

Novel trophic interaction: the scuttle fly *Megaselia scalaris* (Diptera: Phoridae) is a facultative parasitoid of the desert scorpion *Mesobuthus eupeus mongolicus* (Scorpiones: Buthidae)

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ABSTRACT

Clear knowledge about trophic interactions among species contributes to understanding biodiversity structuring and ecosystem functioning. However, identification of host-parasitoid interactions is often impeded by the hyper-diversity of parasitoid community and their immature stages under study. As a consequence, our knowledge on host-parasitoid interactions is rather incomplete and many trophic links are still missing. In this study, we discovered that the scuttle fly *Megaselia scalaris* (Loew 1866) facultatively infested the scorpions of *Mesobuthus eupeus mongolicus* (Birula, 1911). We monitored the parasitoidism process in laboratory and obtained the parasitoid adults. The parasitoids were identified by examination of morphological characteristics and genetic analyses of mitochondrial DNA sequences from both larvae and adults. Ecological niche modelling revealed that climatically suitable areas for both parasitoids and scorpions stretch in northwest China. Our results unveiled the missing trophic links between Phoridae and Buthidae, and our morphological description and genetic inventory will provide the basic data for future studies on the exceptionally polyphagous and cosmopolitan insect species, *M. scalaris*.

ARTICLE HISTORY



Received 13 January 2016
Accepted 1 September 2016
Online 10 October 2016

KEYWORDS


Trophic interaction;
parasitoids; hosts; DNA-
barcodes; ecological niche
modelling

Introduction

Knowledge on trophic interactions is pivotal to understand the ecological role of species in ecosystems and to decipher the processes that maintain biodiversity. Particularly, parasitoidism, a special trophic interaction falling between predacious and parasitic lifestyles, is the most widespread form of trophic interactions and is

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 Supplemental data for this article can be accessed [here](#).

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subjected to increasing ecological and evolutionary investigations. Parasitoids are a group of insects whose adults are free-living but larvae develop by feeding in or on the body of an arthropod host and eventually killing it (Eggleton and Belshaw 1992; Godfray 1994). More than 75% of parasitoid species are found in the order of Hymenoptera, and an estimated 16,000 species in the order Diptera are parasitoids which account for approximately 20% of the total number of species with this lifestyle (Eggleton and Belshaw 1992; Feener and Brown 1997). Parasitoids comprise some 10% or more of all metazoan species (Hassell 2000). Consequently, they play a critical ecological role by modulating host population dynamics, being a biological control agent or being a pest itself. In recent years, parasitoids have been increasingly used as model systems to examine fundamental questions in behavioural and evolutionary ecology. In-depth understanding of parasitoid behavioural ecology and parasitoid-host population dynamics have also renewed interest in using parasitoids as biological control agents (Hochberg and Hawkins 1992; Hawkins et al. 1993; Hawkins and Cornell 1994; Hassell 2000). Although, the unparalleled opportunities brought by parasitoid-host model systems have been highly appreciated, our knowledge on such systems is still rather incomplete given the extreme species diversity of parasitoids and complex interactions between parasitoids and their hosts.

In fact, trophic interaction between parasitoids and scorpions seems to be completely overlooked. There is no report of scorpions as hosts for insect parasitoids (McCormick and Polis 1990). This is surprising considering the hyper-diversity of parasitoids and their diverse host spectrum together with the high biomass in communities and long evolutionary history of scorpions (Polis 1990; Polis and Yamashita 1991). Scorpions are an unusual and iconic group of arthropods with great ecological and medical importance. All of them are predators and play a key role in arthropod communities, especially in deserts. An amazing suite of biochemical, physiological, behavioural and ecological adaptations to diverse habitats have ensured scorpions continued evolutionary success over the past 450 million years (Polis 1990). Most prominently, scorpions have evolved venoms that increased their predation success (Castilla et al. 2015). Venoms of about 30 species, all but one species belonging to the family Buthidae, are also dangerous to humans (Chippaux and Goyffon 2008). Envenomation by these scorpions poses a threat to more than 2 billion people worldwide with annual number of stings exceeding a million, 0.27% of which eventually led to death (Chippaux and Goyffon 2008; Isbister and Bawaskar 2014). Although envenomation by scorpions represents a scourge of human beings, venoms of scorpions are a rich source of bioactive molecules with high medical significance (Goudet et al. 2002; Rodriguez de la Vega and Possani 2005) and insecticidal potentials (Smith et al. 2013). Armed with a venomous sting (telson) and a pair of powerful pedipalps, scorpions are presumed to be at the top of the trophic hierarchy in the arthropod communities. This might underlie the neglect of scorpions in host-parasitoid interaction studies.

