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REVIEW

Do the mechanisms modulating host preference in holometabolous phytophagous insects depend on their host plant specialization? A quantitative literature analysis

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Abstract In holometabolous phytophagous insects, adult females and larvae determine host plant selection through oviposition and feeding preferences. Pre-imaginal and/or imaginal experiences with plant chemical cues can modulate these preferences. Various studies found evidence, or not, of host preference modulation through previous experience but they appear to contradict each other. Most probably, modulation of host preference depends on the degree of specialization of the insects. Our literature analysis revealed that the positive influence of experience in the modulation of host plant preference occurred equally in polyphagous, oligophagous and monophagous species, but was significantly more influenced by the phylogeny of the insect and the developmental stage involved in plant cue experience. Identification of phylogenic and developmental stage factors of "host learning" abilities appeared to be key information for predicting the response of species to habitat modifications rather than the insect's degree of host plant specialization. The signification of this output on the fact that some insect species or populations shifted from the wild to cultivated habitats to become important pests is discussed.

Keywords host plant range · Sensory experience · Host preference induction · Hopkins' host selection principle · Neo-Hopkins principle · Chemical legacy · Shift from the wild to cultivated habitats · Pest risk appearance

Key message

- This literature analysis investigates the role of insect's experience on the modulation of host preference in holometabolous phytophagous insects, according to the host range, the phylogenetic dependence, and the developmental stage(s) exposed to the experience.
- Understanding the mechanisms involved in host plant selection by insects is a crucial issue to better understand why some insects shifted from the wild to cultivated habitats to become important pests. Our study indicates that host plant selection is largely conditioned by insect's experience.
- The phylogeny of the insect and the developmental stage involved affected the positive influence of experience on the modulation of host plant preference, while the host range did not. Therefore the capacity of an insect to become a pest is not linked to its polyphagy.

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Introduction

Host plant selection in phytophagous insects is a crucial event since it has a direct effect on development and survival (Bernays and Chapman 1994; Schoonhoven et al. 2005). For holometabolous insects, host selection is usually determined by the ovipositing female (Bernays and Chapman 1994; Schoonhoven et al. 2005) except for highly mobile larvae of some Lepidoptera species (Wiklund 1975; Bernays and Chapman 1994; Berdegué and Trumble 1996). Both feeding and oviposition behaviors are influenced by plant chemical cues (Schoonhoven et al. 2005 for review). Finding a suitable host plant can be difficult given the large spatial and temporal variation in plant resources and availability of plants (Carrasco et al. 2015). Preference can be modulated by experience with plant cues during the different stages of their life (Anderson and Anton 2014). Ability to retain information on feeding preference during lifetime is particularly intriguing in holometabolous insects. For most of them, feeding strategy differs dramatically between life stages.

Walsh (1864) and Hopkins (1916) were the first to study the influence of natal host plants on host preference modulation in holometabolous phytophagous insects. Hopkins (1916) working with bark beetles stated that “a species which breeds in two or more hosts will prefer to continue to breed in the host to which it has become adapted”. This was called the Hopkins’ Host Selection Principle (HHSP) until Thorpe and Jones (1937) renamed it pre-imaginal conditioning. Various studies were conducted on different species belonging mainly to the Lepidoptera, Coleoptera and Diptera families to demonstrate or invalidate the effect of pre-imaginal conditioning on habitat preference (see Table A1). Some studies demonstrated that pre-imaginal conditioning influenced larval feeding and oviposition site preference (see Table A1 in ESM appendix) whereby the sensitivity of chemical cues is memorized in the central nervous system during the larval stage and then maintained through metamorphosis to the adult stage. However, some researchers questioned this neuronal memory hypothesis given that the metamorphosis involves a major restructurating of the central nervous system which “erases” the transfer of the memory of their sensitivity of chemical cues to the adult stage (Tissot and Stocker 2000; Blackiston et al. 2008). Jaenike (1983) showed that, in contrast to conditioning at the imago stage, pre-imaginal conditioning had no influence on the oviposition site preference in *Drosophila melanogaster* (Diptera: Drosophilidae). This imaginal conditioning mechanism was named the neo-Hopkins principle. It states that the newly emerged adult detects the chemical cues present in its immediate environment, ‘memorizes’ them, and looks for similar ones when in search for oviposition or feeding sites. An alternative mechanism named chemical legacy, which allows transmission of host preference through metamorphosis, was proposed by Corbet (1985). He stated that the chemical cues coming from the natal habitat are stored in the hemolymph of the larva or at the surface of the pupa. The memorisation of the sensitivity of these chemical cues can then be transmitted through metamorphosis and be detected by the adult insect during emergence.

