (Bartley *et al.*, 2019; Manlick *et al.*, 2024). Thus, trophic interactions unify the study of biodiversity and ecosystem function (Thompson *et al.*, 2012). Clear knowledge of trophic interactions informs the ecological role of species and the processes that maintain biodiversity and ecosystem function (Zhang *et al.*, 2017). However, what was poorly documented is the trophic interactions between scorpions and insects, representing a fundamental gap in our understanding of arthropod food webs.

Scorpions and insects are two charismatic lineages of arthropods. Both evolved from aquatic ancestors of comparable

evolutionary ages, scorpions and insects have terrestrialized independently. The earliest scorpion lived around 430 million years ago with a combination of primitive marine chelicerate and derived arachnid characteristics (Wendruff *et al.*, 2020). The oldest insect lived approximately 410 million years ago with derived characters shared with winged insects (Engel & Grimaldi, 2004). While scorpions are well known for morphological conservatism and diversity depauperation with only about 2800 extant species having been reported (Su *et al.*, 2024), insects epitomize diversity both in terms of morphology and number of species with over one million species having been described (Stork, 2018). Despite the sharp contrasting diversity patterns, scorpions and insects have adapted to diverse habitats and survived the drastic environmental changes over the past 400 million years. Given insects occur everywhere and scorpions are widely distributed, they have extensive overlapping geographical distribution, ecological niche, and ecosystem function. Consequently, interactions between scorpions and insects are inevitable.

Fossil records suggest that scorpions potentially constituted a component of the earliest faunas of terrestrial ecosystems, along with myriapods and insects at least by the early Devonian (Howard *et al.*, 2019). Such a long coevolutionary history implies that trophic interactions between scorpions and insects would be pervasive and diverse. However, while many nutrient types have evolved and repeatedly evolved in insects, scorpions are exclusively predators, generally feeding on other arthropods and occasionally small vertebrates. Like insects, scorpions are widely distributed, occurring on all major landmasses except Antarctica, with high abundance and diversity in tropical and subtropical regions. In general, scorpions are highly successful in desert habitats, with the greatest abundance and diversity of scorpions happening in the desert, semidesert, and savanna habitats (Polis, 1988). In some areas, population density can be as high as 10000/ha (Due & Polis, 1986). The mega-diversity of insects and the high biomass of scorpions in the arthropod community imply that trophic interactions between these groups are pivotal to the arthropod communities.

To narrow the knowledge gap in trophic interactions between scorpions and insects, we assembled a data set of insect preys, predators, and parasitoids of scorpions from literature to build trophic links within arthropod food webs. The limited records on trophic interactions between scorpions and insects enable us to link them through predatory and parasitoidism interactions.

2 Materials and methods

2.1 Data acquisition

We aimed to compile all records of interactions between scorpions and insects currently available in published scientific literature. To do so, we performed searches on Web of Science with queries consisted of the keywords “scorpion” AND “insect”, the operator OR and one of the following interaction keywords: “predat*”, “prey”, “parasit*”. For the returned hits, we included all associations with genus-level resolution of both scorpions and insects. This procedure enables us to obtain the most precise trophic links between scorpions and insects. In addition, information on trophic interactions between scorpions and insects from our direct field observations was also included. For field observations, we only recorded the case in which the predator-prey relationship can be reliably justified. These only included the cases in which scorpions consuming insects were observed on the spot. Cases in which scorpions and insects sharing a shelter or burrow were excluded.

2.2 Data analyses

Three types of trophic interactions, predator-prey, prey-predator and host-parasitoid, between scorpions and insects were considered. For predator-prey interaction types, we group scorpions to family level while insects to order level and calculated their interaction frequency. As the cases for host-parasitoid interactions were rare, we group both scorpions and insects to family levels. Trophic interactions were described and visualized by bipartite networks using R package bipartiteD3.

3 Results

3.1 Prey of scorpions

Predator-prey interaction was the most common trophic interaction type between scorpions and insects. Documented

records include 45 scorpion species from 9 families predating on 79 insect species from 11 orders (Fig. 1 and Table 1). Insects of Coleoptera were the dominant prey of scorpions, making up 30.38% (24/79) of known prey species. This was followed by insects of Orthoptera (15.19%), Hymenoptera (13.92%), Lepidoptera (10.13%), Blattodea (10.13%), and Hemiptera (8.86%). Insects of Diptera, Mantodea, Neuroptera, Embioptera, and Dermaptera appeared less frequently predated by scorpions. More than half (53.33%, 24/45) of known scorpion predators of insects belonged to the family Buthidae, which widely predated on insects from 10 orders. It was recorded that two scorpion species of Vaejovidae predated on insects from 6 orders, and 9 species of Scorpionidae fed on 4 insect orders. The prey of other scorpion families was poorly documented.

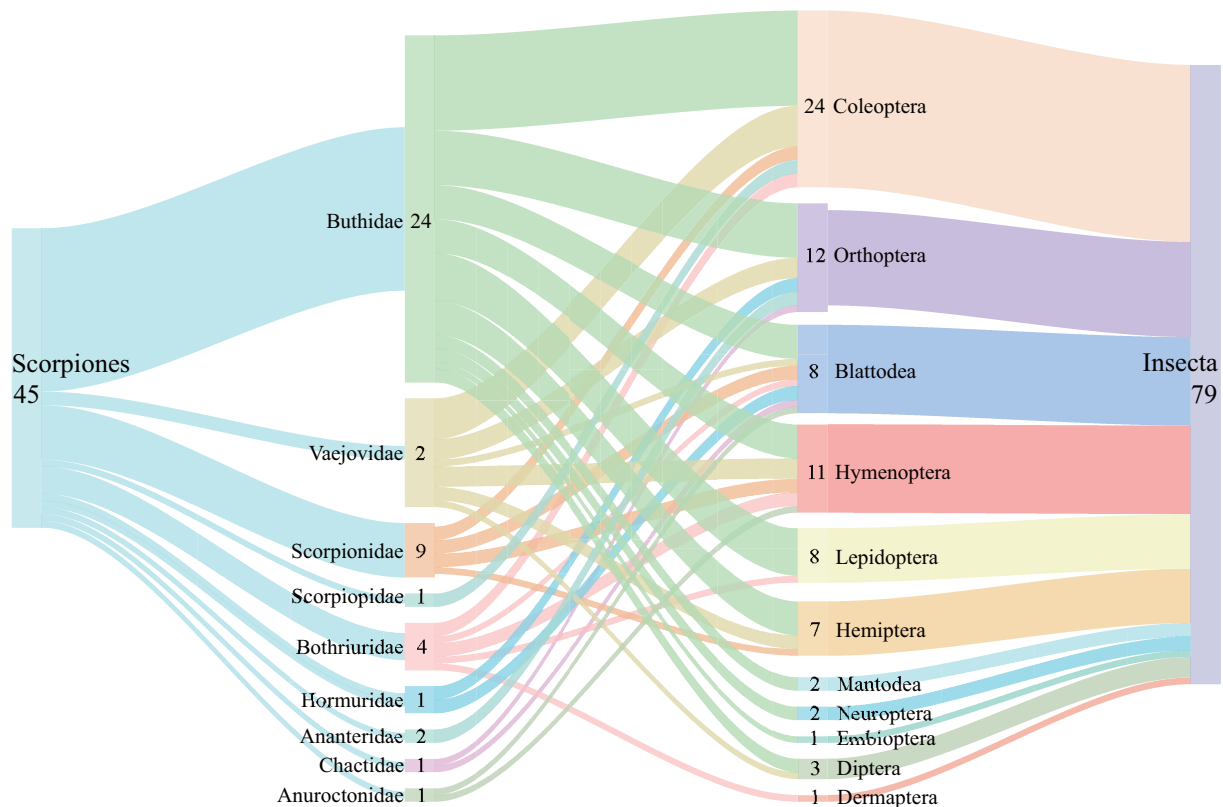


Figure 1. The predator-prey interactions between scorpions and insects.