Accurate identification of parasitoids is not only fundamental to estimate parasitoid diversity but also crucial for understanding host specificity and food web structure of communities. A clear description of host-parasitoid interactions would contribute to decipher the underlying ecological mechanism sustaining food web function and to reveal the likely evolutionary processes that mould, shape and transform trophic interactions. However, species identification of parasitoids is

seriously impeded by the hyper-diversity of the parasitoid community and the fact that only their immature stages are involved in most cases. The availability of genetic data has boosted our abilities to recognise parasitoid biodiversity. With the ever-increasing availability of genetic data, particularly in the form of DNA barcodes, biodiversity studies are witnessing a surge in the discoveries of new species and new species interactions (Meier et al. 2006; Hrcek et al. 2011; Santos et al. 2011), although some discrepancy exists about the thresholds for inter- and intra-specific DNA variability (e.g. Meier et al. 2006; Collins and Cruickshank 2014; Downton et al. 2014). In the present study, combining rearing observation, DNA-based species identification and ecological niche modeling, we set up a host-parasitoid association between the desert scorpion *Mesobuthus eupeus mongolicus* (Birula, 1911) (Figure 1 (a)) and the scuttle fly *Megaselia scalaris* (Loew, 1866) in northwest China. This could represent a missing link in the arthropod trophic web which signals a virgin field in host-parasitoid studies and has immediate implications in biological conservation.



Figure 1. Scorpion, *Mesobuthus eupeus mongolicus* (a) and its parasitoid scuttle fly, *Megaselia scalaris* (b–e): (a) a female scorpion; (b) larvae of fly emerging from the genital operculum of scorpion; (c) fly larva; (d) fly pupa; (e) a male fly.

Materials and methods

Scorpion collection and parasitoids sampling

Scorpions were collected at night using a portable ultraviolet (UV) light from a desert c. 60 km east of Alxa Youqi (39.1°N, 102.3°E), Inner Mongolia, China. The collected scorpions were kept in plastic bottles (750 mL) with pores pierced in the lids for ventilation. It has been reported that *M. eupeus* is the only scorpion species in this sampling region and can be easily identified based on the descriptions of Shi et al. (2007). A previous biogeographic study based on both mitochondrial and nuclear DNA markers found that scorpions from this region clustered in an eastern lineage of *M. eupeus*, which ranged from eastern Tajikistan to southern Mongolia and northwest China (Shi et al. 2013). Based on morphological characteristics and geographical distribution, this lineage is identified as the subspecies *M. eupeus mongolicus* (Birula, 1911). Maggots emerging from dead scorpions were reared into adulthood in a climatic chamber at 27°C, 75% relative humidity (RH) and natural lighting. A total of 70 adult flies were obtained at the end of rearing. Flies were identified morphologically by G.C. Liu.

Molecular protocols and genetic analyses

We randomly sampled four larvae and five adults for molecular identification. Genomic DNA was extracted using a modified phenol-chloroform extraction protocol (Zhang and Hewitt 1998). The mitochondrial cytochrome C oxidase I gene (*mtCOI*) was polymerase chain reaction (PCR) amplified using the primers pair LCO1490 (Folmer et al. 1994) and Nancy (Simon et al. 1994), which flanks a 676-bp region spanning positions 1457–2132 of the mitochondrial genome in the scuttle fly, *M. scalaris* (NC_023794.1). The protocols for PCR amplification and DNA sequencing were essentially as described by Shi et al. (2013). All the voucher specimens and DNA extracts are deposited at the Laboratory of Molecular Ecology and Evolution, Institute of Zoology (MEE-IOZ), Chinese Academy of Sciences, Beijing. All nucleotide sequences are deposited in GenBank under accession numbers KX832630–KX832638.