All three mechanisms contribute to the behavioral phenotypic plasticity of host preference in phytophagous insects. They differ in the developmental stage(s) when conditioning takes place. However, it is not easy to differentiate them experimentally (Barron 2001). For example, it is difficult to separate the pre-imaginal conditioning from the chemical legacy. Attempts to separate the influence of these two mechanisms by rinsing the pupae with water only worked if the semiochemicals stored at the surface of the pupae are water-soluble (Thiéry and Moreau 2013). In addition, if chemical cues are stored in the hemolymph as suggested by the chemical legacy, the differentiation between pre-imaginal conditioning and chemical legacy is even more difficult to achieve (Barron 2001). Due to this difficulty to distinguish these two mechanisms, Davis and Stamps (2004) merged pre-imaginal conditioning and chemical legacy under the notion of Natal Habitat Preference Induction (NHPI). This notion is more general andhas been applied to many animal taxa such as mammals, birds and reptiles. NHPI states that animals prefer to develop in a habitat similar to their natal one.

In an environment with large spatial and temporal heterogeneity, a behavioral phenotypic plasticity based upon experienced host cues is advantageous over an innate ability to find a host (Anderson and Anton 2014). In the literature, the studies conducted on NHPI covered various insect species with different host plant ranges varying from mono-, oligo- to polyphagous. We hypothesized that differences in NHPI would exist across the spectrum of diet breaths. Compared to oligo- and monophagous insects, polyphagous insects demonstrate a stronger phenotypic plasticity to feed on a larger diet spectrum. Therefore, they should adopt a new substrate (or a new plant) more readily than oligo- and monophagous species. Through a literature analysis, we have tested the hypothesis that modulation of host preference by previous experience most probably depends on the degree of specialization of the insects.

Methods

In our literature analysis, which included 196 studies, we analyzed NHPI in three behaviors related to host preference, namely larval feeding site preference, adult feeding site preference and oviposition site preference. Since it was difficult to separate the mechanisms that modulate host preference (pre-imaginal conditioning, neo-Hopkins principle, chemical legacy and NHPI), and as the information was not always provided accurately, the developmental stages (larvae, pupae and adults) were taken into consideration rather than the mechanism itself. Furthermore, the experimental data varied in several other co-variables putatively affecting the response variable (RV, i.e. the insect's ability to change its host preference after being exposed to the host), among them the cue used for experience (entire plants, plant organs, isolated chemicals, etc.), and whether the trait was evaluated in choice or non-choice tests. In this context, a Markov Chain Monte Carlo generalized linear mixed model (MCMCglmm) multivariate comparative analysis methodology was used to distinguish between the effects of theses co-variables and the effect of phylogeny on RV.

Data collection

All available studies since 1939, which have attempted to determine the mechanism(s) that modulate host preference after larval, pupal and/or imaginal experience in holometabolous phytophagous insects, were considered. RV was a binary trait recording the existence of an adaptive change in preference between experienced versus inexperienced individuals. The definitions of Bernays and Chapman (1994) were used to attribute the degree of plant's specialization of each insect. Monophagous species feed on different plant species within a single plant genus, oligophagous species on different genera of plants within one plant family, and polyphagous species feed on different genera of plants from different plant families. Because the behavior of an insect varies with its developmental stage and depends on whether it is looking for food or an oviposition site (Bell 1990), the information was separated into three types of activities, namely larval feeding, adult feeding and oviposition, and split according to the developmental stages at which the experience took place (larvae, adult, pupae, pupae + adult, larvae + pupae + adult). For all insect species, the *cytochrome oxidase I* (*COI*) and the *elongation factor-1* (*EF-1*) genes available at GenBank (http://www.ncbi.nlm.nih.gov/genbank/, last access 20 March, 2015) were used to determine the phylogenetic relationships. Studies were not included in the analysis when:

1. the activity (i.e. oviposition or feeding) tested was not specified;
2. the conditioning was not done during the entire developmental stage considered;
3. the molecular data of the species were not available;

The studies considered are listed in the Table A1 and the corresponding references in the annex. Accession numbers for *COI* and *EF-1* sequences of these species are given in Table A2 of the ESM appendix.

