

# 1 Testing host-plant driven speciation in phytophagous insects : a phylogenetic perspective

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11

## 12 Abstract

13 During the last two decades, ecological speciation has been a major research theme in  
14 evolutionary biology. Ecological speciation occurs when reproductive isolation between  
15 populations evolves as a result of niche differentiation. Phytophagous insects represent model  
16 systems for the study of this evolutionary process. The host-plants on which these insects feed and  
17 often spend parts of their life cycle constitute ideal agents of divergent selection for these  
18 organisms. Adaptation to feeding on different host-plant species can potentially lead to ecological  
19 specialization of populations and subsequent speciation. This process is thought to have given  
20 birth to the astonishing diversity of phytophagous insects and is often put forward in  
21 macroevolutionary scenarios of insect diversification. Consequently, numerous phylogenetic  
22 studies on phytophagous insects have aimed at testing whether speciation driven by host-plant  
23 adaptation is the main pathway for the diversification of the groups under investigation. The  
24 increasing availability of comprehensive and well-resolved phylogenies and the recent  
25 developments in phylogenetic comparative methods are offering an unprecedented opportunity to  
26 test hypotheses on insect diversification at a macroevolutionary scale, in a robust phylogenetic  
27 framework. Our purpose here is to review the contribution of phylogenetic analyses to investigate  
28 the importance of plant-mediated speciation in the diversification of phytophagous insects and to  
29 present suggestions for future developments in this field.

30

31 **Introduction**

32 The idea according to which new species arise through **adaption** to different ecological  
33 niches constitutes the core of Darwin's work. This process is now termed ecological speciation  
34 and its study has become an intense field of research in evolutionary biology (Nosil 2012; Nosil *et*  
35 *al.* 2002; Rundle & Nosil 2005; Schluter 2009). **Phytophagous insects**\*<sup>1</sup> have always been at the  
36 forefront of these investigations (Drès & Mallet 2002; Elias *et al.* 2012; Forbes *et al.* 2017; Funk  
37 *et al.* 2002; Matsubayashi *et al.* 2010). The hypothesis of ecological speciation resulting from  
38 divergent selection exerted by host-plants was put forward a long time ago to explain the  
39 formation of new species of insects (Brues 1924; Walsh 1864). There are several model systems  
40 on which this scenario has been explored. One text-book example of host-plant driven incipient  
41 speciation is the apple maggot (*Rhagoletis pomonella* complex) in which the evolution of new  
42 feeding preferences on the recently introduced domesticated apple (*Malus pumila*) has supposedly  
43 led to the emergence of specialized host races (Berlocher 2000; Bush 1975; Powell *et al.* 2014).  
44 Stick insects, leaf beetles (Nosil *et al.* 2012; Rundle *et al.* 2000), butterflies (McBride & Singer  
45 2010), and the pea aphid also star among model systems in the study of host-driven speciation  
46 (Via *et al.* 2000; Caillaud & Via 2000; Peccoud *et al.* 2009; Smadja *et al.* 2012). In all these  
47 examples, the speciation scenario hypothesizes that: 1) the restricted utilization of distinct sets of  
48 host-plant species by insect populations is the result of adaptive trade-offs; 2) hybrids with  
49 intermediate phenotypes (in terms of traits involved in **host-plant adaptation**\*) fare poorly on  
50 parental host-plants and therefore gene flow between populations is reduced; 3) gene flow can be  
51 further reduced through the evolution of assortative mating, especially when host-plants also  
52 represent mating sites. In support of this scenario, many studies show the existence of genetically  
53 differentiated host races in insect species. Some studies have quantified selection against hybrids  
54 (McBride & Singer 2010; Gow *et al.* 2007) and some studies have uncovered genomic regions  
55 that determine host-plant preference and performance on alternative hosts (Egan *et al.* 2008;  
56 Smadja *et al.* 2012; Soria-Carrasco *et al.* 2014).