The newly obtained sequences were used as queries in the BLAST program to search for homologous sequences in the National Center for Biotechnology Information collection (Altschul et al. 1990). We retrieved all homologous sequences with query coverage > 80% (> 500 bp) and similarity > 90%. This threshold for similarity is larger than the maximum within-species divergence (9.71%) found in flies (Jiang et al. 2014). From GenBank, we also obtained *mtCOI* sequences from other species of the genus *Megaselia*. Sequences from *Drosophila cuaso* (EF569993) and *Drosophila dunni* (HM006882) were used as outgroups. All sequences were aligned using Clustal X 1.83 (Thompson et al. 1997). Phylogenetic analyses were performed using both maximum likelihood (ML) and Bayesian methods with the best-fit DNA evolution model selected by ModelTest 3.7 (Posada and Crandall 1998) according to the Akaike information criterion. ML analysis was carried out using PHYML 3.0 (Guindon and Gascuel 2003) and topological robustness was assessed through 1000 bootstrap replicates. Bayesian inference implemented in MrBayes version 3.1.2 (Ronquist and Huelsenbeck 2003) was initiated with random starting trees and run for 5×10^6 generations with four Markov chains

employed. Trees were sampled every 500 generations. The first 25% of the trees were discarded as burn-in. Genetic distances, p -distance and Kimura's two-parameter (K2P) distances (based on Kimura's two-parameter model), were calculated between groups with MEGA 5.05 (Tamura et al. 2011). NeighborNet network based on p -distances was constructed for the unique haplotypes of focusing species using SplitsTree4 version 4.12.3 (Huson and Bryant 2006). To establish an accurate threshold to distinguish inter- and intra-specific variation, we used the taxonomic name-based threshold optimisation technique, *threshOpt*, in the Spider package for R (Brown et al. 2012).

Ecological niche modeling

Ecological niche theory predicts that environmental conditions at the place where the parasitoidism occurs should be suitable for both the parasitoids and the hosts. We test this prediction through ecological niche modeling (ENM) with the maximum entropy algorithm implemented in MaxEnt version 3.3.3k (Phillips et al. 2006). We compiled geographic coordinates for occurrence of the scuttle fly from the Global Biodiversity Inventory Facility (GBIF, <http://www.gbif.org>) online database and from the primary literature. The occurrence data were spatially filtered to include those at least 30 km apart in order to reduce sampling biases. We only used eight bioclimatic variables (BIO1: annual mean temperature; BIO4: temperature seasonality; BIO10: mean temperature of warmest quarter; BIO11: mean temperature of coldest quarter; BIO12: annual precipitation; BIO15: precipitation seasonality; BIO16: precipitation of wettest quarter; and BIO17: precipitation of driest quarter) that summarise temperature and precipitation dimensions of the environment at a 2.5 arc-minute resolution (c. 5×5 km) in the WorldClim data set (Hijmans et al. 2005) in our ENM to reduce effects of over fitting and multi-collinearity of predictors. MaxEnt was run with a convergence threshold of 10^{-5} and maximum number of iterations of 10,000 for 10 replicates with subsample. Model performance was assessed via the area under the receiver operating characteristic curve (AUC) statistic and the importance of variables was assessed by jackknife tests. We employed the minimum training presence threshold and the 10 percentile training presence threshold to convert continuous models to binary predictions. The minimum training presence threshold allows no training omission, while the 10 percentile training presence threshold permits a training omission rate of 10%. The ENM for the scorpion (*M. eupeus mongolicus*) reconstructed in Shi, Liang, et al. (2015) was also converted into a binary map and overlaid on that of the scuttle fly for visual examination.

Results

Morphology and diagnosis

The parasitoid was identified as *M. scalaris* (Figure 1(b–e)) by the following features of adults: frons yellowish brown, with dense, fine microsetae; mesopleuron bare; scutellum with two pair of bristles; costa extends more than half wing length, vein R_{2+3} present; haltere yellow; hind tibia without differentiated antero-dorsal hairs; hind femur yellow with a brown tip; hypopygium dark brown and anal tube yellow; hairs at tip of proctiger bristle-like and feathered; female tergite VI short and wide, being clearly

wider than tergite V, and largely yellow in middle third; tergite VII wider than length and all brown.

Among the 39 scorpions collected from the field, we found seven that were infested with scuttle fly larvae. These fly-infested scorpions appeared sluggish, with their tails sprawled even after disturbances. Multiple maggots emerged from a single opening near the genital operculum of dead scorpions (Figure 1(b)). When the larvae were allowed to develop at 27°C and 75% RH, the pupal duration lasted for 8–10 days. Finally, we obtained 70 adult flies (Figure 1(e)).