3.2 Predation of scorpions by insects

Predatory insects are diverse and abundant in natural environments, many of which are used as biological control agents. We found 11 insect species from 4 orders (Hemiptera, Hymenoptera, Coleoptera, and Orthoptera) predate on 11 scorpion species (Fig. 2 and Table 2). Most insect predators (5 species) of scorpions belong to Hymenoptera, which was followed by Hemiptera (3 species). While orthopterans are among the most common prey of scorpions, a katydid, *Hyperomerus* sp. (Orthoptera: Tettigoniidae) was found to predate scorpions of Chactidae in terra firme forest of the western Amazon region in Brazil (Almeida *et al.*, 2022).

3.3 Parasitoids of scorpions

Parasitoids are insects whose larvae feed in or on an arthropod host and eventually kill it but adults are free-living. Approximately 10% of all described insect species are parasitoids (Eggleton & Belshaw, 1992). Records about parasitoids of scorpions are extremely rare. Only four species of parasitoids infecting scorpions have been reported, all of which are Diptera (Fig. 3 and Table 3). Two species of Sarcophagidae (*Sarcodexia stemodontis*, *Sarcophaga dux*) were found to parasitize scorpions of Buthidae (Townsend, 1893; Shi *et al.*, 2015b). The tachinid fly *Spilochaetosoma californicum* (Tachinidae) parasitizes scorpions of both Anuroctonidae and Vaejovidae. The desert scorpion *Mesobuthus mongolicus* was parasitized by larvae of the scuttle fly *Megaselia scalaris* (Phoridae) (Zhang *et al.*, 2017).

Table 1. Insect preys consumed by scorpions.

Scorpions	Insect Preys			References
	Species	Order	Family	
Ananteridae				
<i>Ananteris balzani</i>	<i>Acheta</i> sp.	Orthoptera	Gryllidae	García-Hernandez & Machado, 2020
<i>Ananteris mauryi</i>	<i>Gryllus assimilis</i>	Orthoptera	Gryllidae	Feitosa <i>et al.</i> , 2022
Anuroctonidae				
<i>Anuroctonus phaiodactylus</i>	<i>Blatta orientalis</i>	Blattodea	Blattidae	Williams <i>et al.</i> , 1990
	<i>Apis mellifera</i>	Hymenoptera	Apidae	Williams <i>et al.</i> , 1990
Bothriuridae				
<i>Bothriurus bonariensis</i>	<i>Blatta orientalis</i>	Blattodea	Blattidae	Simone <i>et al.</i> , 2018
	<i>Forficula auricularia</i>	Dermoptera	Forficulidae	Simone <i>et al.</i> , 2018
<i>Brachistosternus cekalovici</i>	<i>Gyriosomus luzotii</i>	Coleoptera	Tenebrionidae	Ojanguren <i>et al.</i> , 2016
<i>Brachistosternus paposo</i>	<i>Gyriosomus kingi</i>	Coleoptera	Tenebrionidae	Ojanguren <i>et al.</i> , 2016
<i>Centromachetes pococki</i>	<i>Dalaca pallens</i>	Lepidoptera	Hepialidae	Cekalovic, 1968
	<i>Apis mellifera</i>	Hymenoptera	Apidae	Cekalovic, 1968
	<i>Camponotus</i> sp.	Hymenoptera	Formicidae	Cekalovic, 1968
Buthidae				
<i>Androctonus finitimus</i>	<i>Musca domestica</i>	Diptera	Musca	Tobassum <i>et al.</i> , 2018
	<i>Manduca quinquemaculata</i>	Lepidoptera	Sphingidae	Tobassum <i>et al.</i> , 2018
	<i>Acheta domestica</i>	Orthoptera	Acrididae	Tobassum <i>et al.</i> , 2018
	<i>Acrida conica</i>	Orthoptera	Gryllidae	Tobassum <i>et al.</i> , 2018
<i>Buthacus tadmorensis</i>	<i>Erodium</i> sp.	Coleoptera	Tenebrionidae	Shehab <i>et al.</i> , 2011
	<i>Pimelia</i> sp.	Coleoptera	Tenebrionidae	Shehab <i>et al.</i> , 2011
	<i>Trachyderma hispida</i>	Coleoptera	Tenebrionidae	Shehab <i>et al.</i> , 2011
	<i>Eremiaphila</i> sp.	Mantodea	Eremiaphilidae	Shehab <i>et al.</i> , 2011
<i>Buthacus yotvatensis</i>	<i>Synclisis baetica</i>	Neuroptera	Mymeleontidae	Segev <i>et al.</i> , 2019
<i>Buthus occitanus</i>	<i>Alphasida</i> sp.	Coleoptera	Tenebrionidae	Sanchez-Pinero & Urbano-Tenorio, 2016
	<i>Cardiophorus</i> sp.	Coleoptera	Elateridae	Sanchez-Pinero & Urbano-Tenorio, 2016
	<i>Cycloderes glabratus</i>	Coleoptera	Curculionidae	Sanchez-Pinero & Urbano-Tenorio, 2016
	<i>Morica hybrida</i>	Coleoptera	Tenebrionidae	Sanchez-Pinero & Urbano-Tenorio, 2016
	<i>Pimelia</i> sp.	Coleoptera	Tenebrionidae	Sanchez-Pinero & Urbano-Tenorio, 2016
	<i>Haploembia palaui</i>	Embiopoda	Oligotomidae	Sanchez-Pinero & Urbano-Tenorio, 2016
	<i>Camptopus lateralis</i>	Hemiptera	Alydidae	Sanchez-Pinero & Urbano-Tenorio, 2016

Table 1 (continued)