Data analysis

The phylogenetic relationships of the insect species considered in this analysis were estimated using Bayesian inference. The best partitions of molecular evolution model among the sequences and codon position was determined using the software PartitionFinder (Lanfear et al. 2012). The best-fit model of substitution for each partition was determined using the Bayesian information criterion. The phylogenetic relationships were estimated with Bayesian inference using the program MrBayes v.3.2.1 (Ronquist and Huelsenbeck 2003). The run consisted of two independent analyses with the following settings: four Markov chains of 20 million generations, random starting trees, default priors, and trees sampled every 100 generations (branch lengths were also saved). A burn-in period of 4 million generations was used. Node support was estimated by clade posterior probability (CPP). The resulting tree was transformed to its ultrametric form using the chronogram maximum likelihood calibration method (Paradis 2013).

The effect of phylogenetic relatedness and the different co-variables on binary RV (change in host preference after plant's cue experience as compared to inexperienced control) was analyzed with Bayesian inference of multivariate phylogenetic mixed model using the MCMCglmm R package (Hadfield and Nakagawa 2010). Fixed effects (=co-variables) were (see table's legend for the description of index value):

- degree of the plant's specialization (polyphagous, oligophagous or monophagous) (first column of Table A1);
- the type of activity tested during conditioning (larval feeding, oviposition, or adult feeding) (2nd column of Table A1);
- experimental design (no choice or choice tests) (3rd column of Table A1);
- the wildness of the insect (whether it is a field insect or a pure laboratory strain) (4th column of Table A1);
- the level of evolutionary interaction between the insect and the plant's cues used for experiment (5th column of Table A1);
- the delay between experience period and test period (6th column of Table A1);
- the developmental stage experienced (at larval, pupal and/or imaginal stages) (7th column of Table A1);
- the year of the publication (last column of Table A1).

Phylogeny was inversed and considered as random effect (Hadfield and Nakagawa 2010). Prior normal distributions with zero means were considered for all fixed effects. Prior variances of 10 were found to produce lower posterior variances for all variables. The degree of evolutionary adaptation and the year of publication, which exhibited particularly peaked posteriors as compared to prior's variances, could be reduced to 1 and 0.01, respectively, to improve the power of analysis without introducing a bias. The proportion of the variance due to phylogeny (de Villemereuil and Nakagawa 2014) was estimated to evaluate the phylogenetic signal for the RV. The posterior distribution of this statistics was analyzed.

Results

A phylogenetic Bayesian tree was performed on the insect species used in the 196 studies used for the literature analysis (Fig. 1). The number of studies was not the same as the number of insect species because several studies used the same insect species or the same species was tested in more than one study or several times within the same study. The tree confirmed the monophyly of each genus.

Information on both the type of activity and developmental stage involved was available for 114 studies involving polyphagous, 67 involving oligophagous and 15 involving monophagous species (Fig. 2, host plant range). Among the studies, 71, 64 and 40% of the polyphagous, oligophagous and monophagous species, respectively, showed significant modulation of host preference.

Considering the type of activity tested within host plant range (Fig. 2, type of activity), most studies were carried out on oviposition, at the rate of 59% for polyphagous, 83% for oligophagous, and 87% for monophagous species. Considering the developmental stage exposed, 60–70% of the studies were done after both larval and imaginal conditioning regardless of the degree of specialization of the insect and the type of activity tested (Fig. 2, developmental stage(s) exposed: adult feeding and oviposition).

A significant influence of the phylogeny on the RV (i.e. the insect's ability to change its host preference after being exposed to the host) was observed in the phylogenetic mixed model, which treated phylogeny as random effect and several independent variables as fixed effect. Posterior distribution of proportion of variance due to phylogeny (Fig. A1) had a modal value at 0.986, median at 0.963 and quantile 5% at 0.427 showing significant effect of phylogeny. Traces of posterior parameters confirmed the random effects for phylogeny (Fig. A2) and the convergence for all the fixed effects (Fig. A3). Among the fixed effects (Table 1), larval and adult but not pupal experiences to plant cues, as well as year of the study, exhibited significant effects ($P < 0.001$, $P < 0.001$ and $P < 0.05$, respectively). The posterior probability distribution curves for these parameters excluded zero values, showing they are significantly different from zero (Fig. A3). In contrast, none of the study effects was significant (72 categories). Experimental design (choice or no-choice tests) and the wildness of the insect (whether field-collected or a pure laboratory strain) did not affect significantly the RV. Whether the insect was polyphagous or oligophagous did not change significantly the RV. The different activity tested, food larvae, oviposition and adult feeding responded similarly. The degree of adaptation to the plant's cues used for insect's experience, experimental design (choice or no-choice tests) and the delay between experience period and the test period also did not affect the RV.