Genetic analyses

A 676 bp fragment of the *mtCOI* gene was amplified from nine flies (four larvae and five adults) and sequenced. Indel mutations or premature stop codons were not found in the alignment of the *mtCOI* gene fragment. BLAST analysis revealed that our sequences were homologous to the *mtCOI* sequences of *M. scalaris* with more than 97% nucleotide identity (Table S1).

The aligned matrix comprised 49 sequences and contained 161 (25%) parsimony-informative sites. GTR + I + G was selected as the best fit model for DNA evolution. The phylogenetic trees constructed using ML and Bayesian methods were highly congruent with respect to the major clade clustering. The ML tree is shown in Figure 2 with the Bayesian posterior probabilities displayed together with the ML bootstrap support values at the corresponding nodes. Our sequences for scorpion parasitoids clustered within a strongly supported (100/1.00 for ML bootstrap support and Bayesian posterior probabilities, respectively) monophyletic clade including all sequences from *M. scalaris*, except KC192982 which formed a distinct clade with the sequence from *M. abdita* Schmitz, 1959 (GU075399). The rest of the sequences from other species formed exclusive monophyletic clades (100/1.00), but the inter-clade relationships were largely unresolved in both phylogenetic analyses. Nevertheless, monophyly of the ingroup was strongly supported (99/1.00). The genetic distances are shown in Table 1. The mean K2P distances between species ranged from 4.9 to 13.7%, and within-species distances ranged from 0 to 1.2%. The mean *p*-distances (4.8–12.5%) were smaller than the respective K2P distances. The smallest genetic distance between *M. scalaris* and other *Megaselia* species was 10.6% for the K2P model (*p*-distance, 9.9%). The mean within-species distance for *M. scalaris* was 1.2% (N = 18). Based on the taxonomic names illustrated in Figure 2, we obtained an optimised threshold of 3.84% for our data using *threshOpt* in the Spider package.

The 18 sequences clustered in clade *M. scalaris* harbour eight haplotypes with a gene diversity of 0.75 and nucleotide diversity (π) of 0.01. Relationships among these unique haplotypes are shown by NeighborNet (Figure 3). All the sequences of flies from scorpions were collapsed into Hap8 situated near the centre of network and diverged from other

Figure 2. The maximum likelihood tree of *Megaselia* scuttle fly species inferred from *mtCOI* sequences. Robustness of branches is indicated by maximum likelihood (ML) bootstrap support from 1000 replicates along with Bayesian posterior probabilities. Black dots denote scuttle flies from scorpion *Mesobuthus eupeus mongolicus*. *Sequence KC192982 was originally labeled *M. scalaris* but its sequence is identical to the sequence of *M. abdita* (GU075399).

