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Research paper

Host range patterning of parasitoid wasps Aphidiinae (Hymenoptera: Braconidae)

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ABSTRACT

Aphidiinae are exclusive endoparasitoids of aphids and together with particular plant species form tritrophic complexes. Parasitoid wasps show different levels of host specificity, which is a very important fact since they have been used in biological control programs. We present a new approach to aphid parasitoid host specificity applied on 505 species from 38 genera, covering all valid species in the world fauna excluding synonyms. For this purpose, the artificial neural network visualization was performed to show the distribution and interconnections between and among members of five *a posteriory* selected groups of parasitoids. The results showed that about half of the analysed species (225) belong to the group of strict specialists, consisting of monophagous parasitoids that attack only one aphid species. The group of generalists assembled 58 species with mainly Palaearctic distribution. Between specialists and generalists are the oligophagous species which are clustered in three categories: narrow, moderate and broad oligophagous. Generally, host specificity in Aphidiinae is weakly connected with their phylogeny, suggesting that the parallel evolution of aphidiines must have occurred. Host specificity mainly depends on aphid hosts which follow host plant distribution.

1. Introduction

Insect parasitoids, their phytophagous hosts and their host plants compose a major proportion of the world's biodiversity (Hawkins, 1994). Aphidiinae are solitary koinobionts, endoparasitoids that lay a single egg into the aphid body (Aphididae, Hemiptera) (Völkl and Mackauer, 2000). They represent one of the most important and best investigated groups because of their significant role in biocontrol as aphid natural enemies. Previous studies of Aphidiinae have included their morphology, taxonomy and phylogeny (Smith et al., 1999) as well as behaviour and ecology (Völkl and Mackauer, 2000).

A large number of patterns in host-parasitoid interactions can be designed taking into account many different parameters (Hawkins, 1994). Host specificity is defined as a continuum from extreme specialists with a host-range restricted to a single host species to those which have a broad host-range, considered as generalists. In addition, the term host-range, applied to an insect, represents the sum of plant or animal species which are its hosts (van Klinken, 1999). Information regarding the trophic associations between parasitoids and their hosts is very important, especially for the biological control programs (e.g., Starý, 1970; Hågvar and Hofsvang, 1991; Trdan, 2005). Aphidiinae show very different range in host specificity, even among the species belonging to the same genus. In response to selective pressures, some populations of the same parasitoid species may follow different evolutionary trajectories (Hufbauer and Roderick, 2005). Zepeda-Paulo et al. (2013) investigated the existence of local host adaptation in *Aphidius ervi* (Haliday, 1834) by examining relevant traits related to infectivity and virulence on different hosts (native and alochtonous aphid species) showing significant variability of parasitoid fitness.

A large number of patterns in host-parasitoid interactions aiming to explain host specificity have been published, in the first place it is the host range of parasitoids. In addition, Starý (1981a) split aphidiines into five host specificity groups using its host range: (1) a single host species, (2) two or more species of the same aphid genus, (3) species of two or more genera of the same aphid subfamily, (4) species of two or more genera of two or more subfamilies of the same aphid family, (5) species of several genera of two or more aphid families. This classification mostly relies on aphid phylogeny, taking into account phylogenetic relations among aphid hosts (related genera and families, nowadays aphid subfamilies). Based on this classification, various strategies and/or aphid's biological control programs have been proposed by Starý

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and Rejmánek (1981), and later by Boivin et al. (2012). Until today, many authors worldwide (e.g., Starý 1979, 2006; Shi and Chen, 2001; Kavallieratos et al., 2004; Žikić et al., 2012; Rakhshani et al., 2012; Barahoei et al., 2014) have invested much effort into investigating pattern tritrophic chains. Thus, new connections between plants, aphids, and parasitoids have been revealed over trophic associations, solving the problem of previous synonymization.

After almost 35 years since previous publications concerning aphidiines host specificity (Starý, 1981a), there is a need to revise this topic, having in mind that many new taxa of Aphidiinae have been described. Also, many species have been introduced in new niches intentionally, through various biological control programs, or unintentionally, by importing plants from one geographical region to another. Development of new methods in ecology allows the consideration and integration of a very large number of parameters which are possible to estimate nowadays.

Having all this in mind, the main goal of this study was to test host specificity over the host range of all valid species of Aphidiinae in the world fauna, including the species of the southern hemisphere. The aim was to define the classes and thresholds of host specificity for Aphidiinae wasps, using the specific spectre of host species, genera and subfamilies which they prefer. To achieve this, the following tasks were set: (1) to examine the host range for each parasitoid species over quantification of used data, not taking into account the phylogenetic relations among aphid hosts, (2) to pattern parasitoid host specificity which rely on host range, (3) to present a vast dataset in the most effective way through visible and comparable output graphs, (4) to test how diversity of plant species as members of tritrophic associations, as well as the Aphidiinae distributional gradient affect the host range among parasitoids and (5) to examine host specificity patterns along the phylogenetic tree.