57 The role of host-plant-mediated speciation in the diversification of phytophagous insect  
58 lineages is also largely emphasized in the literature on large-scale patterns of insect diversity:  
59 macroevolutionary perspectives on phytophagous insect evolution have attributed their  
60 extraordinary diversification to selective responses to their host-plants (Ehrlich & Raven 1964;

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<sup>1</sup> See glossary

61 Janz 2011; Winkler & Mitter 2008; Yokoyama 1995). However, these macroevolutionary  
62 scenarios are often presented in the literature as narratives for specific lineages commenting a  
63 phylogenetic reconstruction of the history of host-plant associations. Many phylogenetic studies  
64 still fail to clearly formulate hypotheses and predictions about the speciation processes that  
65 underlie the observed patterns and the role played by host-plant adaptation in those. The reason  
66 might be that the macroevolutionary patterns that arise when **host-plant specialization\*** is the  
67 driver of speciation events are not always clear. There is no review on what to expect and how to  
68 formally test these predictions.

69 The increasing availability of robust molecular phylogenies and recent developments in  
70 phylogenetic comparative methods are offering an unprecedented opportunity to test evolutionary  
71 hypotheses in a robust phylogenetic framework. Our purpose here is to present the  
72 macroevolutionary scenarios for the diversification of phytophagous insects that have been put  
73 forward in the literature, decipher the role that ecological speciation driven by host-plant  
74 adaptation play in them and synthesize predictions from these scenarios. We then identify tools  
75 from the “comparative phylogenetic toolbox” that provide ways to test some of these predictions.

76 This toolbox can be divided into three compartments: 

77 1) comparisons of the phylogenetic histories of insects and their associated plants: the  
78 congruence (in terms of dates of divergence and branching patterns and) of the phylogenetic  
79 histories of plant-feeding insects and their host-plants can be tested in robust statistical  
80 frameworks and illuminate how herbivores track the diversification of their hosts;

81 2) ancestral character state reconstructions: the evolutionary trajectory of host-associations,  
82 host breadth and host-plant adapted traits can be inferred using ancestral character state  
83 reconstruction methods and statistical tests can determine whether their distribution throughout the  
84 phylogenetic trees follow the predictions of scenarios involving ecological speciation mediated by  
85 host-plant adaptation;

86 3) diversification analyses: the recent developments of methods to study the **diversification**  
87 **dynamics\*** of entire clades using phylogenetic trees provide ways to test how shifts to new host-  
88 plant species or changes in host breadth have impacted speciation rates in phytophagous insects.

89 We review papers that have adopted these approaches. We then present suggestions for future  
90 research that should help linking microevolutionary studies on host-plant adaptation and  
91 macroevolutionary perspectives on phytophagous insect diversification.

## 92 **I Macroevolutionary scenarios of phytophagous insect diversification**

### 93 **I.1) *Escape and radiate* (Figure 1 a)**

94 More than 50 years ago, Ehrlich & Raven (1964) put forward a macroevolutionary  
95 scenario that inspired most of the current research on plant-feeding insect diversification: it is  
96 known as “***Escape and radiate***” (Thompson 1989). They hypothesized that when insects acquire  
97 the ability to circumvent the chemical defenses of a plant group, it promotes their rapid  
98 diversification by ecological release, *i.e.* the availability of novel resources and reduction in direct  
99 competition. Insects undergo an **adaptive radiation**\*. In this scenario, adaptation towards host-  
100 plants is the driving force of insect species formation. The “*Escape and radiate*” scenario also  
101 hypothesizes that, in response to phytophagous insect predation, plants acquire novel chemical  
102 defenses which allow them in turn to diversify very rapidly (Marquis *et al.* 2016). Ehrlich &  
103 Raven’s seminal study suffers from several shortcomings that have been pinpointed before (Janz  
104 2011). First, although the authors frame their theory within the concept of adaptive radiation, they  
105 do not explicitly lay out speciation mechanisms for both partners of the interaction. Following  
106 their scenario, a trade-off in resource use and specialization towards specific host-plants is  
107 necessary to explain the formation of numerous insect species (*i.e.* species radiation) following the  
108 capture of a new host-plant lineage. Such a trade-off is not mentioned in the original paper (Janz  
109 2011). In addition, as underlined by contemporary researchers of Erlich and Raven’s, it is difficult  
110 to conceive how the selection pressures exerted by insects on plant defences can drive plant  
111 speciation (Jermy 1976, Jermy 1984). Plant traits that reduce phytophagous insect attacks are  
112 rarely linked with reproductive isolation between plant populations (but see Marquis *et al.* 2016  
113 for a review of scenarios of herbivore-induced speciation in plants) and the evidence for bursts of  
114 speciation in plants following the evolution of chemical defence is scant (Futuyma & Agrawal  
115 2009). However this study has been and remains a great source of inspiration for studies on the  
116 diversification of plant-insect associations. This is probably because it is one of the first studies  
117 that attempts to explain how microevolutionary processes (host-plant adaptation) translate into  
118 macroevolutionary patterns (radiation onto newly acquired plant lineages). Several predictions that  
119 can be tested on phylogenetic trees arise from the *Escape & Radiate* scenario (Table 1).