Scorpions	Insect Preys			References
	Species	Order	Family	
	<i>Emblethis parvus</i>	Hemiptera	Rhyparochromidae	Sanchez-Pinero & Urbano-Tenorio, 2016
	<i>Plinthisus</i> sp.	Hemiptera	Rhopalidae	Sanchez-Pinero & Urbano-Tenorio, 2016
	<i>Rhopalus parumpunctatus</i>	Hemiptera	Rhopalidae	Sanchez-Pinero & Urbano-Tenorio, 2016
	<i>Camponotus foreli</i>	Hymenoptera	Formicidae	Sanchez-Pinero & Urbano-Tenorio, 2016
	<i>Crematogaster auberti</i>	Hymenoptera	Formicidae	Sanchez-Pinero & Urbano-Tenorio, 2016
	<i>Messor sexual</i>	Hymenoptera	Formicidae	Sanchez-Pinero & Urbano-Tenorio, 2016
	<i>Aglossa pinguinalis</i>	Lepidoptera	Pyralidae	Sanchez-Pinero & Urbano-Tenorio, 2016
	<i>Agrotis</i> sp.	Lepidoptera	Noctuidae	Sanchez-Pinero & Urbano-Tenorio, 2016
<i>Centruroides edwardsii</i>	<i>Blaptica dubia</i>	Blattodea	Blaberidae	Díaz <i>et al.</i> , 2019
	<i>Periplaneta australasiae</i>	Blattodea	Blaberidae	Díaz <i>et al.</i> , 2019
	<i>Phyllophaga</i> sp.	Coleoptera	Scarabaeidae	Díaz <i>et al.</i> , 2019
	<i>Tenebrio molitor</i>	Coleoptera	Tenebrionidae	Díaz <i>et al.</i> , 2019
	<i>Peckia</i> sp.	Diptera	Sarcophagidae	Díaz <i>et al.</i> , 2019
	<i>Atta</i> sp.	Hymenoptera	Formicidae	Díaz <i>et al.</i> , 2019
	<i>Camponotus</i> sp.	Hymenoptera	Formicidae	Díaz <i>et al.</i> , 2019
	<i>Acheta assimilis</i>	Orthoptera	Gryllidae	Díaz <i>et al.</i> , 2019
	<i>Acheta domesticus</i>	Orthoptera	Gryllidae	Díaz <i>et al.</i> , 2019
<i>Centruroides granosus</i>	<i>Acheta domesticus</i>	Orthoptera	Gryllidae	Garcia <i>et al.</i> , 2022
<i>Centruroides hentzi</i>	<i>Gryllodes sigillatus</i>	Orthoptera	Gryllidae	Ward <i>et al.</i> , 2018
<i>Centruroides vittatus</i>	<i>Acheta domesticus</i>	Orthoptera	Gryllidae	Rowe & Carlson, 2009
	<i>Tenebrio molitor</i>	Coleoptera	Tenebrionidae	Rowe & Carlson, 2009
	<i>Zoophobas morio</i>	Coleoptera	Tenebrionidae	Rowe & Carlson, 2009
<i>Centruroides sculpturatus</i>	<i>Acheta domesticus</i>	Orthoptera	Gryllidae	Webber & Rodríguez-Robles, 2013
<i>Hottentotta judaicus</i>	<i>Schistocerca gregaria</i>	Orthoptera	Acrididae	Raviv & Gefen, 2021
<i>Hottentotta tamulus</i>	<i>Manduca quinquemaculata</i>	Lepidoptera	Sphingidae	Tobassum <i>et al.</i> , 2018
	<i>Acrida conica</i>	Orthoptera	Acrididae	Tobassum <i>et al.</i> , 2018
	<i>Acheta domestica</i>	Orthoptera	Gryllidae	Tobassum <i>et al.</i> , 2018
	<i>Musca domestica</i>	Diptera	Musca	Tobassum <i>et al.</i> , 2018
<i>Jaguajir rochae</i>	<i>Phoetalia circumvagans</i>	Orthoptera	Gryllidae	Silva <i>et al.</i> , 2019
<i>Mesobuthus mongilicus</i>	<i>Acheta domesticus</i>	Orthoptera	Gryllidae	Prevost & Stemme, 2020
	<i>Harpalus amplicollis</i>	Coleoptera	Carabidae	Shi <i>et al.</i> , 2015a
	<i>Harpalus froelichii</i>	Coleoptera	Carabidae	Shi <i>et al.</i> , 2015a

Table 1 (continued)

Scorpions	Insect Preys			References
	Species	Order	Family	
<i>Mesobuthus gibbosus</i>	<i>Carabus banoni</i>	Coleoptera	Carabidae	Birula, 1917
<i>Mesobuthus martensii</i>	<i>Eupolyphaga sinensis</i>	Blattodea	Corydidae	Lv, 1981
	<i>Tenebrio molitor</i>	Coleoptera	Tenebrionidae	Lv, 1981
	<i>Ulomoides dermestoides</i>	Coleoptera	Tenebrionidae	Lv, 1981
	<i>Corcyra cephalonica</i>	Lepidoptera	Galleriidae	Lv, 1981
	<i>Ostrinia nubilalis</i>	Lepidoptera	Pyralidae	Lv, 1981
	<i>Plodia interpunctella</i>	Lepidoptera	Pyralidae	Lv, 1981
	<i>Plutella xylostella</i>	Lepidoptera	Plutellidae	Xu <i>et al.</i> , 2013
	<i>Mantis religiosa</i>	Mantodea	Mantidae	Lv, 1981
	<i>Odontobuthus odonturus</i>	<i>Musca domestica</i>	Diptera	Musca
<i>Orthochirus scrobiculosus</i>	<i>Mymeleon</i> sp.	Neuroptera	Myrmeleontidae	Segev <i>et al.</i> , 2019
<i>Tityus fuhrmanni</i>	<i>Periplaneta americana</i>	Blattodea	Blattidae	Arroyave-Muñoz <i>et al.</i> , 2022
	<i>Acheta domesticus</i>	Orthoptera	Gryllidae	Arroyave-Muñoz <i>et al.</i> , 2022
<i>Tityus neibae</i>	<i>Acheta domestica</i>	Orthoptera	Gryllidae	Silva-Júnior <i>et al.</i> , 2022
<i>Tityus pusillus</i>	<i>Gryllus assimilis</i>	Orthoptera	Gryllidae	Feitosa <i>et al.</i> , 2022
	<i>Nauphoeta cinerea</i>	Blattodea	Blaberidae	Lira <i>et al.</i> , 2020
<i>Tityus serrulatus</i>	<i>Nauphoeta cinerea</i>	Blattodea	Blaberidae	Pucca <i>et al.</i> , 2014
	<i>Tenebrio molitor</i>	Coleoptera	Tenebrionidae	Mineo & Del-Claro, 2006
	<i>Ulomoides dermestoides</i>	Coleoptera	Tenebrionidae	Pucca <i>et al.</i> , 2014
	<i>Zophobas morio</i>	Coleoptera	Tenebrionidae	Pucca <i>et al.</i> , 2014
	<i>Grilus</i> sp.	Orthoptera	Gryllidae	Pucca <i>et al.</i> , 2014
<i>Tityus</i> sp.	<i>Blaptica dubia</i>	Blattodea	Blaberidae	Garcia <i>et al.</i> , 2022
<i>Uroplectes lineatus</i>	<i>Temnopteryx phalerata</i>	Blattodea	Ectobiidae	Eastwood, 1978
<i>Uroplectes insignis</i>	<i>Temnopteryx phalerata</i>	Blattodea	Ectobiidae	Eastwood, 1978
Chactidae				
<i>Chactas</i> sp.	<i>Acheta domesticus</i>	Orthoptera	Gryllidae	Garcia <i>et al.</i> , 2022
	<i>Blaptica dubia</i>	Blattodea	Blaberidae	Garcia <i>et al.</i> , 2022
Hormuridae				
<i>Opisthacanthus elatus</i>	<i>Acheta domesticus</i>	Orthoptera	Gryllidae	Garcia <i>et al.</i> , 2022
	<i>Blaptica dubia</i>	Blattodea	Blaberidae	Garcia <i>et al.</i> , 2022