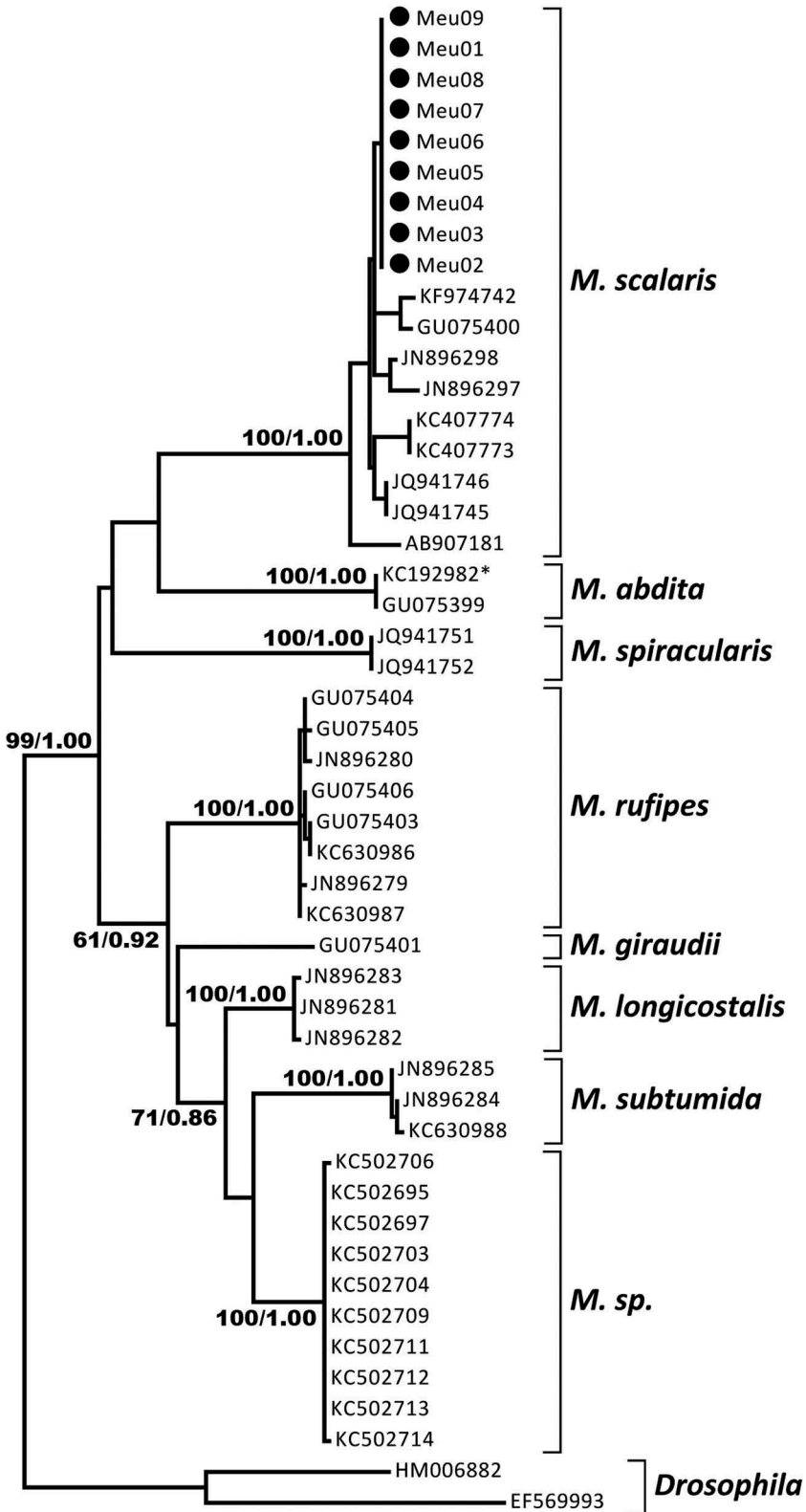


Table 1. Genetic distance estimates between scuttle fly species. The bold numbers on the diagonal represent mean distances within species. The means of Kimura's two-parameter (K2P) distances are shown below the diagonal and p -distances above the diagonal. N, sample size. n/c, not possible to estimate. Abbreviations of species names: *Mscs*, *Megaselia. scalaris*; *Mlon*, *M. longicostalis*; *Msp*, *M. sp*; *Mabd*, *M. abdita*; *Msub*, *M. subtumida*; *Mgir*, *M. giraudii*; *Mrug*, *M. rugipes*; *Mspi*, *M. spiracularis*.

	N	<i>Mscs</i>	<i>Mlon</i>	<i>Msp</i>	<i>Mabd</i>	<i>Msub</i>	<i>Mgir</i>	<i>Mrug</i>	<i>Mspi</i>
<i>Mscs</i>	18	0.012	0.099	0.100	0.102	0.105	0.111	0.112	0.115
<i>Mlon</i>	3	0.106	0.002	0.048	0.098	0.059	0.069	0.068	0.114
<i>Msp</i>	10	0.108	0.049	0.001	0.098	0.061	0.075	0.072	0.117
<i>Mabd</i>	2	0.110	0.106	0.105	0.000	0.113	0.102	0.099	0.116
<i>Msub</i>	3	0.113	0.062	0.064	0.122	0.002	0.093	0.081	0.125
<i>Mgir</i>	1	0.120	0.073	0.079	0.110	0.099	n/c	0.078	0.097
<i>Mrug</i>	8	0.121	0.071	0.076	0.106	0.086	0.082	0.003	0.101
<i>Mspi</i>	2	0.125	0.124	0.127	0.126	0.137	0.103	0.108	0.000