120 In the years following its publication, “*Escape and radiate*” was often interpreted as  
121 generating **cospeciation**\* patterns; however it is now recognized that it rather predicts the  
122 sequential speciation of insects onto an already diversified plant lineage (Janz 2011; Suchan &  
123 Alvarez 2015). According to this prediction: 1) the reconstruction of the history of host-plant  
124 associations on the phylogenetic trees of insects should reveal host-plant conservatism, *i.e.* the use  
125 related plant species by related insects (Mitter & Brooks 1983; Winkler & Mitter 2008); 2) the  
126 phylogenies of herbivorous insects and their host-plants should be more congruent than expected

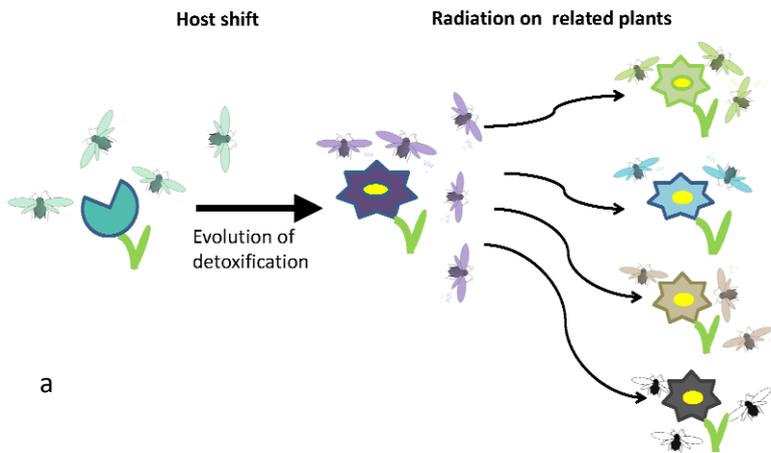
127 by chance and the diversification of the insects should lag behind that of their host-plants; this is  
128 called sequential evolution (Jermy 1976) or “*host tracking*”. Nevertheless, when the association  
129 between insects and their host plants is species-specific, a pattern of cospeciation can be expected  
130 through simple co-vicariance: geographic barriers affect the differentiation of populations of  
131 interacting lineages in a similar way and cause simultaneous speciation events (Althoff *et al.* 2012;  
132 Brookes *et al.* 2015; Martínez-Aquino 2016). In these cases, it is geographic isolation and not  
133 natural selection that initiates the reproductive isolation of insect populations and subsequent  
134 speciation. However, the specificity of the insects and host-adapted traits enhance the probability  
135 of shared vicariant events.