Table 1 (continued)

Scorpions	Insect Preys			References
	Species	Order	Family	
Scorpionidae				
<i>Heterometrus fulvipes</i>	<i>Periplaneta americana</i>	Blattodea	Blattidae	Kalarani <i>et al.</i> , 1992
<i>Heterometrus petersii</i>	<i>Tenebrio molitor</i>	Coleoptera	Tenebrionidae	Jiao, 2009
	<i>Zophobas morio</i>	Coleoptera	Tenebrionidae	Jiao, 2009
<i>Heterometrus spinifer</i>	<i>Gromphadorhina portentosa</i>	Blattodea	Blaberidae	Chandler <i>et al.</i> , 2020
<i>Opisthophthalmus capensis</i>	<i>Dorylinus helvolus</i>	Hymenoptera	Formicidae	Eastwood, 1978
	<i>Temnopteryx phalerata</i>	Blattodea	Ectobiidae	Eastwood, 1978
<i>Scorpio maurus</i>	<i>Mesor</i> sp.	Hymenoptera	Formicidae	Shachak & Brand, 1983
<i>Urodacus armatus</i>	<i>Periplaneta americana</i>	Blattodea	Blattidae	Quinlan <i>et al.</i> , 1995
<i>Urodacus novaehollandiae</i>	<i>Periplaneta americana</i>	Blattodea	Blattidae	Quinlan <i>et al.</i> , 1995
<i>Urodacus yaschenkoi</i>	<i>Acyrtosiphon pisum</i>	Hemiptera	Aphididae	Luna-Ramirez <i>et al.</i> , 2017
Scorpiopidae				
<i>Scorpiops luridus</i>	<i>Tenebrio molitor</i>	Coleoptera	Tenebrionidae	Jiao, 2010
	<i>Zophobas morio</i>	Coleoptera	Tenebrionidae	Jiao, 2010
Vaejovidae				
<i>Paruroctonus mesaensis</i>	<i>Arenievaga investigata</i>	Blattodea	Blattidae	Polis, 1979
	<i>Batulius</i> sp.	Coleoptera	Tenebrionidae	Polis, 1979
	<i>Edrotes ventricosus</i>	Coleoptera	Tenebrionidae	Polis, 1979
	<i>Eupsophulus castaneus</i>	Coleoptera	Tenebrionidae	Polis, 1979
	<i>Eussatus muricatus</i>	Coleoptera	Tenebrionidae	Polis, 1979
	<i>Telabis</i> sp.	Coleoptera	Tenebrionidae	Polis, 1979
	<i>Trigonoscuta</i> sp.	Coleoptera	Curculionidae	Polis, 1979
	<i>Proctacanthella</i> sp.	Diptera	Asilidae	Polis, 1979
	<i>Chlorochroa</i> sp.	Hemiptera	Pentatomidae	Polis, 1979
	<i>Ligyrocoris</i> sp.	Hemiptera	Lygaeidae	Polis, 1979
	<i>Photopsis</i> sp.	Hymenoptera	Mutillidae	Polis, 1979
	<i>Pogonotmyrtex californicus</i>	Hymenoptera	Formicidae	Polis, 1979
	<i>Solenopsis xyloni</i>	Hymenoptera	Formicidae	Polis, 1979
	<i>Macrobaenetes valgum</i>	Orthoptera	Gryllacrididae	Polis, 1979
	<i>Stenopelmatius coahuilerisis</i>	Orthoptera	Stenopelmatidae	Polis, 1979
	<i>Vaejovis carolinianus</i>	<i>Acheta domesticus</i>	Orthoptera	Gryllidae

Table 2. Insect predators of scorpions.

Scorpions	Insect Predators			References
	Species	Order	Family	
Ananteridae				
<i>Ananteris leilae</i>	<i>Agelais centralis</i>	Hymenoptera	Vespidae	Miranda <i>et al.</i> , 2021
	<i>Leptogenys cuneata</i>	Hymenoptera	Formicidae	Miranda <i>et al.</i> , 2021
<i>Ananteris mauryi</i>	<i>Ectatomma planidens</i>	Hymenoptera	Formicidae	Dionisio-da-Silva & Lira, 2019
Anuroctonidae				
<i>Anuroctonus phaiodactylus</i>	<i>Eleodes grandicoliis</i>	Coleoptera	Tenebrionidae	Williams, 1966
	<i>Stenopelmatus</i> sp.	Orthoptera	Stenopelmatidae	Williams, 1966
Buthidae				
<i>Centruroides hentzi</i>	<i>Microtomus purcis</i>	Hemiptera	Reduviidae	Stevenson & Stohlgren, 2015
<i>Physoctonus debilis</i>	<i>Microtomus tibialis</i>	Hemiptera	Reduviidae	Silva-Júnior <i>et al.</i> , 2023
<i>Tityus pusillus</i>	Harpactorini sp.	Hemiptera	Reduviidae	Lira <i>et al.</i> , 2016
<i>Tityus stigmurus</i>	<i>Dinoponera quadriceps</i>	Hymenoptera	Formicidae	Santos <i>et al.</i> , 2017
Chactidae				
<i>Chactopsis</i> sp.	<i>Hyperomerus</i> sp.	Orthoptera	Tettigoniidae	Almeida <i>et al.</i> , 2022
Vaejovidae				
<i>Paruroctonus boreus</i>	<i>Stenopelmatus</i> sp.	Orthoptera	Stenopelmatidae	Tourtlotte, 1974
<i>Paruroctonus luteolus</i>	<i>Pogonomyrmex rugosus</i>	Hymenoptera	Formicidae	Polis <i>et al.</i> , 1981
<i>Paruroctonus mesaensis</i>	<i>Pogonomyrmex rugosus</i>	Hymenoptera	Formicidae	Polis <i>et al.</i> , 1981

Table 3. Insect parasitoids of scorpions.