Discussion

This analysis provides a first quantitative synthesis of the studies carried out on the role of insect experience on modulation of host preference according to different effects, including, the year of publication, the degree of plant's specialization, the phylogeny and the developmental stage at which the conditioning took place.

The effect of year of the study was significant, suggesting important autocorrelation effects that may be due to the fact that studies including several species in the same paper were carried out and under the same experimental conditions. A reduced statistical power of recent studies to detect learning due to fewer repetitions in the experimental design could also explain this significant negative effect of the year of the study on learning ability.

The majority of the studies retrieved from the literature on this subject used polyphagous species, although phytophagous insects are generally more oligophagous or monophagous than polyphagous (Bernays and Chapman 1994; Schoonhoven et al. 2005). Our analysis indicates that modulation of host preference after larval, pupal and/or imaginal experience did not depend on the degree of plant specialization of the species and was not more common in polyphagous than in oligophagous or monophagous insects. The preference performance hypothesis suggests a lower constraint on host preference in polyphagous species (Bernays 2001) and an easier adaptation to a new host plant in polyphagous insects as compared to specialist insects (Pentzold et al. 2014). We would therefore expect a higher ability to "learn" preference for a new host after experiencing this host in polyphagous than oligo- or monophagous insects, as has been shown by Petit et al. (2015) on Lepidoptera stem borers. But this is not the case, as concluded in this analysis. We must take into account that a species generally exists on a scale of diet specialization;