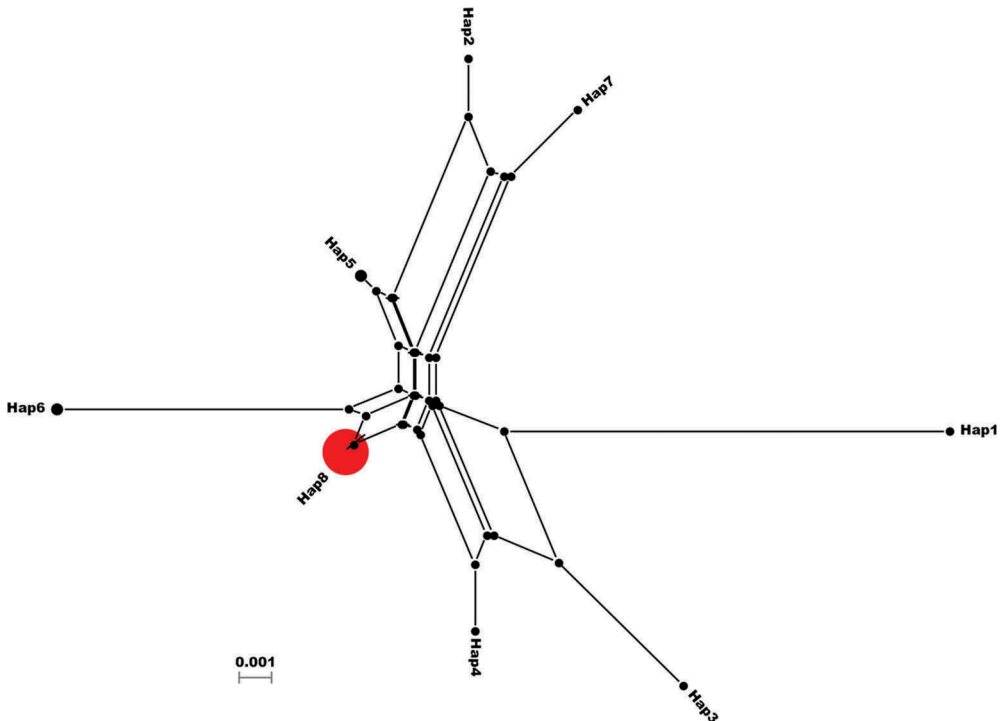


Figure 3. Genetic divergences among the haplotypes of *Megaselia scalaris* are shown as NeighborNet based on p -distances of *mtCOI* sequences. Circle sizes are proportional to the number of isolates sharing the haplotypes. Isolates from the scorpion *Mesobuthus eupeus mongolicus* are all included in Hap8.

haplotypes by p -distances of 0.7–2.1%. The p -distances between other haplotypes ranged from 0.7% (Hap2 vs Hap8 and Hap4 vs Hap7) to 2.7% (Hap1 vs Hap2 and Hap7).

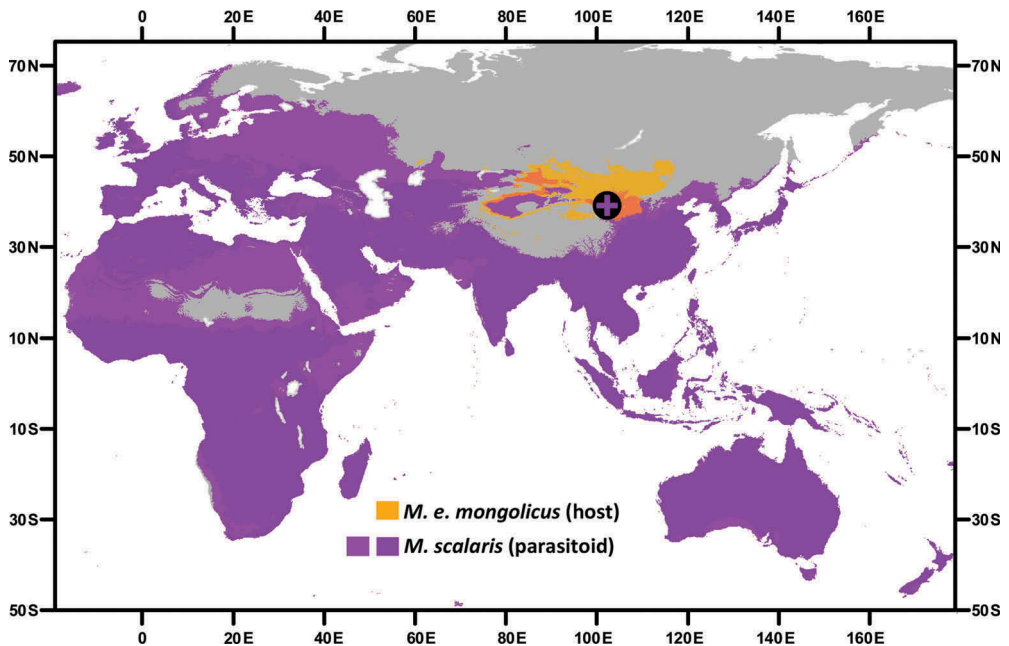


Figure 4. Suitable distributional areas for the scuttle fly *Megaselia scalaris* and the scorpion *Mesobuthus eupeus mongolicus* predicted with ecological niche modeling. The map shows the climatically suitable range for the scuttle fly under the minimum training presence threshold which included all known training occurrence points and under 10 percentile training presence threshold in which 10% of the occurrence points used in training models was omitted. Distribution for *M. eupeus mongolicus* was generated from Shi, Liang, et al. (2015). The crossed circle indicates the place where parasitised scorpions were collected.