Scorpions	Insect Parasitoids			References
	Species	Order	Family	
Anuroctonidae				
<i>Anuroctonus phaiodactylus</i>	<i>Spilochaetosoma californicum</i>	Diptera	Tachinidae	Williams <i>et al.</i> , 1990
Buthidae				
<i>Centruroides edwardsii</i>	<i>Sarcodexia stemodontis</i>	Diptera	Sarcophagidae	Townsend, 1893
<i>Mesobuthus martensii</i>	<i>Sarcophaga dux</i>	Diptera	Sarcophagidae	Shi <i>et al.</i> , 2015b
<i>Mesobuthus mongolicus</i>	<i>Megaselia scalaris</i>	Diptera	Phoridae	Zhang <i>et al.</i> , 2017
Vaejovide				
<i>Vaejovis spinigeru</i>	<i>Spilochaetosoma californicum</i>	Diptera	Tachinidae	Wood, 1987

4 Discussion

Trophic interactions are the links of food webs that are at the nexus of biodiversity, functioning, and stability (Potapov *et al.*, 2023). They are key determinants of population abundance and dynamics, the structure and persistence of communities, and the rate and sustainability of ecosystem processes (Woodward *et al.*, 2010). A comprehensive grasp of trophic interactions is instrumental in elucidating the structure and functioning of biodiversity. However, the current knowledge of scorpion-insect interactions in the arthropod food webs is highly fragmentary and incomplete. A major reason for such a knowledge gap is the nocturnal nature of scorpions. While the nocturnal nature of scorpions makes the establishment of trophic links in food webs particularly challenging, poor recognition of scorpions' ecological role is responsible for the long-term overlook of scorpions in food web studies.

Our survey here revealed scorpions predate at least 79 insect species belonging to 11 orders (Fig. 1). Besides, it has been reported that items of Isoptera was consumed by scorpion *Troglorhopalurus lacrau*, of Phasmatodea was consumed by *Tityus pusillus*, and of Zygentoma was consumed by *Jaguajir rochae* and *Physoctonus debilis* in Brazil (Dionisio-da-Silva *et al.*, 2024). Although the prey insects were not identified to the genus level, these observations accumulated the total

number of insect prey orders of scorpions to 13. At the same time, scorpions were predated by 11 insect species from four orders (Fig. 2), and were parasitized by four species of Diptera (Fig. 3). Given the generalism of predation as indicated by scorpion of Buthidae and the high diversity of insect parasitoids and predators, as well as the high biomass of scorpions in some ecosystems, it can predict that trophic interactions between scorpions and insects would be pervasive. A history of over 410 million years of evolution side by side would imply that interactions between scorpions and insects are extensive. Thus,

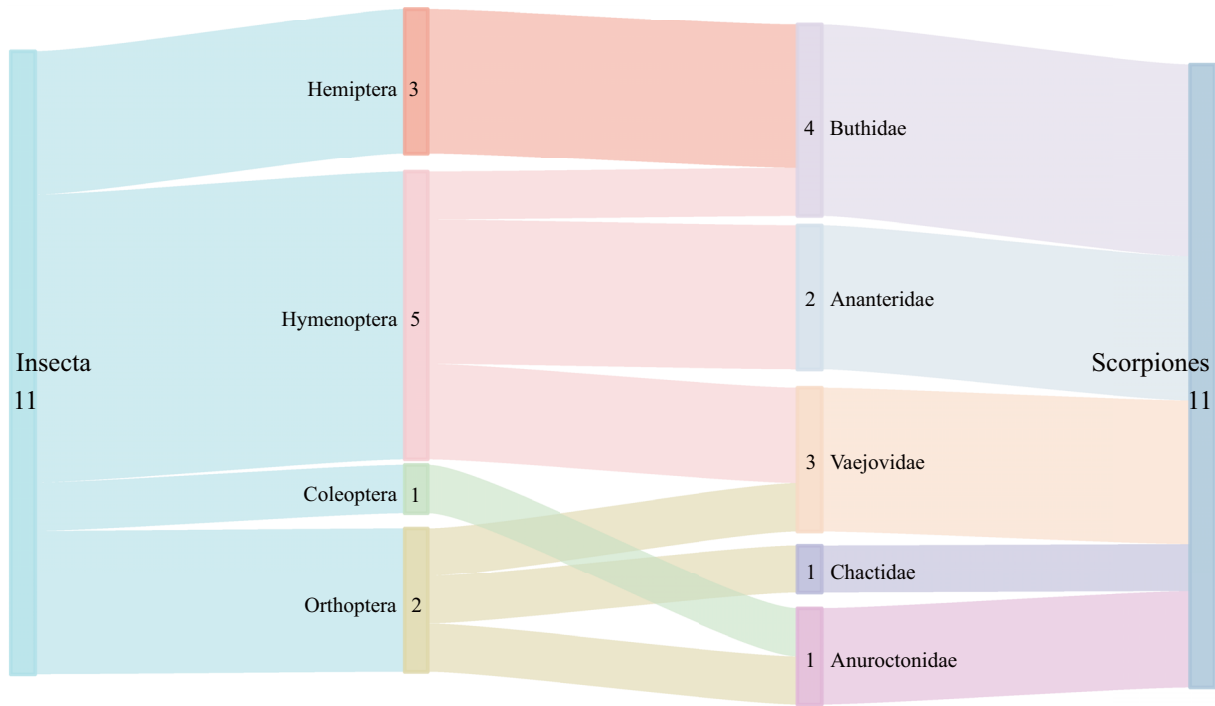


Figure 2. The prey-predator interactions between scorpions and insects.

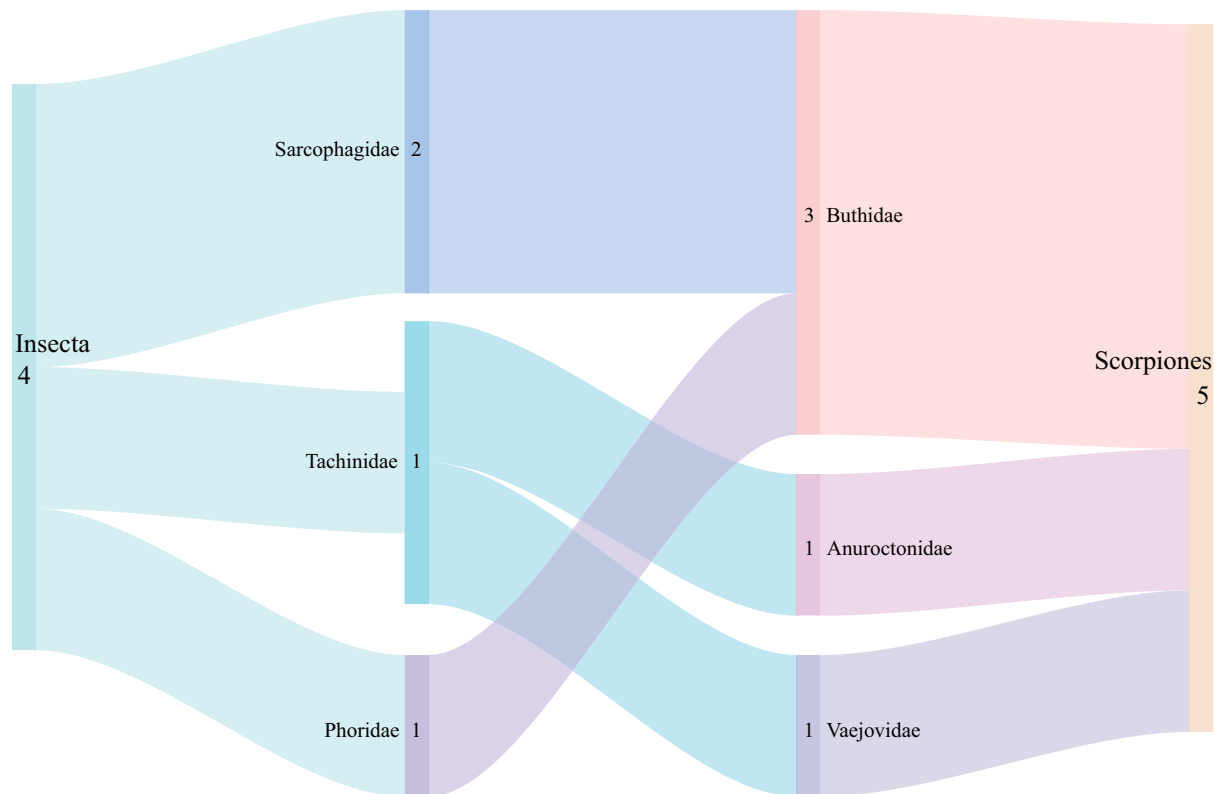


Figure 3. The host-parasitoid interactions between scorpions and insects.

it is very likely that we have only observed a tiny fraction of complex interactions between scorpions and insects.