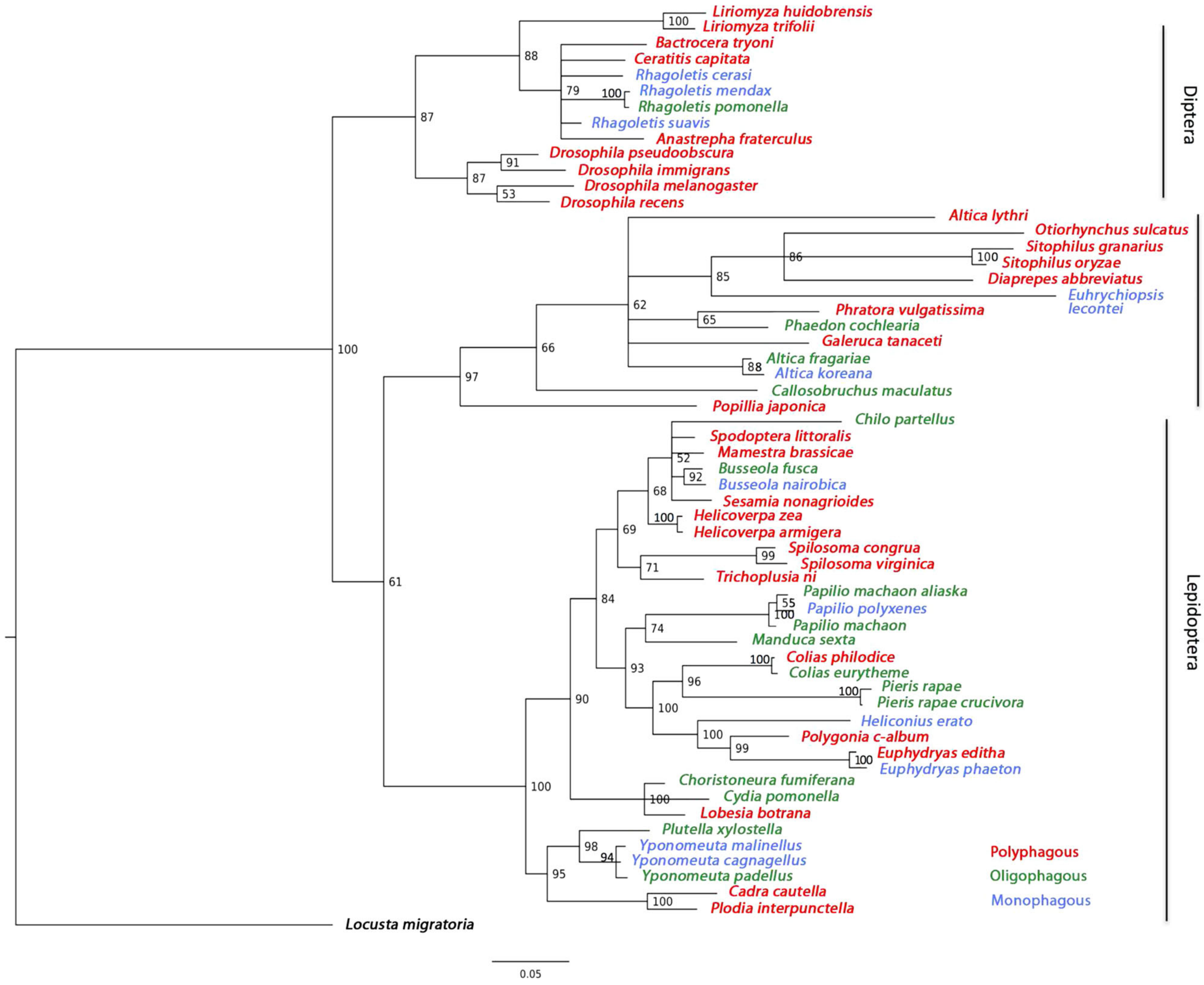
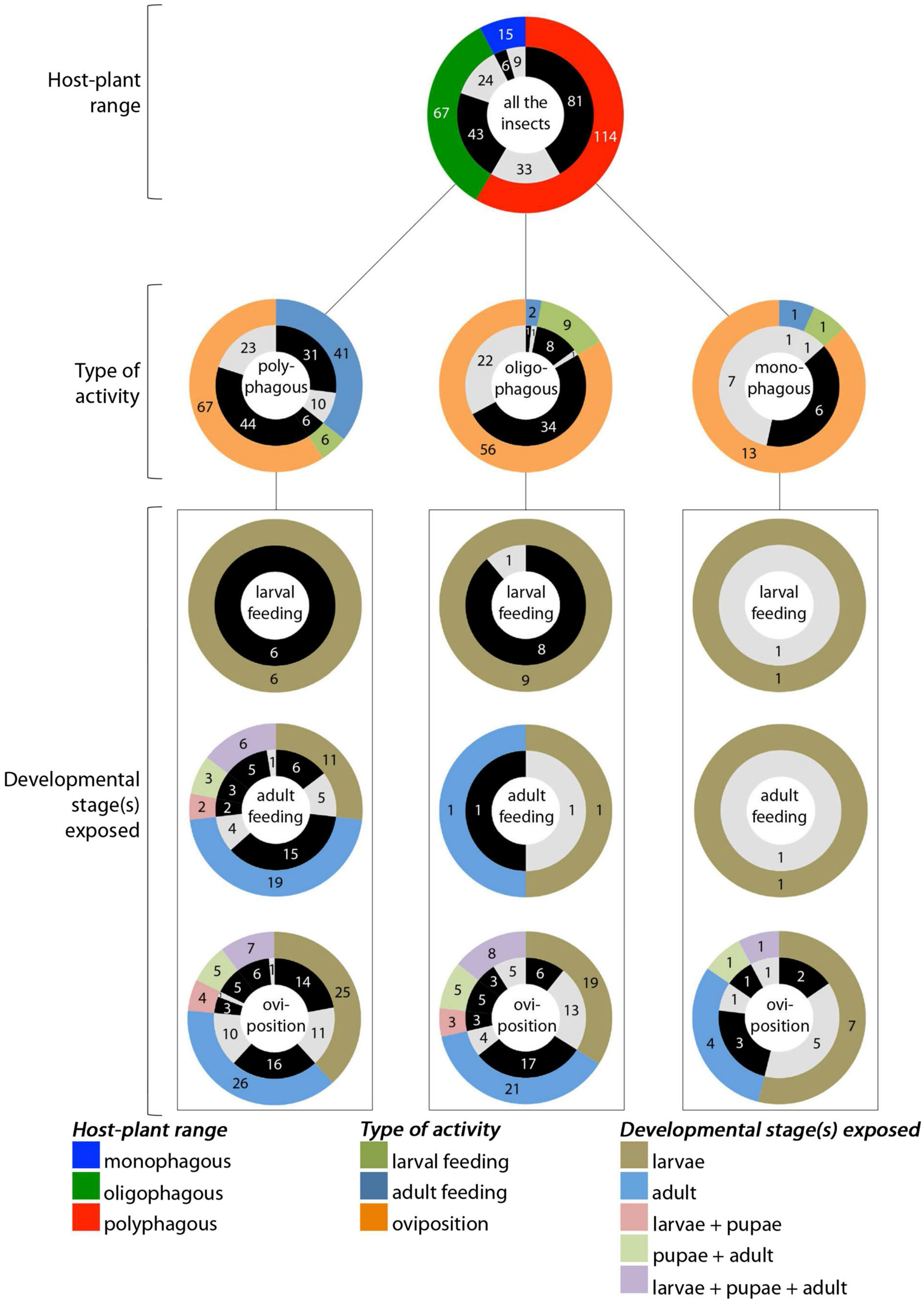


