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PSYLLID HOST-PLANTS (HEMIPTERA: PSYLLOIDEA): RESOLVING A SEMANTIC PROBLEM

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ABSTRACT

Evolutionary and biological patterns can be obscured by inadequate or ill-defined terminology. An example is the generally very specific relationship between the sap-feeding hemipteran group, psyllids, and their breeding plants, commonly called host-plants. The literature is clogged with references to so called 'hosts', which are often merely plants on which psyllids were found accidentally, and no immature development was detected. Recently the term host has also been applied by some authors to any plant on which immature or adults feed. Here we propose a terminology to clarify associated plant definitions, and we suggest restricting the use of the term *host-plant* to plants on which a psyllid species completes its immature to adult life cycle. For the other plant associations we suggest the terms *overwintering* or *shelter plant* (plants on which adult psyllids overwinter and on which they may feed), *food plant* (plants on which adult psyllids feed, but do not breed and do not spend an extended period of time) and *casual plant* (plants on which adult psyllids land but do not feed).

Key Words: jumping plant-lice, psyllids, host-plant, terminology

RESUMEN

Patrones evolutivos y biológicos pueden ser oscurecidas por la terminología inadecuada o mal definida. Un ejemplo es la relación generalmente muy específica entre el grupo de hemípteros chupadores de savia, los psílidos, y sus plantas de desarrollo, generalmente llamadas 'plantas hospederas'. La literatura está obstruido con referencias a los denominados 'hospederos', que a menudo se limita a las plantas en el que los psílidos, donde encontró por accidente y no se detectó el desarrollo inmaduro. Recientemente el térmo 'hospedero' también ha sido aplicado por algunos autores a cualquier planta en la que inmaduros o adultos se alimentan. Aquí se propone una terminología para aclarar las definiciones de plantas asociadas, y sugerimos restringir el uso del término *planta hospedera* a las plantas en los que una especie de psílido completa su ciclo de vida del inmaduro hasta el adulto. Para el resto de asociaciones con las plantas sugerimos los términos *planta de hibernación* o *refugio* (las plantas en el que los psílidos adultos pasan el invierno y en la que se pueden alimentar), *planta de alimentacion* (plantas sobre las que los psílidos adultos se alimentan, pero no se reproducen y no pasan un largo período de tiempo) y de la *planta casual* (plantas sobre que los psílidos adultos se posan, pero no se alimentan).

Palabras Clave: psillidos, planta hospedera, terminología

Psyllids or jumping plant-lice (Hemiptera, Psylloidea) constitute a small group (~3800 species) of highly specialized plant sap-feeding Sternorrhyncha. The immature development involves five instars, usually called larvae or nymphs. As both these terms are used in the psyllid literature, and elsewhere convey different meanings depending on the insect order, we will here call these stages 'immatures' in order to avoid any confusion. The number of host-plants on which the immature to adult life cycle is completed is usually restricted to one or a few closely related plant species, hence the reputation of psyllids as highly host specific. In addition, closely related psyllid species tend to develop on closely related plant species (Burckhardt & Basset 2000; Percy et al. 2004). Psyllids represent, therefore, a potentially ideal model group for addressing evolutionary aspects of insect-plant relationships (Hodkinson 1974, 2009; Hollis 1987; Hollis & Broomfield 1989; Percy 2003; Percy et al. 2004; Burckhardt 2005).

Such comparative studies strongly rely on the availability and quality of host-plant data. Reliable information on host-plants is also needed in the management of agricultural or forestry pests, in applied biological control programs, and for making biosecurity decisions (e.g., customs and import regulations). In the majority of psyllid literature (Burckhardt 1987a, 1987b, 1988; Burckhardt & Lauterer 1997; Burckhardt & Queiroz 2012; Hodkinson 2009; Hodkinson & Hollis 1987; Hollis 1984, 1987, 2004; Lauterer 1991; Lauterer & Malenovský 2002; Percy 2002; Percy et al. 2012) the term 'host-plant' is used for plant taxa on which a particular psyllid species completes its immature development. Hence for immature stages this information is easy to acquire: the plant on which the last instar immatures are found constitutes the host-plant. The last stage 5th instar is considered an important indicator because in some cases where oviposition mistakes are made, nymphs can develop through to the early stages, although the evidence for this comes mainly from agricultural or no choice experiments. Experiments and trials performed by van Klinken (2000) showed that females of *Prosopidopsylla flava* Burckhardt, 1987 laid eggs on 58 test-plant species different from the known *Prosopis* host, but development was arrested and no adults resulted from these eggs. The situation is more complex for adults that are fairly mobile and tend to disperse, particularly when adult densities are high. Adult psyllids are winged, which the immatures are not, and they can disperse via active flight or passively when blown by wind over shorter or longer distances. With the exception of some economically important vector species (Čermák & Lauterer 2008; Grafton-Cardwell et al. 2013) little is known about the flight behaviour of psyllids, but whether actively or passively dispersing, they may land on any plant in the vicinity. The literature is clogged with reports of incidental or accidental resting plants as 'hosts' suggesting that particular species, often economically important pests, are polyphagous. Some literature surveys have produced long lists of 'host-plants' from which it is not clear which ones are breeding plants and which are not (e.g., Al-Jabr 1999 for *Bactericera cockerelli* (Šulc, 1909)).