While understanding of the diversity of scorpions and insects has greatly accelerated with DNA-based species recognition approaches, DNA-based methods also provide new opportunities for systematically studying trophic interaction between them (King *et al.*, 2008). We believe that diet DNA metabarcoding based on the next generation sequencing technologies (de Sousa *et al.*, 2019) will enable research on trophic interactions between scorpions and insects to go beyond the taxonomic framework of description of dietary composition. Further efforts should be directed at understanding why a certain insect is prey for a given scorpion species and to characterize the ecological role of their trophic interaction in sustaining biodiversity and ecosystem function.

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References

- Ahsan, M.M., Tahir, H.M. 2016. Foraging behaviour of *Hottentotta tumulus* (Fabricius, 1798) and *Odontobuthus odonturus* (Pocock, 1897). *Zoological Society of Pakistan*, 48(6): 1811–1811.
- Åkesson, A., Curtsdotter, A., Eklöf, A., Ebenman, B., Norberg, J., Barabás, G. 2021. The importance of species interactions in eco-evolutionary community dynamics under climate change. *Nature Communications*, 12: 4759.
- Almeida, M.R.N., Nascimento, J.A.F., Machado, E.O., Lira, A.F.A. 2022. Once a prey, now a predator: an unusual record of a scorpion (Scorpiones: Chactidae) predated by a katydid (Orthoptera: Tettigoniidae) in the western Brazilian Amazon. *Acta Amazonica*, 52(3): 229–231.
- Arroyave-Muñoz, A., Meijden, A., Estrada-Gómez, S., García, L.F. 2022. Linking toxicity and predation in a venomous arthropod: the case of *Tityus fuhrmanni* (Scorpiones: Buthidae), a generalist predator scorpion. *Journal of Venomous Animals and Toxins Including Tropical Diseases*, 28(1): 1–10.
- Bartley, T.J., McCann, K.S., Bieg, C., Cazelles, K., Granados, M., Guzzo, M.M., MacDougall, A.S., Tunney, T.D., McMeans, B.C. 2019. Food web rewiring in a changing world. *Nature Ecology & Evolution*, 3: 345–354.
- Birula, A.A. 1917. *Arthrogastric Arachnids of Caucasia, Part I, Scorpion*. Israel Program of Scientific Translations, Jerusalem. 170 pp.
- Cekalovic, T. K. 1968. Alimentación y habitan de *Centromachetes pocock* (Kraepelin), 1984 (Scorpionida-Bothriuridae). *Boletín de la Sociedad de Biología de Concepción*, 40: 27–32.
- Chandler, K.L., Davis, J., Wolford, D. 2020. Arthropod Thunderdome: Antipredator responses of *Gromphadorhina portentosa* in relation to predator species and relative size differential. In: *The Society for Integrative and Comparative Biology. 2020 Annual Meeting Abstracts*. JW Marriott Austin, Austin. p. e294.t
- de Sousa, L.L., Silva, S.M., Xavier, R. 2019. DNA metabarcoding in diet studies: Unveiling ecological aspects in aquatic and terrestrial ecosystems. *Environmental DNA*, 1: 199–214.
- Díaz, C., Rivera, J., Lomonte, B., Bonilla, F., Diego-García, E., Camacho, E., Tytgat, J., Sasa, M. 2019. Venom characterization of the bark scorpion *Centruroides edwardsii* (Gervais 1843): Composition, biochemical activities and in vivo toxicity for potential prey. *Toxicon*, 171: 7–19.
- Dionisio-da-Silva, W., Foerster, S.Á.A., Gallão, J.E., Lira, A.F.A. 2024. What's for dinner? Prey consumption by neotropical scorpions across contrasting environments. *The Journal of Arachnology*, 52: 26–30.
- Dionisio-da-Silva, W., Lira, A. 2019. Record of *Ananteris mauryi* (Scorpiones: Buthidae) Preyed Upon by *Ectatomma planidens* (Hymenoptera: Formicidae) in the Brazilian Atlantic Rainforest. *Biology, Environmental Science Proceedings of the Entomological Society of Washington*, 128: 497–503.
- Due, A.D., Polis, G.A. 1986. Trends in scorpion diversity along the Baja California peninsula. *The American Naturalist*, 128(4): 460–468.
- Dyer, L.A., Walla, T.R., Greeney, H.F., III, J.O.S., Hazen, R.F. 2010. Diversity of interactions: A metric for studies of biodiversity. *Biotropica*, 42(3): 281–289.
- Eastwood, E.B. 1978. Notes on the scorpion fauna of the Cape. Part 3. Some observations on the distribution and biology of scorpions on Table Mountain. *Annals of the South African Museum. Annale van die Suid-Afrikaanse Museum*, 74: 229–248.
- Eggleton, P., Belshaw, R. 1992. Insect parasitoids: An evolutionary overview. *Philosophical Transactions of the Royal Society B Biological Science*, 337(1279): 1–20.
- Engel, M.S., Grimaldi, D.A. 2004. New light shed on the oldest insect. *Nature*, 427: 627–630.
- Feitosa, M.L.B., Dionisio-da-Silva, W., Lira, A.F.A., Teles-Pontes, W.J. 2022. Fear as an enemy? Behavioral changes of *Ananteris mauryi* (Scorpiones: Buthidae) triggered by chemical cues from an intraguild predator. *Canadian Journal of Zoology*, 100: 488–493.