Fig. 1 Phylogenetic Bayesian tree using 1896 bp (*COI* + *EF-1*) of the species used in the literature analysis (see Table A1). Posterior probabilities are given at nodes. *Locusta migratoria* is used as outgroup

thus, there exist "composite generalist" species where a polyphagous species produces specialized populations (Rossiter 1987). This may explain why modulation of host preference after larval, pupal and/or imaginal experience can occur regardless of the degree of plant specialization.

In addition, understanding the mechanisms involved in host plant selection by insects is a crucial issue to better understand why some insects shifted from the wild to cultivated habitats to become important pests. Our literature analysis revealed that host plant selection is finally largely conditioned by the insect's experience. Natal host plant conditioning could be an important part of host use divergence and of insects shifting from the wild to cultivated habitats. Natal host plant conditioning may break down some of the historical inertia that may otherwise inhibit host switching and thereby facilitate the establishment of populations on a new host plant (Brown et al. 1995; Agosta 2006). A shift of host can occur when natal host plant conditioning leads to the loss of previous host associations or to host range expansion (Tabashnik 1983; Bernays and Chapman 1994; Izzo et al. 2014). This might explain why some insect species or populations shifted from the wild to cultivated habitats, i.e. through ecological fitting or host range expansion processes; and become important pests. Thus, innate behavioral responses modulated by experience enable the insect to cope with environmental variations (Jaenike 1988; Papaj and Prokopy 1989; Cunningham et al. 1999; Via 1999; Dukas 2008). Such host shifts can occur in all host plant range types. Examples of insects shifting from the wild to cultivated habitats have been reported in polyphagous insects such as the African sugar cane borer *Eldana saccharina* Walker (Lepidoptera: Pyralidae), which shifted from *Cyperus* sp. to become an important pest of sugar cane in South Africa and maize in West Africa (Atkinson 1980), and *Caryedon serratus* (Coleoptera: Bruchidae) which shifted from wild


Host-plant range
Type of activity
Developmental stage(s) exposed
all the insects
15
9
6
24
81
67
114
43
33
poly-phagous
23
31
41
67
10
44
6
6
oligo-phagous
2
9
1
1
8
22
1
34
56
mono-phagous
1
1
1
1
7
6
13
larval feeding
6
6
larval feeding
1
8
9
larval feeding
1
1
adult feeding
6
11
1
5
6
3
3
5
2
2
4
15
19
adult feeding
1
1
1
1
adult feeding
1
1
ovi-position
7
5
6
1
14
25
5
4
3
10
11
16
26
ovi-position
8
5
6
19
3
5
5
13
3
3
4
17
21
ovi-position
1
1
1
2
1
1
7
4
3
5
Host-plant range
🟦 monophagous
🟩 oligophagous
🟥 polyphagous
Type of activity
🟩 larval feeding
🟦 adult feeding
🟧 oviposition
Developmental stage(s) exposed
🟫 larvae
🟦 adult
🟥 larvae + pupae
🟩 pupae + adult
🟪 larvae + pupae + adult

◀**Fig. 2** Representation of the number of studies which did (*black*) or did not (*gray*) validate the effect of previous experience on modulation of host preference (*inner doughnut charts*) according to three following criteria (*outer doughnut charts*): host plant range of the insect (mono-, oligo- and polyphagous); type of activity analyzed (larval feeding, adult feeding and oviposition); developmental stage(s) exposed to the experience (larvae, adult, pupae or combinations)