As stated by Civolani et al. (2011), very little is known about plant choice mechanisms in psyllids (see Soroker et al. 2004 for a review), which appear to differ among species (Hodkinson 2009). Furthermore, the available studies on sex attraction mechanisms deal mainly with a few pear psyllid species and can hardly be generalized to the entire superfamily (e.g., Soroker et al. 2004; Horton & Landolt 2007; Guédot et al. 2011). In Northern temperate and subarctic regions, about half of the psyllid species migrate as adults on to conifers on which they overwinter. When the ambient temperature is high enough they may also feed on these overwintering plants (sometimes referred to as shelter plants), though studies are inconclusive or incomplete on this point (Hodkinson 2009; Valterova et al. 1997). A few authors use the word 'host' for all plants on which immature and adult psyllids feed in the terms 'summer host plant', 'winter host plant' and 'shelter host plant' (Nehlin et al. 1994; Valterova et al. 1997) or 'reproduction host plants' and 'overwintering host plants' (Mayer et al. 2011). This generalized use of the term 'host' in the psyllid literature creates unnecessary confusion and obscures the analyses of patterns between psyllids and their host-plants, confounding accurate analyses of the systematic and evolutionary patterns on insect–plant associations, a situation known also from other phytophagous insects (Mound 2013), and preventing a thorough understanding of the observed specialization in this group.

In comparison with other Sternorrhyncha, the concept of host-plant is often more well-defined in scale insects (Coccoidea) because of the typically sedentary lifestyle. The situation in whiteflies (Aleyrodidae) is similar to psyllids, with winged adults and sessile immature stages, facilitating the identification of the host-plant. In aphids (Aphidomorpha), the host-plant is often revealed by the presence of a colony of wingless immatures and adults, but there is the added complication of primary and secondary hosts that need to be identified by studying the life cycle. Inconsistencies in the literature are more common in aphids, with species described multiple times from different hosts and/or only the primary or secondary host recorded (Eastop 1972).

In the present paper, we propose a terminology and define a series of terms for plants on which psyllids are found covering the range of known psyllid–plant relationships. We hope that this will clarify any ambiguities and lead to a more consistent use of terminology in the literature.

Literature Data

In the literature, the term 'host-plant' is used inconsistently creating some unnecessary confusion.

In the taxonomic literature (catalogues of Klimaszewski 1973; Hodkinson & White 1981; Hodkinson 1983, 1986, 1988; Gegechkori & Loginova 1990; Hollis 2004; Burckhardt & Queiroz 2012; Percy et al. 2012) the standard is to use the term 'host' for the plant on which a particular psyllid species completes its immature to adult development. Erroneous host information may result from the misidentification of the host-plant or from collections of adults from plants that are mistaken as hosts where the presence of immature stages is not established, or simply from unconsidered use of the term 'host' by collector and/or author. An example for the former case is the Brazilian

Gyropsylla cannela described by Crawford (1925) from 'cannela amarella' which was interpreted by Costa Lima (1942) as *Nectandra* sp. 'Cannela' is a common name used for several *Nectandra*, *Ocotea* and *Persea* species (Lauraceae). Burckhardt & Queiroz (2013) found that the host of *G. cannela* is in fact *Ilex microdonta* (Aquifoliaceae), a host which is consistent with that of other congeners, and *Nectandra* is a misidentification. An example for the latter case, where the immature stages were not known, is the Mediterranean *Agonoscena cisti* (Puton, 1882), which develops on several *Pistacia* spp. (Anacardiaceae). The type series was collected on *Cistus*, which was mistaken as the breeding plant. *Cistus* constitutes, together with *Pistacia*, a common component of Mediterranean maquis vegetation and thus this case illustrates how the incidental capture of psyllids often occurs on common or dominant plant species in the local region. Errors of these kinds, where the host-plants of congeners are all in a different plant group to the cited 'host', or when the cited 'host' is a common plant in the region, can be more easy to spot. However, the veracity of these records still needs to be checked and in such cases, it would be better for authors to qualify the uncertainty of the host data recorded, preferably using the terminology proposed here.