Ecological niche models

After filtering out the records that were less than 30 km apart, a total of 64 point occurrence data were used to construct ENMs for the scuttle fly *M. scalaris*. ENMs maintained a high AUC statistic (0.81 ± 0.05), indicating the good performance of these models. Of the eight climate variables used, mean temperature of coldest quarter (BIO11) and annual precipitation (BIO12) contributed to the models most with mean relative contributions of 34.8 and 30.8%, respectively; these were followed by annual mean temperature (BIO1, 15%). ENMs predicted climatically suitable areas based on two thresholds (the minimum training presence threshold: 0.1284; the 10-percentile training presence threshold: 0.2556); these are shown in Figure 4 for the region under discussion (see Figure S1 for worldwide prediction). Overlaying the scorpion ENM with the fly ENM, an overlapping belt occurred in northwest China, where climatic conditions were suitable for both the scorpion and the fly. Our sampling sites located exactly on the overlapped region (Figure 4) when assuming the minimum training presence threshold.

Discussion

In this study, we documented a case of parasitoidism of the scuttle fly, *M. scalaris*, on the scorpion *M. eupeus mongolicus* (Figure 1(a)). This is the first recorded case showing such an association between these two species. *M. scalaris* is a highly synanthropic fly species with a cosmopolitan distribution (Figure S1), feeding on an exceptionally wide range of decomposing organic matter of both animals and plants. Its larvae could also lead a life as facultative predators, parasites and parasitoids (Disney 2008). Accidental cases of myiasis were also reported in human beings (Singh et al. 1988; Meinhardt and Disney 1989; Singh and Rana 1989; Hira et al. 2004), reptiles (Silva et al. 1999) and amphibians (Zwart et al. 2005). Field reports have demonstrated the ability of this fly to infest a wide range of living invertebrates, including insects of the orders Coleoptera (Harrison and Gardner 1991; Arredondo-Bernal and Trujillo-Arriaga 1994), Diptera (Batista-Da-Silva 2012), Dictyoptera (Koch et al. 2013), Hemiptera (Costa et al. 2007), Hymenoptera (Soares et al. 2006), Lepidoptera (Robinson 1971; Ulloa and Hernandez 1981) and Orthoptera (De Gregorio and Leonide 1980), and ticks (Ixodida, Andreotti et al. 2003), spiders (Araneae, Disney 1994; Machkour-M'Rabet et al. 2015) and snails (Gastropoda, Idris and Abdullah 1997). Laboratory cultures of arthropods were often the targets of infestation by this fly (Robinson 1975; Miranda-Miranda et al. 2011; Cazorla-Perfetti et al. 2012).

A reliable identification of parasitoid species is pivotal to recognise host-parasitoid interactions, and, in turn, to understand food web structure and dynamics. *Megaselia* is the largest genus of the mega-diverse dipterous family Phoridae, with around 1400 named species, but in all likelihood most species are still undescribed (Disney 2008). Such huge species diversity greatly challenged the traditional species inventory based solely on morphological characteristics. In addition, as manifested by *M. scalaris*, some species are exceptionally widespread and infesting multiple host species. It is often unclear whether parasitoids under study from different geographic locations represent a single genetically coherent species or comprise multiple cryptic species which have distinct evolutionary trajectories. For instance, recent genetic inventories using DNA barcodes revealed that many presumed polyphagous parasitoid flies actually included several cryptic host-specific species (Smith et al. 2006, 2007). Our molecular phylogenetic analyses revealed that the *mtCOI* sequences for the scuttle flies infesting scorpions clustered with all homologs for *M. scalaris* from GenBank and formed a strongly supported (100/1.00) monophyletic clade, except the sequence KC192982 which clustered with the sequence GU075399 from *M. abdita* (Figure 2). The overlap region between these two sequences had identical nucleotide sequences. In contrast, the *M. scalaris* and *M. abdita* clades were highly divergent with a K2P distance of 11%, which is well above the interspecific genetic distance in Diptera (Table 1). This situation suggested that either the specimen for KC192982 was misidentified or mitochondrial introgression has occurred between two species very recently. The upper within-species genetic distance (2.7%) for the *M. scalaris* clade was larger than the threshold (2.2%) used by the Barcode Index Number (BIN) algorithm of the BOLD (Barcode of Life Data) System (Ratnasingham and Hebert 2013) and the optimum threshold (2.13%) obtained from other dipteran species (Collins and Cruickshank 2014). The optimum threshold inferred by Spider was even larger (3.84%) for our data. Considering the extremely