Caesalpiniaceae to groundnuts in West Africa (Delobel 1995). Several examples of such shifts have also been reported in oligo- and monophagous insects. For oligophagous insects, several examples are given in the literature. The Lepidoptera stem borer *Busseola fusca* (Lepidoptera: Noctuidae) became an important pest of maize in sub-Saharan Africa since the introduction of this crop to this continent (Kfir et al. 2002). Similarly, the diamondback moth *Plutella xylostella* L. (Lepidoptera: Plutellidae) was found on sugar peas in Kenya (Löhr 2001), the apple maggot fly *Rhagoletis pomonella* (Walsh) (Diptera, Tephritidae) shifted from the native hawthorn (*Crataegus* sp.) to apple (*Malus* sp.) (Bush 1969) and the legume-feeding butterfly *Colias philodice eriphyle* (Lepidoptera: Pieridae) expanded its host plant range to *Medicago sativa* L. (Fabacae) (Tabashnik 1983), a plant cultivated for livestock feed around the world. An example for monophagous insects, *Conicofrontia sesamoides* Hampson (Lepidoptera: Noctuidae), specialized to *Miscanthus capensis* (Poaceae), was recently found as a pest on sugar cane in South Africa (Le Ru et al. 2015).

According to the importance of the insect's developmental stage on the modulation of host plant preference, we found that both larval and adult but not pupal experiences to plant cues exhibited significant effects. Barron (2001) concluded that experience within the adult stage has a greater influence on the pattern of host uses than preimaginal experience. In our study, both the fixed effects (larval and imaginal experiences) exhibited the same significant *P* value (Table 1). Therefore, it is suggested that preimaginal experience has a similar influence on the pattern of host uses as adults. Moreover, although the repetitions in the experimental design using pupae were fewer as compared to larvae and adults, this study indicated, for the first time, that pupal conditioning seems not to be involved in NHPI.

In conclusion, our study revealed that early host experience positively biases subsequent host use and host seeking behaviors. However, this ability varies between species and is largely influenced by the phylogeny of the insect rather than by the degrees of host plant specialization. Accounting for phylogenetic relationships may therefore help to predict an ability to adapt to habitat modifications by modulating host preference and thus to become a pest.

When involving neuronal processes, host preference may integrate information not only on the natal host but also on the habitat's complexity. Indeed, this ability to change host preference after being conditioned to a natal host may be advantageous for insects when hosts are always present and spatially and temporally homogenous, but may be disadvantageous when hosts are unavailable and changing during the life span. In the former situation, "preference induction by experience" would reduce effective feeding or oviposition time. If natal hosts are

Table 1 Results of the general linear mixed models with MCMCglmm

Fixed effects	Post mean	Lower-95% credible interval	Upper-95% credible interval	Effect sample	*P* value	Significance
(Intercept)	52.52	4.60	105.06	327.4	0.029	*
Degree of specialization (oligophagous)	−0.29	−1.45	0.81	263.8	0.631	
Degree of specialization (polyphagous)	0.71	−0.46	1.80	467.5	0.202	
Experimental design (no choice or choice tests)	0.38	−0.57	1.31	236.1	0.428	
Activity tested (food larvae)	0.85	−0.37	2.01	344.8	0.176	
Activity tested (oviposition)	−0.47	−1.28	0.39	274.6	0.304	
Degree of adaptation to the plant's cues used for insect's experience	−0.02	−0.22	0.22	213.2	0.893	
Wildness of the insect	0.24	−0.18	0.74	331.6	0.273	
Larval experience	2.85	1.99	3.69	130.3	0.0002	***
Pupal experience	0.31	−0.67	1.30	334.3	0.553	
Imaginal experience	3.98	3.14	4.92	215.6	0.0002	***
Delay between experience period and test period	0.04	−0.49	0.55	142.0	0.836	
Year	−0.03	−0.05	−0.004	327.1	0.021	*

* p-value < 0.05; *** p-value < 0.001

unavailable, "preference induction by experience" is detrimental (e.g., Jahner et al. 2011). "Learning" may be more important for insects when available host species do not vary in time and space than when they vary. Experiments addressing this effect of environmental complexity on effects of "host impregnation" on host preference may help in untangling this complex, which is probably linked to multifactorial responses of the insect.

Author contributions

CP and SD contributed equally to this research.

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Compliance with ethical standards

Conflict of interest Authors Christophe Petit, Stéphane Dupas, Denis Thiéry, Claire Capdevielle-Dulac, Bruno Le Ru, Myriam Harry and Paul-André Calatayud declare that they have no conflict of interest.

Ethical approval This article does not contain any studies with human participants or animals performed by any of the authors.

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