- Garcia, L.F., Valenzuela-Rojas, J.C., Gonzalez-Gomez, J.C., Lacava, M., van der Meijden, A. 2022. Pinching or stinging? Comparing prey capture among scorpions with contrasting morphologies. *Journal of Venomous Animals and Toxins including Tropical Diseases*, 28: e20210037.
- Howard, R.J., Edgecombe, G.D., Legg, D.A., Pisani, D., Lozano-Fernandez, J. 2019. Exploring the evolution and terrestrialization of scorpions (Arachnida: Scorpiones) with rocks and clocks. *Organisms Diversity & Evolution*, 19: 71–86.
- Jiao G. B, Zhu M, H. 2009. Prey Capture Behavior in *Heterometrus petersii* (Thorell, 1876) (Scorpiones: Scorpionidae). *Euscorpius*, 80: 1–5.
- Jiao G. B, Zhu M, H. 2010. Cleaning behaviors in four scorpion species. *Journal of Venomous Animals and Toxins including Tropical Diseases*, 16(2): 375–381.
- Kalarani, V., Murali Mohan, P., Davies, R.W. 1992. Thermal acclimation and metabolism of the hepatopancreas in the tropical scorpion, *Heterometrus fulvipes*. *Journal of Thermal Biology*, 17(3): 141–146.
- King, R.A., Read, D.S., Traugott, M., Symondson, W.O.C. 2008. Molecular analysis of predation: a review of best practice for DNA-based approaches. *Molecular Ecology*, 17: 947–963.
- Lira, A.F.A., Araújo, V.L.N., Albuquerque, C.M.R. 2016. Predation of a scorpion (Scorpiones: Buthidae) by an assassin bug (Heteroptera: Reduviidae) in the Brazilian Atlantic Forest. *Turkish Journal of Zoology*, 40: 294–296.
- Lira, A.F.A., Almeida, F.M.F., Albuquerque, C.M.R. 2020. Reaction under the risk of predation: effects of age and sexual plasticity on defensive behavior in scorpion *Tityus pusillus* (Scorpiones: Buthidae). *Journal of Ethology*, 38(1): 13–19.
- Luna-Ramirez, K., Skaljic, M., Grotmann, J., Kirfel, P., Vilcinskis, A. 2017. Orally delivered scorpion antimicrobial peptides exhibit activity against pea aphid (*Acyrtosiphon pisum*) and its bacterial symbionts. *Toxins (Basel)*, 9(9): 261.
- Lv, X.X. 1981. A preliminary study of the food of the *Mesonuthus martensii*. *Journal of Zoology*, 16(1): 28–31.
- Manlick, P.J., Perryman, N.L., Koltz, A.M., Cook, J.A., Newsome, S.D. 2024. Climate warming restructures food webs and carbon flow in high-latitude ecosystems. *Nature Climate Change*, 14: 184–189.
- Mineo, M.F., Del-Claro, K. 2006. Mechanoreceptive function of pectines in the Brazilian yellow scorpion *Tityus serrulatus*: Perception of substrate-borne vibrations and prey detection. *Acta Ethologica*, 9(2): 79–85.
- Miranda, R.J., Armas, L.F.D., Cambra, R. 2021. Predation of *Ananteris* spp. (Scorpiones: Buthidae) by ants and a social wasp (Hymenoptera: Formicidae, Vespidae) in Panama, Central America. *Euscorpius*, 329: 1–4.
- Nelsen, D.R., David, E.M., Harty, C.N., Hector, J.B., Corbit, A.G. 2020. Risk assessment and the effects of refuge availability on the defensive behaviors of the southern unstriped scorpion (*Vaejovis carolinianus*). *Toxins (Basel)*, 12(9): 1–21.
- Ojanguren, A., Botero-Trujillo, R., Castex, A., Pizarro-Araya, J. 2016. Biological aspects of the genus *Brachistosternus* (Bothriuridae) in the Atacama Desert (Chile), with the description of a new type of pedipalp macroseta. *Gayana*, 80(2): 169–174.
- Padial, J.M., Miralles, A., de la Riva, I., Vences, M. 2010. The integrative future of taxonomy. *Frontiers in Zoology*, 7(1): 16.
- Polis, G.A. 1979. Prey and feeding phenology of the desert sand scorpion *Pamroctonus mesaensis* (Scorpionidae : Vaejovidae). *Journal of Zoology*, 188(3): 333–346.
- Polis, G.A. 1988. Foraging and evolutionary responses of desert scorpions to harsh environmental periods of food stress. *Journal of Arid Environments*, 14(2): 123–134.
- Polis, G.A., Sissom, W.D., McCormick, S.J. 1981. Predators of scorpions: field data and a review. *Journal of Arid Environments*, 4: 309–326.
- Potapov, A., Lindo, Z., Buchkowski, R.W., Geisen, S. 2023. Multiple dimensions of soil food-web research: History and prospects. *European Journal of Soil Biology*, 117: 103494.
- Pucca, M.B., Amorim, F.G., Cerni, F.A., Bordon K.C.F., Cardoso, I.A., Anjolette, F.A.P., Arantes, E.C. 2014. Influence of post-starvation extraction time and prey-specific diet in *Tityus serrulatus* scorpion venom composition and hyaluronidase activity. *Toxicon*, 90: 326–336.
- Quinlan, T.G., Calver, M.C., Smithz, G.T. 1995. Relationships between morphology and feeding behaviour in the syntopic scorpions *Urodacus armatus* Pocock and *Urodacus novaehollandiae* Peters (Scorpiones: Scorpionidae). *Journal of the Australian Entomological Society*, 34: 277–279.
- Ratzke, C., Barrere, J., Gore, J. 2020. Strength of species interactions determines biodiversity and stability in microbial communities. *Nature Ecology & Evolution*, 4: 376–383.
- Raviv, D., Gefen, E. 2021. Post-feeding thermophily in a scorpion is associated with rapid digestion and recovery of maximal nocturnal activity. *Journal of Insect Physiology*, 129(2021): 104–155.
- Rowe, M.P., Carlson, B.E. 2009. Temperature and desiccation effects on the antipredator behavior of *Centruroides vittatus* (Scorpiones: Buthidae). *Journal of Arachnology*, 37: 321–330.
- Sanchez-Pinero, F., Urbano-Tenorio, F. 2016. Watch out for your neighbor: climbing onto shrubs is related to risk of cannibalism in the scorpion *Buthus cf. occitanus*. *PLoS One*, 11(9): e0161747.
- Sandall, E.L., Maureaud, A.A., Guralnick, R., McGeoch, M.A., Sica, Y.V., Rogan, M.S., Booher, D.B., Edwards, R., Franz, N., Ingenloff, K., Lucas, M., Marsh, C.J., McGowan, J., Pinkert, S., Ranipeta, A., Uetz, P., Wiczorek, J., Jetz, W. 2023. A globally integrated structure of taxonomy to support biodiversity science and conservation. *Trends in Ecology & Evolution*, 38(12): 1143–1153.
- Santos, G.C.S.G., Lira, A.F.A., de Albuquerque, C.M.R. 2017. Record of *Tityus stigmurus* (Scorpiones: Buthidae) predation by *Dinoponera quadricaps* (Hymenoptera: Formicidae) in the Caatinga biome, Brazil. *Revista Ibérica de Aracnología*, 31: 145–146.