136 The diversification dynamics of insects should follow the typical pattern of adaptive  
137 radiations (Janz 2011), *i.e.* they should show an acceleration of speciation rate upon the capture of  
138 new plant lineages or the evolution of detoxification mechanisms (Wheat *et al.* 2007) and then  
139 slow down when their niches are saturated (when species diversity is reaching the carrying  
140 capacity of the host-plant lineage) (Rabosky & Lovette 2008). Furthermore, the capture of a  
141 species-rich clade of plants should result in higher speciation rates than the capture of lineages  
142 encompassing less species (Roskam 1985; Janz *et al.* 2006).

### 143 **I.2) The ‘*Oscillation Hypothesis*’ (Figure 1b)**

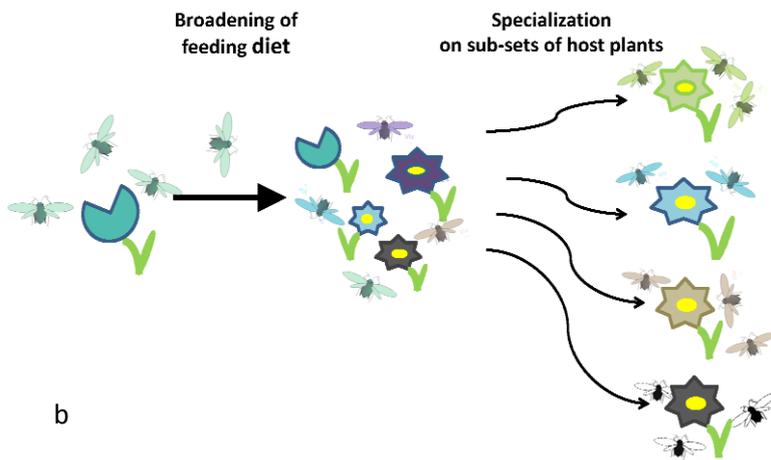
144 The “*Escape and radiate*” scenario was revisited more than a decade ago by Janz and  
145 collaborators (Janz *et al.* 2001, Janz & Nylin 2008; Janz *et al.* 2006; Nylin & Janz 2009). Using  
146 butterflies as study systems, they stated that expansions in diet breadth followed by specialisation  
147 onto new host-plant species constantly fuel the diversification of phytophagous insects. This has  
148 been termed the ‘*Oscillation Hypothesis*’ (Janz & Nylin 2008). It stipulates that transitions  
149 towards a generalist diet generally open up a new adaptive zone, which favours the capture of new  
150 host-plants. In this scenario, expansions in diet are enabled by the phenotypic plasticity of insects  
151 with respect to host-plants (Nylin & Janz 2009). Population fragmentation and their specialisation  
152 onto newly captured host-plants then lead to the formation of new species. Hence this scenario  
153 explicitly predicts that species formation results from insect populations evolving towards the  
154 utilization of a restricted set of host-plants. Nevertheless, it suggests that this specialization  
155 process is often a consequence of the geographic isolation of generalist insect populations in areas  
156 inhabited by different host-plant species (Janz *et al.* 2006). Therefore the “*Oscillation hypothesis*”  
157 does not necessarily postulate that natural selection is the main driving force of species formation.

**Escape and Radiate** (Erich & Raven 1964)



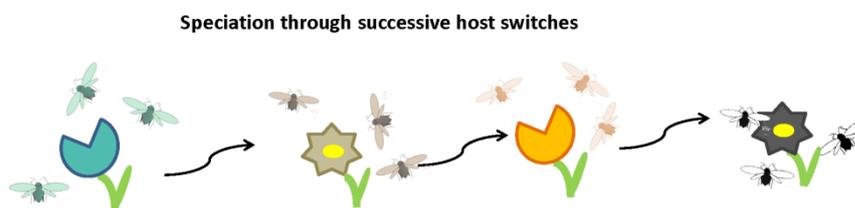
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**Oscillation hypothesis** (Janz & Nylin 2008)



159

**Musical chairs** (Hardy & Otto 2014)



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161

162 Fig 1: Schematic illustrations of the macroevolutionary scenarios of phytophagous insect  
163 diversification.

164

165 However, subsequent papers quoting this scenario emphasize the central role of host-plant  
166 specialisation (Hardy & Otto 2014; Nakadai 2017; Wang *et al.* 2017; Hardy 2017).