diverse niches occupied by *M. scalaris* and the geographically limited intraspecific samples used in our analysis, the largest intraspecific distance we observed should not be the representative for the maximum intraspecific variation in this fly species. Although some intraspecific genetic distances seemed marginally larger, the network for *M. scalaris* haplotypes was highly reticulated (Figure 3). Such a poorly sorted intraspecific genealogy suggested that all the samples belonged to a large randomly breeding population. This evolutionary scenario is feasible for a species with high dispersal potential, such as *M. scalaris*.

Scorpions are large predators situated at the top of the food chain in arthropod communities. The high biomass of scorpions implies that they play a key role in ecosystems, especially in arid regions (Polis 1990; Polis and Yamashita 1991). Thus, natural enemies of scorpions would be expected to exert an influence on ecosystem health through the trophic cascades. However, our knowledge about natural enemies of scorpions is very limited. Hitherto only a few species of fungi (e.g. Santana-Neto et al. 2010), nematodes (e.g. Gouge and Snyder 2005) and mites (e.g. Lourenço 1982; Ibrahim and Abdel-Rahman 2011) have been described infesting scorpions. The recent finding of the flesh fly, *Sarcophaga dux*, might represent the first parasitoid of scorpions currently known (Shi, Zhang, et al. 2015). As *M. scalaris* has an extraordinary capacity to penetrate seemingly closed containers (Disney 2008), it remains to be directly demonstrated that scorpions are targeted by *M. scalaris* in the field.

However, given the extremely wide geographic distribution (Figures 4 and S1) and the exceptionally broad diet and host spectrum of the scuttle fly (Disney 1994, 2008) together with the high biomass of scorpions in arthropod communities (Polis 1990; Polis and Yamashita 1991), it is possible that parasitoidism could naturally occur. In particular, our results for ENM indicated that there are sizable areas where climatic conditions are suitable for both the scuttle fly and the scorpion (Figure 4). Those overlapping ecological niches would provide a necessary condition of coexistence that is required by parasitoidism. It should be noted that we only compared the distribution of the subspecies *M. eupeus mongolicus* with the scuttle fly. If considering the desert scorpion *M. eupeus* as a whole, the overlap between ranges of the scorpion and the scuttle fly will be quite extensive. *M. eupeus* is widespread, ranging from east Anatolia to southern Mongolia and northwest China (Shi et al. 2007). In addition, both the scuttle fly (Disney 2008) and the scorpion (Shi et al. 2007; Shi, Liang, et al. 2015) invade indoor habitats. This would improve the likelihood of occurrence for parasitoidism. Our observation of successful development of *M. scalaris* suggests that the scuttle fly can finish its life cycle with no difficulty in the body of scorpions.

In summary, our preliminary study unveiled that the scuttle fly is a facultative parasitoid of scorpions, representing a missing trophic link between two unusual groups of arthropods, Phoridae and Buthidae. It remains untested how the parasitoids located the scorpions in the field. Nevertheless, given the hyper-diversity of parasitoids, such a trophic interaction should not be overlooked in any scorpion conservational efforts and rearing practices. Future efforts should be directed towards understanding the pervasiveness of host-parasitoid interactions between scorpions and flies, and to evaluating the likely consequences of such trophic links on spatial spread of the parasitoids and on scorpion population dynamics.

Acknowledgements

The authors are grateful to Mr. Zhiyuan Su for his assistance in scorpion collection. We are also grateful to the two anonymous reviewers for their constructive comments and suggestions.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This work was supported by the Natural Science Foundation of China [grant numbers 31370041 and 31372245]; and the Breakthrough Project of Strategic Priority Program of the Chinese Academy of Sciences [grant number XDB13030200].

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