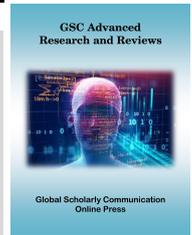




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(RESEARCH ARTICLE)

Testing for congruence between the oviposition behaviour of leaf-mining insects and the degree of phylogenetic relatedness among either mining species or hosts species: a case study within the mining moth genus *Phyllonorycter* (Lepidoptera: Gracillariidae)

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Abstract

In leaf-mining insects, the oviposition behaviour is especially critical for the welfare of the future brood, the latter being usually doomed to develop entirely within the host-leaf selected for egg-laying by the ovipositing females. As, moreover, oviposition behaviour in leaf miners depends upon the taxonomic identities of both the mining-insect and the host, one can thus speculate that the patterns of oviposition behaviour of different leaf-mining species could be more or less congruent with either the degree of phylogenetic relatedness of the leaf-mining species themselves or the degree of phylogenetic relatedness of their respective host-species. Here, I test successively these two hypotheses – the “miners phylogenetic relatedness” hypothesis and the “hosts phylogenetic relatedness” hypothesis – by addressing a system insect-plant involving four mining moth species (all four belonging to the genus *Phyllonorycter*) and the three corresponding host-tree species, all included within the family Betulaceae. It turns out that, for this system at least, neither of the two previous hypotheses is actually supported. Possible reasons for this double rejection are discussed accordingly.

Keywords: Egg-laying behaviour; Selectivity; Host acceptance

1. Introduction

Quantitative aspects of the oviposition behaviour in leaf-mining insects – the *severity* of ovipositing mothers in *selecting* host-leaves accepted for subsequent egg-laying (the “*leaf-acceptance ratio*”) and the average *clutch-size* – both play significant role in determining the future successful development of offspring and, thereby, are intended to have direct influence on the intensity of the resulting mining attack [1, 2]. These behavioural traits are reactions of ovipositing females following leaf probing and, accordingly, these behavioural traits should depend upon both:

- (i) the *foliage quality* of the host species, as perceived “in the eyes of the mining-species” [3] (i.e. a *host-related* parameter) and
- (ii) the corresponding level of requirement of mothers themselves, as regards the minimal quality of the host-leaf judged by mothers as being acceptable for subsequent egg-laying (i.e. an *insect-related* parameter).

Accordingly, any significant behavioural differences that might be disclosed between different mining-species within a same mining genus attacking different hosts species, would likely result from difference regarding *either* the *host* and/or the *mining species*.

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Now, the shared responsibilities of the insect and of the host-plant in this respect may be tracked by seeking for the existence of a possible congruence between:

- (i) the respective *oviposition behaviours* of different mining species and
- (ii) the pattern of *phylogenetic relatedness* either among these *mining species* themselves (the “*miners* phylogenetic relatedness” hypothesis) or among the corresponding *hosts species* (the “*hosts* phylogenetic relatedness” hypothesis).

Hereafter, I successively address and test these two hypotheses. The system {insects-hosts} considered for this study involves four moth species, all belonging to the genus *Phyllonorycter*, mining the leaves of one or the other of three host species representative of the family Betulaceae (*Alnus glutinosa*, *Carpinus betulus*, *Corylus avellana*). This system was chosen because we dispose of recent phylogenies published for *Phyllonorycter* [4] and for Betulaceae [5].

2. Material and methods

As already mentioned, egg-laying behaviour of leaf-mining mothers may be characterised by two major quantitative parameters: the *leaf-acceptance ratio* ‘ α ’ that reflect the degree of mothers’ selectivity for leaf quality prior to oviposition and the average *clutch-size* ‘ n_c ’ (the number of eggs deposited as a single bout on a previously accepted host-leaf). These behavioural parameters are, yet, very difficult to directly observe reliably under field conditions. It is possible, however, to trace back to these parameters by subsequently considering the resulting pattern of mines distribution among host-leaves. Accordingly, a specific approach, the so-called “*Melba*” procedure, has been developed in this purpose [6 - 12]. This procedure was implemented here and successively applied to 19 stands supporting mining attacks of:

- *Phyllonorycter coryli* (Nicelli, 1851) (7 stands) and *Ph. nicellii* (Stainton, 1851) (5 stands) on *Corylus avellana* L.,
- *Ph. esperella* (Goeze, 1783) (6 stands) on *Carpinus betulus* L. and
- *Ph. rajella* (Linnaeus, 1758) (1 stand) on *Alnus glutinosa* (L.) Gaertner.