167 Most of the predictions from the *Escape and Radiate* scenario are valid under the  
168 “Oscillation hypothesis” (Hardy *et al.* 2017), however it yields several new predictions (Table 1):

169 - **generalist\*** diets should be “transient and repeatedly disappear in favour of specialization  
170 onto a limited set of related plants” (Nylin *et al.* 2014);

171 - gains of new host plants are associated with host breadth expansion (Janz *et al.* 2001);

172 - the amplitude of the oscillation determines the number of potential host-plant species;  
173 therefore, insect clades with the most diverse host-use (the highest number of host-plant species)  
174 are expected to be more speciose than clades using less host species (Janz *et al.* 2006); and along  
175 the same lines insect clades that encompass species that exhibit large host breadths should have  
176 higher diversification rates (Hardy & Otto 2014; Weingartner *et al.* 2006);

177 - shifts from a generalist diet to a specialist one should be associated with an acceleration  
178 of diversification rates. In other words, patterns of diversification should follow a model where  
179 cladogenetic events are associated with host breadth reduction (Hardy & Otto 2014);

180 - generalists have larger geographic ranges as they are able to colonize more habitats and  
181 can expand more easily (Slove & Janz 2011).

### 182 **I.3) The *Musical Chairs* (Figure 1c)**

183 Hardy and Otto (2014) have recently put forward a scenario where speciation in  
184 herbivorous insects is driven by specialisation onto newly captured host-plants without any  
185 transitions in diet breadth: insects speciate by successive switches to new host-plants. The authors  
186 named their scenario “*the Musical Chairs*” (Hardy & Otto 2014). They explicitly state that  
187 specialization onto a few host plant species explains species diversification in phytophagous  
188 insect.

189 The “*musical chairs*” hypothesis yields several predictions that differentiate it from the  
190 “*Oscillation hypothesis*” (Table 1):

191 - gains of new hosts are not associated with host breath expansion (Hardy 2017):

192 - host breadth contraction is not associated with cladogenetic events (Hardy & Otto 2014);

193 - speciation rates should be higher in lineages showing no conservatism in host-plant  
194 associations (Hardy & Otto 2014);

195 - lineages showing many transitions from generalist to specialist feeding diets should not  
196 be more speciose than lineages that only encompass specialist species (Hardy & Otto 2014).

197            However, several authors have pointed out that it will be difficult to tell apart the “*Musical*  
198 *Chairs*” from “the *Oscillation Hypothesis*”. If generalism is indeed ephemeral as expected when  
199 specialization towards host-plants is adaptive, it will be difficult to reconstruct its history  
200 accurately on phylogenetic trees (Janz *et al.* 2016). Consequently, the relationships between host-  
201 range size and speciation rates will be difficult to explore and the set of predictions that  
202 differentiate the *musical chairs* from the *oscillation hypothesis* will not always be testable.

203            Phylogenetic comparative methods (Pennell & Harmon 2013) including increasingly  
204 sophisticated diversification models (Beaulieu & O’Meara 2016; O’Meara & Beaulieu 2016;  
205 Rabosky 2006; Rabosky & Goldberg 2015; Stadler 2013; Stadler & Bokma 2013) can now be  
206 deployed to reconstruct ancestral character states, investigate the diversification dynamics of  
207 insect lineages and test whether shifts in diversification rates are associated with transitions in  
208 character states. Below we review how these methods have been used to investigate the evolution  
209 of plant/insect associations and test the predictions of host-driven speciation scenarios.