2. Material and methods

We sampled data of the world fauna of Aphidiinae subfamily counting 505 species belonging to 38 genera. Furthermore, there are approximately 5000 described species of aphids distributed in 250 genera and 20 subfamilies (Remaudière and Remaudiere, 1997), with the major percentage described in the temperate zones (Blackman and Eastop, 2006). The diversity of plants as first trophic members in this analysis was presented with more than 6500 species (Table S1). For this research we sampled as much recent literature as possible concerning trophic associations between parasitoid wasps and aphid hosts, covering a large part of the world and the main geographical regions:

Western Palaearctic: Balkans (Kavallieratos et al., 2004), Bulgaria (Atanasova, 1997), Czech Republic (Starý, 2006), Malta (Mifsud and Starý, 2011; Rakhshani et al., 2015), Serbia, Montenegro (Žikić et al., 2012), Ukraine (Kaliuzhna and Zubenko, 2013).

Eastern Palaearctic: Central Asia (Starý, 1979), China (Shi and Chen, 2001; Wei et al., 2005), Georgia (Achvlediani, 1981), Iraq (Starý and Kaddou, 1971), Iran (Starý et al., 2000; Rakhshani et al., 2007, 2008, 2012; Barahoei et al., 2014), Japan (Takada, 1968, 2002), Kazakhstan (Starý and Juchnevič, 1978), Russia, Siberia (Davidian and Gavrilyuk, 2014), Turkey (Uysal et al., 2004; Tomanović et al., 2008).

Nearctic: Canada, USA (Pike et al., 2000; Smith, 2012; Tomanović et al., 2012), Mexico (Starý, 1983).

Afrotropical: Algeria (Laamari et al., 2012), Kenya (Starý and Schmutterer, 1973), Tunisia (Boukhris-Bouhachem, 2011).

Neotropical: General (Starý et al., 2014), Argentina (Starý and Delfino, 1986), Costa Rica (Zemora Mejías et al., 2010), Cuba (Starý, 1981b), Mexico (Starý and Remaudière, 1983), Venezuela (Starý and Cermeli, 1989).

Oriental: India (Raychaudhuri, 1990; Akhtar et al., 2011; Ahmad and Wani, 2014), Malaysia (Sook and Starỳ, 1986), Pakistan (Starỳ et al., 1998; Naeem et al., 2005), Thailand (Starý et al., 2008, 2010).

Australasia: Australia (Carver and Starý, 1974).

Oceanic: New Zealand (Valentine and Walker, 1991).

All data on parasitoids, hosts, plants and theirs geographical distribution were checked, compared and uniformed using two general databases: Fauna Europaea (van Achterberg, 2015) and Taxapad (Yu and Achterberg, 2012). For each parasitoid species the data on the number of aphid species, aphid genera, and aphid subfamilies they parasitized is given (Table S1). Also, parasitoids were classified based on the tribal level and the distribution in eight geographical regions. The full names of parasitoids were coded for more effective visualization on the artificial neural network. For the classification of parasitoids on the tribe level we used the following abbreviations: ACL = Aclitini, APH = Aphidiini, EPH = Ephedrini, PRA = Praini and TRI = Trioxini (Belshaw and Quicke, 1997). For still unranked genera *Pseudephedrus*, also *Parephedrus*, relatively close to the tribe Ephedrini the abbreviations UR1 = *Pseudephedrus* and UR2 = *Parephedrus* were used. The host range is represented over the model (species/genera/subfamilies). Also in the Table S1 the third trophic member, plants, was organized over the host plant range using the same model, number of (species/genera/families) completing the tritrophic chain (parasitoid/host/plant).

2.1. Data analysis

In order to pattern autecological information of the 505 Aphidiinae species regarding the trophic specialisation the Kohonen unsupervised artificial neural network, also known as a self-organizing map (SOM), was used (Kohonen, 1982). When applied to host specificity data, the SOM can visualize and explore linear and nonlinear relationships in high-dimensional datasets. The input matrix for the SOM in our study consists of 505 rows (species of Aphidiinae) and 3 columns (number of aphid host species-genus-subfamily). Ordination and classification of such huge data set could not be possible with traditional multivariate techniques. On the other hand, the SOM is not limited when large data sets are introduced in the analysis since, for visual presentation, this method makes full use of the available map space. The aphid diversity data was log-transformed ($\log(x+1)$) and then normalized. Each input vector, each species of Aphidiinae defined by three parameters (aphid host species, genus and subfamily) was introduced into the SOM during the training process. The output of the SOM is a two-dimensional grid (SOM map) composed of hexagonal neurons. Once the training process is completed, all species will be attached to the output neurons of the trained SOM map regarding a pattern depending on the model of trophic specificity. The species placed in the same output neuron are characterised by the same trophic specificity model. The increase of the distance between neurons in the SOM map is in accordance with the decrease of similarities in the host specificity. To create subsets of neurons on the trained SOM map the k-means method was used (Jain and Dubes, 1988). This method clusters aphid species carried by neurons with similar ecological traits (host range). The number of groups was set *a priory* following the Starý's five host specificity groups.

The distribution of each parameter (number of aphid host species, genus and subfamily) along the SOM map could be presented by a visualization technique named Component Planes, produced by SOM software in the form of a greyness gradient. The component planes of factors were used to provide more detailed description on the obtained clusters in terms of aphid diversity at different taxonomical level. The map resolution (the number of output neurons) was *a priori* determined following two most recommended methods (Vesanto et al., 2000; Park et al., 2003), and avoiding a large number of empty output neurons (Penczak et al.,

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