Running the “*Melba*” procedure provides estimations of the leaf-acceptance ratio ‘ α ’ and the average *clutch-size* ‘ n_c ’ for each of the sampled stands. Pooled results are presented in figure1.

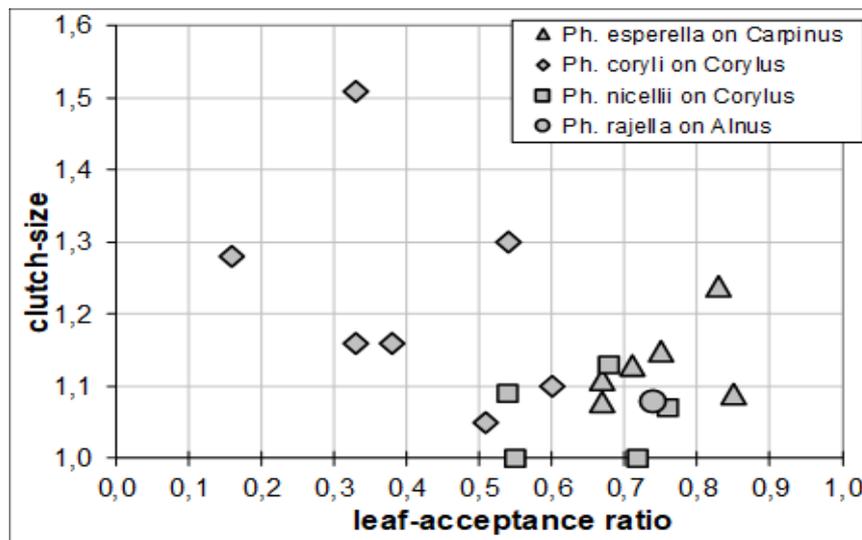


Figure 1 The distribution of (i) the leaf-acceptance ratio α and (ii) the average clutch-size n_c for *Phyllonorycter coryli* (7 stands) and *Ph. nicellii* (5 stands) on *Corylus avellana*; for *Ph. esperella* (6 stands) on *Carpinus betulus* and for *Ph. rajella* (1 stand) on *Alnus glutinosa*.

3. Results and discussion

3.1. Testing for the congruence between insect behaviour and the corresponding host-tree phylogenetic relatedness (within Betulaceae)

The three genus *Alnus*, *Carpinus* and *Corylus* all belong to the family Betulaceae, but *Alnus* on the one hand and *Carpinus* and *Corylus* on the other hand are members of well differentiated tribes within Betulaceae: Betuloideae for *Alnus*, Coryloideae for *Carpinus* and *Corylus* [5].

The pattern of combined distribution of the two oviposition behaviour parameters – the leaf-acceptance ratio ' α ' and the average clutch-size ' n_c ' – (figure 1) hardly mirrors the respective degrees of phylogenetic relatedness between the corresponding host-tree species (figure 2). Thus, the distribution of combined values [α , n_c] for *Ph. nicellii* is closer to the corresponding distributions for *Ph. esperella* and *Ph. rajella* than it is to the distribution for *Ph. coryli*. And this, although *Ph. nicellii* and *Ph. coryli* share the same host-species, *Corylus avellana*, while *Ph. nicellii*, *Ph. esperella* and *Ph. rajella* are mining different host-species, including *Alnus*, belonging to a different tribe. Therefore, no congruence occurs between the respective patterns of behavioural parameters of each of the four moth species and the pattern of phylogenetic relatedness among their respective host-species. Thus, here, the "hosts phylogenetic relatedness" hypothesis is not supported.