## 210 **II Phylogenetic approaches for testing ecological speciation scenarios**

### 211 **II.1) Comparing the phylogenies of plants and insects**

212            Many phylogenetic studies have compared the phylogenies of herbivorous insect and their  
213 host-plants and have investigated cospeciation and host tracking patterns. They have used tools  
214 such as tree reconciliation analyses (Conow *et al.* 2010; Page 1994) and distance-based methods  
215 for tree comparisons (Legendre *et al.* 2002). A pattern of cospeciation has been found between  
216 figs and their phytophagous pollinating wasps (Cruaud *et al.* 2012; Rønsted *et al.* 2005; Weiblen  
217 & Bush 2002) as predicted by early taxonomic studies on this biological system (Ramirez 1974;  
218 Wiebes 1979), but also between figs and some of the non-pollinating galling wasps that are highly  
219 specific to their hosts (Jousselin *et al.* 2008). Reciprocal adaptations of plants and insects (i.e.  
220 **coevolution\***) have been unravelled in this study system (Jousselin *et al.* 2003; Weiblen 2004).  
221 However, it is not known whether the cospeciation patterns observed are the sole result of this  
222 coevolution (i.e. whether reciprocal selection exerted by both partners has driven the reproductive  
223 isolation of interacting populations; Althoff *et al.* 2014; Hembry *et al.* 2014) or whether matching  
224 speciation events have arisen through co-vicariance. In the other iconic model system for the study  
225 of plant/insect **coevolutionary diversification\***, the *Yucca*–*Yucca* moth interaction (Pellmyr  
226 2003), **pollinating and non-pollinating moths phylogenetic histories** parallel some parts of the  
227 evolutionary history of their hosts. Some studies suggest that these patterns are the results of  
228 coevolution (Godsoe *et al.* 2009) while others hint towards co-vicariance (Althoff *et al.* 2012)..

229 Table 1: Predictions from the different scenarios involving host-plant driven speciation: the first column indicates the evolutionary hypotheses tested  
 230 and the headers of the other columns indicate phylogenetic comparative approaches used for testing them.

	<b>Insect and host tree comparison</b>	<b>Evolution of host associations</b>	<b>Evolution of host breadth</b>	<b>Insect diversification dynamics</b>
<b>Speciation driven by host-plant specialization</b>	Cospeciation if the insects play a role in their host-plant reproductive isolation	No overlap in host use among sister-species (Nyman <i>et al.</i> 2010).	Predominance of specialists over generalists (Janz <i>et al.</i> 2001, Winkler & Mitter 2008).	- herbivorous insects are more diverse than their non-herbivorous relatives (Mitter <i>et al.</i> 1988) - the diversification dynamic of phytophagous insects follows a pattern of adaptive radiation (Janz 2011) - the number of species within an insect clade positively correlates with the number of host-plant species (Janz 2006)
<b>Macroevolutionary scenarios</b>				
<i>Escape and radiate</i>	Host tracking (Jermy 1976, Mitter & Brooks 1983).	Phylogenetic conservatism of host-plant lineages or host-plants with similar defences (Winkler & Mitter 2008).	No prediction	Increase in speciation rates upon the capture of new plant lineages or detoxification mechanisms (Wheat <i>et al.</i> 2007; Fordyce 2010).
<i>Oscillation</i>	Potentially host tracking following the capture of a new host-plant lineage.	Conservatism of host-plants following the capture of a new plant lineage.	- recurrent transitions in host breadth (Janz <i>et al.</i> 2001, Janz & Nylin 2008) - gain of new host lineages preceded by host breadth expansion (Janz <i>et al.</i> 2001) - host breadth larger in species with large geographic range (Slove & Janz 2011) - speciation events associated with shifts from generalist to specialist (Hardy & Otto 2014)	- clades including generalist species are more speciose than clades with only specialists (Weingartner <i>et al.</i> 2006) - speciation rates higher in lineages showing high lability in host breadth (Hardy & Otto 2014)
<i>Musical chairs</i>	No prediction	High lability in speciose lineages breadth (Hardy & Otto 2014)	Few transitions in host breadth (Hardy & Otto 2014; Hardy 2017)	- no positive association between speciation rates and host breadth lability (Hardy & Otto 2014) - speciation rates positively correlated with lability in host associations (Hardy & Otto 2014)

231 In both interactions, the fact that the phytophagous insects are specific pollinators of their  
232 host-plants and breed inside them necessarily link the reproductive success of the two partners  
233 and increase the likelihood of concomitant speciation events. Therefore host-plant adapted  
234 traits are certainly pivotal in the speciation process of these insects.