- Segev, N., Berger-Tal, O., Gavish-Regev, E. 2019. Sit-and-wait prey first field observations of scorpions preying on antlions (*Neuroptera*). *Article in Israel Journal of Ecology and Evolution*, 66(1–2): 1–6.
- Shachak, M., Brand, S. 1983. The relationship between sit and wait foraging strategy and dispersal in the desert scorpion, *Scorpio maurus palmatus*. *Oecologia*, 60(3): 371–377.
- Shehab, A.H., Amr, Z., Lindsell, J.A. 2011. Ecology and biology of scorpions in Palmyra, Syria. *Turkish Journal of Zoology*, 35(3): 333–341.
- Shi, C.M., Liang, H.B., Altanchimeg, D., Nonnaizab, Chuluunjav, C., Zhang, D.X. 2015a. Climatic niche defines geographical distribution of *Mesobuthus eupeus mongolicus* (Scorpiones: Buthidae) in Gobi desert. *Zoological Systematics*, 40(3): 339–348.
- Shi, C.M., Zhang, X.S., Zhang, D.X. 2015b. Parasitoidism of the *Sarcophaga dux* (Diptera: Sarcophagidae) on the *Mesobuthus martensii* (Scorpiones: Buthidae) and its implications. *Arthropod Biology*, 108(6): 979–985.
- Silva, M.A., Silva, N.A., Lira, A.F.A., Martins, R.D. 2019. Role of venom quantity in the feeding behavior of *Jaguajir rochae* (Scorpiones: Buthidae). *Acta Ethologica*, 22(2): 99–104.
- Silva-Júnior, A.O., Seiter, M., André, F.A.L., Pontes, W.J.T. 2022. Effects of nutritional stress on reproductive output in the scorpion *Tityus pusillus* Pocock, 1893 (Scorpiones, Buthidae). *Invertebrate Reproduction & Development*, 66(3–4): 218–223.
- Silva-Júnior, A.O., Celante, G.L., Silva, A.M., Gil-Santana, H.R., Moura, G.J.B., Lira, A.F.A. 2023. Report of intraguild predation of the scorpion *Physcoctonus debilis* (C.L. Koch, 1840) (Scorpiones: Buthidae) by the assassin bug *Microtomus tibialis* Stichel, 1926 (Hemiptera: Reduviidae). *Revista Chilena De Entomología*, 49(2): 267–270.
- Simone, Y., Meijden, A.V., García, L.F., Lacava, M., Viera, C. 2018. Predatory versatility in females of the scorpion *Bothriurus bonariensis* (Bothriuridae) overcoming prey with different defensive mechanisms. *Journal of Insect Behavior*, 31(5): 1–14.
- Stevenson, D.J., Stohlgren, K.M. 2015. Predation on the scorpion *Centruroides hentzi* (Banks) (Scorpiones: Buthidae) by the assassin bug *Microtomus purcis* (Drury) (Insecta: Hemiptera: Reduviidae). *Southeastern Naturalist*, 14(1): 1–4.
- Stork, N.E. 2018. How many species of insects and other terrestrial arthropods are there on earth? *Annual Review of Entomology*, 63(1): 31–45.
- Su, Y.K., Xiu, M.H., Yang, H.Y., Shi, C.M. 2024. A chromosome-level genome assembly for the desert scorpion *Mesobuthus przewalskii* from Asian drylands. *Journal of Heredity*: esae059.
- Thompson, R.M., Brose, U., Dunne, J.A., Hall Jr., R.O., Hladysz, S., Kitching, R.L., Martinez, N.D., Rantala, H., Romanuk, T.N., Stouffer, D.B., Tilyanakis, J.M. 2012. Food webs: reconciling the structure and function of biodiversity. *Trends in Ecology & Evolution*, 27(12): 689–697.
- Tobassum, S., Tahir, H.M., Zahid, M.T., Gardner, Q.A., Ahsan, M.M. 2018. Effect of milking method, diet, and temperature on venom production in scorpions. *Journal of Insect Science*, 18(4): 1–7.
- Tourtlotte, G.I. 1974. Studies on the biology and ecology of the northern scorpion, *Paruroctonus boreus* (Girard). *Great Basin Naturalist*, 34(3): 167–179.
- Townsend, C.H.T. 1893. A scorpion parasite. *Journal of the Institute of Jamaica*, 1(5): 221.
- Valiente-Banuet, A., Aizen, M.A., Alcántara, J.M., Arroyo, J., Cocucci, A., Galetti, M., García, M.B., García, D., Gómez, J.M., Jordano, P., Medel, R., Navarro, L., Obeso, J.R., Oviedo, R., Ramírez, N., Rey, P.J., Traveset, A., Verdú, M., Zamora, R. 2014. Beyond species loss: the extinction of ecological interactions in a changing world. *Functional Ecology*, 29(3): 299–307.
- Ward, M.J., Ellsworth, S.A., Hogan, M.P., Nystrom, G.S., Martinez, P., Budhdeo, A., Zelaya, R., Perez, A., Powell, B., He, H., Rokyta, D.R. 2018. Female-biased population divergence in the venom of the Hentz striped scorpion (*Centruroides hentzi*). *Toxicon*, 152: 137–149.
- Webber, M.M., Rodríguez-Robles, J.A. 2013. Reproductive tradeoff limits the predatory efficiency of female Arizona Bark Scorpions (*Centruroides sculpturatus*). *BMC Evolutionary Biology*, 13(197): 1–8.
- Wendruff, A.J., Babcock, L.E., Wirkner, C.S., Kluessendorf, J., Mikulic, D.G. 2020. Silurian ancestral scorpion with fossilised internal anatomy illustrating a pathway to arachnid terrestrialisation. *Scientific Reports*, 10: 14.
- Williams, S.C. 1966. Burrowing activities of the scorpion *Anuroctonus phaeodactylus* (Wood) (Scorpionida: Vejovidae). *Proceedings of the California Academy of Sciences*, 34(4): 419–428.
- Williams, S.C., Arnaud, P.H., Lowe, G. 1990. Parasitism of *Anuroctonus phaeodactylus* (Wood) and *Vaejovis spinigerus* (Wood) (Scorpiones: Vejovidae) by *Spilochaetosoma californicum* Smith (Diptera: Tachinidae), and a review of parasitism in scorpions. *Entomology*, 5: 11–27.
- Wood, D.M. 1987. Tachinidae. In: McAlpine, J.F., Peterson, B.V., Shewell, G.E., Teskey, H.J., Vockeroth, J.R., Wood, D.M. (eds), *Manual of Nearctic Diptera*, Vol. 2. Research Branch/Agriculture Canada, Ottawa. pp. 1193–1269.
- Woodward, G., Blanchard, J., Lauridsen, R.B., Edwards, F.K., Jones, J.I., Figueroa, D., Warren, P.H., Petchey, O.L. 2010. Individual-based food webs: species identity, body size and sampling effects. *Advances in Ecological Research*, 43: 211–266.
- Xu, S.C., Liao, L.K., Pan, X.H., Li, J. 2013. Predation of *Buthus martensii* Karsch on *Plutella xylostella*. *Acta Agriculturae Boreali-occidentalis Sinica*, 22(9): 188–191.
- Zhang, X.S., Liu, G.C., Zhang, D.X., Shi, C.M. 2017. Novel trophic interaction: the scuttle fly *Megaselia scalaris* (Diptera: Phoridae) is a facultative parasitoid of the desert scorpion *Mesobuthus eupeus mongolicus* (Scorpiones: Buthidae). *Journal of Natural History*, 51: 1464–5262.