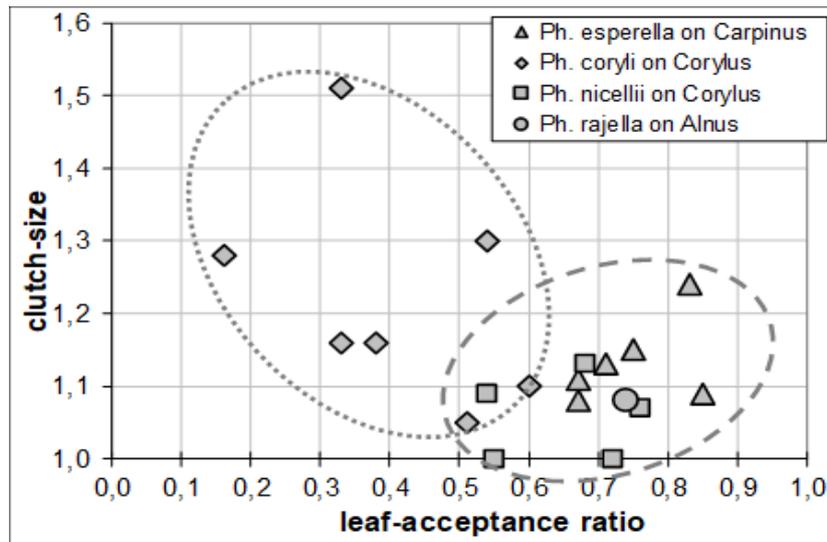


Figure 2 Non-congruence between the pattern of oviposition behaviour (the leaf-acceptance α and clutch-size n_c) and the phylogenetic relatedness of the respective host species [5]. Comments in text.

In figure 2, the dashed contour delimits similar behavioural parameters for three moths, *Ph. nicellii*, *Ph. esperella* and *Ph. rajella*, although each of them is mining different hosts – *Corylus avellana*, *Carpinus betulus*, *Alnus glutinosa* respectively. Moreover, these three host-species belong to different tribes in Betulaceae. On the contrary, *Ph. coryli* (dotted contour) and *Ph. nicellii* (dashed contour) significantly differ in their respective behavioural parameters (Mann & Whitney test, $p < 0.05$ regarding both the differences on leaf-acceptance α and clutch-size n_c) although they share the same host-species, *Corylus avellana*. Accordingly, the "hosts phylogenetic relatedness" hypothesis is not supported.

3.2. Testing for the congruence between insects behaviours and their own phylogenetic relatedness pattern within the genus *Phyllonorycter*

According to [4], closely related *Phyllonorycter* species generally feed on closely related hosts. Yet, I test whether the same holds true for egg-laying behaviour: figure 3.

First, among the four mining species involved, *Ph. coryli* and *Ph. esperella* are closely related [4] and, indeed, share the same (unusual) type of mining habit: upper-surface tentiforme mines. The two other moth species, *Ph. nicellii* and *Ph. rajella* – although being distantly related [4] – yet induce both the (common type) lower-surface tentiforme mines.

Second, the patterns of oviposition behaviours of the four mining moths, in terms of combined values of α and n_c , do not show any appreciable congruence with the degrees of phylogenetic relatedness between them (Figure 3). Thus, here, the “miners phylogenetic relatedness” hypothesis is not supported.

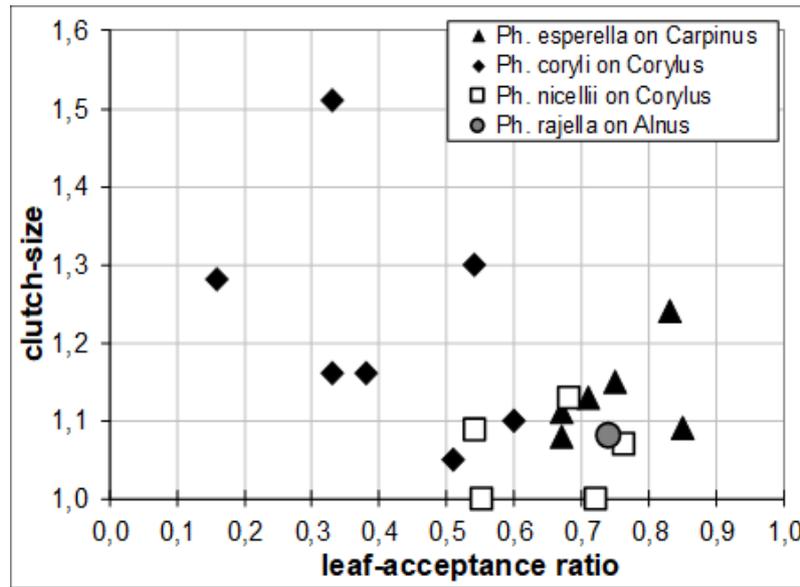


Figure 3 The distribution of combined values of α & n_c of the four mining moths tested against the phylogenetic relatedness between them. Comments in text.