More difficult to judge is the quality of information published in the form of plant lists on which particular psyllids were found. *Bactericera cockerelli*, for instance, is a Nearctic pest on tomatoes, potatoes and other Solanaceae, and this psyllid has been introduced recently into New Zealand (Martin 2008). It is a vector of *Candidatus* Liberibacter solanacearum, the causal agent of the Zebra Chip disease and, therefore, of particular economic concern. Wallis (1955), who examined the host-plant relationship of *B. cockerelli*, listed 41 plant species in three plant families on which *B. cockerelli* could complete its immature development. In addition, Wallis found adult *B. cockerelli* psyllids on 20 different plant families. Repeatedly, the two types of plant data have been combined in a single list under the heading 'host-plants' (Al-Jabr, 1999), implying that *B. cockerelli* is not just unusually polyphagous for a psyllid, which is true, but is an extraordinarily highly polyphagous species, which is not true. Knowing the proper extent of polyphagy in this species is critical to effective control of the species and prevention of the disease (Martin 2008). Some invasive plant-feeding insect pests exhibit an initial expansion of host-plant range on colonization and/or a subsequent contraction of host-plant range after establishment (Rafter & Walter 2013; Susan Halbert pers. comm.), but experimental data is needed to verify whether this can be said of psyllids. Roderick & Percy (2008) compared post colonization host ranges in native species colonizing islands and found that auchenorrhynchan hopper lineages were more likely to have undergone post colonization host range expansions than psyllids.

The Psyl'list online database (Ouvrard 2013), while not yet complete, aims to gather all taxonomic data together with associated data such as host-plants and locality information. The data in Psyl'list is collated from the scientific literature, and host-plants are included as they are recorded in the original publications. In total, as of June 2013, 2957 psyllid species have been entered into the database, of which 2548 are linked with at least one plant. Despite the inconsistencies of host-plant terminology in the literature, the database provides the most comprehensive record of psyllid–plant associations (7420 links between psyllid and plant taxa), and it gives an overall idea of the general patterns of host-plant associations in the Psylloidea (for instance, each psyllid genus is linked with five plant genera on average, and 91% of psyllid genera are associated with less than 10 genera of plants). The definitions given below will be used in the database in order to clarify the issues surrounding host-plant definitions in psyllids and thus provide more relevant datasets for pattern analyses.

Recently, the term 'host' has been applied deliberately by some authors to any plant on which psyllids (immatures and adults) are considered to feed. Many North temperate psyllids overwinter as adults on conifers but breed on other plants. This is the case of *Trioza apicalis* Foerster, 1848, and *Cacopsylla picta* (Foerster, 1848) which develop on *Daucus* (Apiaceae) and *Malus* (Rosaceae), respectively. In an attempt to clarify the situation, different plants terms such as 'reproduction host-plant', 'overwintering host-plant', 'overwintering shelter plant' 'summer host-plant', winter host-plant' or 'shelter host-plant' have been used (Nehlin et al. 1994; Valterova et al., 1997; Mayer et al., 2011; Peccoud et al. 2013). However, even though these definitions add some clarity, they are not in line with the bulk of the psyllid literature, particularly the taxonomic literature where the host-plants are often designated as part of the species description, and, hence, in our opinion introduce additional and unnecessary confusion.

Definitions

We propose the following definitions to clarify, for instance, discussions of evolutionary patterns, or design measures to control pests, and to provide a terminology for the various categories of plants which is consistent with the bulk of the relevant literature. We propose here the following terminology:

Host-plant – a plant on which a psyllid species completes its immature to adult life cycle.

Overwintering or *shelter plant* – a plant on which adult psyllids overwinter, and on which they may feed.

Food plant – a plant on which adult psyllids feed, but do not breed and do not spend an extended period of time (e.g., diapause or winter season).

Casual plant – a plant on which adult psyllids land actively or passively, and on which adults may probe the plant but do not feed.

Conclusions

Using an ambiguous terminology for discussing biological features, such as host-plants, leads to confusion and hampers the assessment of psyllid–plant relationships. We propose restricting the use of the term 'host' to breeding plants on which a psyllid species completes its immature to adult life cycle. Psyllids generally develop on a narrow range of plant species, and applying the term 'host' to any food or shelter plant would blur our interpretation of psyllid host-plant specificity and obscure our understanding of psyllid host-plant interactions.

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