In figure 3 and according to [4], the degree of similarity of colours of figures is intended to mirror the degree of phylogenetic relatedness between mining-moths species: *black* for both the closely related *Ph. coryli* and *Ph. esperella*; *grey* for the distant *Ph. rajella* and *white* for the still more distant *Ph. nicellii*. Instead of being segregated apart, the distributions of values of α & n_c for the distantly related species *Ph. esperella*, *Ph. rajella* and *Ph. nicellii* are included within a same scatter, while the distribution of α and n_c for *Ph. coryli* is segregated apart, in spite of its close relatedness to *Ph. esperella*. Accordingly, the “miners phylogenetic relatedness” hypothesis is not supported.

3.3. Discussion of results

“Pre-hatching maternal-care behaviour” in leaf-miners (involving both (i) the *host-leaf acceptance ratio* for subsequent egg deposit and (ii) the *size of egg-clutch*), is likely intended to (i) selecting the best resource insuring the efficient development of the future brood and (ii) preventing the risk of scramble competition between conspecific larvae within a same host leaf, respectively [1-2]. Accordingly, this pre-hatching maternal-care will arguably contribute to the optimal development of offspring and, thus, deserve attention, in particular regarding the causes of variations in oviposition behaviour among mining species.

As such, these behaviours should account for both the taxonomic identity of the moth and the taxonomic identity of the host. Which may suggest, in turn, that some congruence could exist between the patterns of behavioural parameters of the egg-laying mothers and the patterns of phylogenetic relatedness between either the *mining moth*-species or the corresponding *host*-species [13]. What we called respectively the “miners phylogenetic relatedness” hypothesis and the “hosts phylogenetic relatedness” hypothesis.

Within the system considered here, including four *Phyllonorycter* moths, each of them mining one among three host-species, all belonging to the family Betulaceae, *no congruence* appears between the pattern of differentiated oviposition behaviours of the four mining-moth species and the patterns of phylogenetic relatedness among the mining-moths as well as among their respective host-trees. So that neither the “miners phylogenetic relatedness” hypothesis nor the “hosts phylogenetic relatedness” hypothesis are supported, at least for the limited system investigated here.

This, finally, might not be so surprising. Indeed, a congruence between the patterns of differentiated moth behaviours and the pattern of phylogenetic relatedness of host-trees would likely be expected only if none of the four moths had had enough micro-evolutionary time to undergo *substantial adaptative evolution*, in order to cope at best with their respective preferred hosts. In other words, such congruence might have been expected only if the four moth species had not already undergone substantial evolutive differentiation allowing them to adapt to their respective hosts

independently of the degree of relatedness of the latter: see reference [12] and, here, *Ph. coryli* and *Ph. nicelli* having adapted to mining a same host, *Corylus avellana*, in spite of their own distant relatedness: figure 3). But, on the contrary, it is more likely that each of these mining species is already well advanced in its own micro-evolutive history. So that, difference in oviposition behaviours among the four mining species have less reason to still reflect, at present time, the degree of difference between the phylogenetic traits of their respective hosts.

The same type of argument might explain the lack of congruence between the pattern of oviposition behaviour and the pattern of phylogenetic relatedness among the mining-moths themselves: the micro-evolution of each moth species is intended to adapt each species to its particular host and, thus, tends to reduce, more or less, the differences between the degrees of selectivity expected between moths.

4. Conclusion

No congruence was disclosed between the main descriptors of oviposition behaviour and the degrees of phylogenetic relatedness among the four studied mining species within the mining moth genus *Phyllonorycter*. No congruence either was detected between the main descriptors of oviposition behaviour and the degrees of phylogenetic relatedness among the three host-trees involved in the study. Accordingly, neither the “*miners’* phylogenetic relatedness” hypothesis nor the “*hosts* phylogenetic relatedness” hypothesis are supported in the system insect-host plant considered here. Yet, although some rationale has been suggested to explain this double rejection (i.e. some close and specific miner-host adaptations seem likely to have evolved *independently* in each couple insect-host), it would remain useful to further extend the investigation to a series of other systems of leaf-miners and their associated host-species. Indeed, tentatively generalizing from one case study only – would this generalization might seem rather logical – is still somewhat adventurous.

Compliance with ethical standards

Acknowledgments

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Disclosure of conflict of interest

The author declares no conflict of interest regarding this study.

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