235 Several studies have unravelled a pattern of phylogenetic tracking between  
236 phytophagous insects and their host-plants (*e. g.* Althoff *et al.* 2006; Becerra & Venable 1999;  
237 Farrell & Mitter 1990; Farrell & Mitter 1998; Miller *et al.* 1987; Percy *et al.* 2004; Roskam  
238 1985) suggesting that phytophagous insects in different orders (Coleoptera, Lepidoptera,  
239 Hemiptera) have speciated by switching and specialising onto different subsets of a newly  
240 captured plant lineage, partly mimicking their host-plant phylogenies. All these studies give  
241 credit to the *Escape and Radiate* scenario.

242 In many case studies, the phylogenies of plants and insect groups were not  
243 simultaneously available or the patterns of host associations precluded any possibility of  
244 phylogenetic tracking. The authors have then simply compared the timing of divergence of  
245 plants and associated insects (*e. g.* Brandle *et al.* 2005; Kergoat *et al.* 2011; Kergoat *et al.*  
246 2015; Lopez-Vaamonde *et al.* 2006; McKenna *et al.* 2009; McLeish *et al.* 2013; Pena &  
247 Wahlberg 2008; Segar *et al.* 2012; Stone *et al.* 2009; Vea & Grimaldi 2016; Wahlberg *et al.*  
248 2013). Most of these studies suggest delayed (but sometimes rapid) colonization of already  
249 diversified groups of plants by insects groups at different temporal scales. They are generally  
250 based on mere qualitative comparisons of dates of divergence obtained from fossil calibrated  
251 phylogenies of both plants and insects, but can also include thorough statistical comparisons  
252 of dates obtained through phylogenetic methods (Loss-Oliveira *et al.* 2012; McLeish *et al.*  
253 2013). They are generally framed as supporting the *Escape and radiate* theory. However these  
254 studies do not give any information on the speciation process behind the diversification of the  
255 insect lineages studied; they merely indicate the timing of host plant colonization. The  
256 comparison of the **diversification dynamics**\* of both herbivorous insects and their host-plants  
257 provide a more direct test of host-driven speciation hypotheses: under host-driven adaptive  
258 radiation insects diversification dynamic is expected to roughly follow the diversification of  
259 its host- plant lineage (Kergoat *et al.* 2018) (see II. 3..2).

260

## 261 **II. 2) Reconstructing the evolutionary trajectory of traits involved in host-plant use**

### 262 II.2.1) Evolution of host associations

263 Phylogenetic inferences are now widely used to reconstruct the evolutionary  
264 trajectories of phenotypic traits throughout the diversification of a lineage. Most phylogenetic

265 studies of phytophagous insects map the history of host association onto the resulting trees.  
266 These reconstructions often show host conservatism (see Winkler & Mitter 2008 for a  
267 review). These assertions stem from mere observations of the reconstructions but numerous  
268 studies now include statistical tests. These include the permutation tail probability test (PTP,  
269 Faith & Cranston 1991- *e. g.* Kelley and Farrell 1998), or some index of phylogenetic signal  
270 such as the lambda ( $\lambda$ ) of Pagel (1999) (see for instance Leppanen *et al.* 2012; Lopez-  
271 Vaamonde *et al.* 2003; Wilson *et al.* 2012 for statistical evidence of host conservatism on  
272 respectively: sawflies, leaf-mining moths and geometrid moths).

273 Host conservatism is often interpreted as following the predictions of “*Escape and*  
274 *Radiate*” and therefore evidence that speciation was promoted by host-plant specialization.  
275 However, showing that related insects feed on related plants does not say much about the  
276 process that has generated this pattern nor connects mechanistically host-plant use evolution  
277 to speciation. The use of vague wording such as host-associations *favour* or *constrain*  
278 speciation is commonly found when discussing host-conservatism in the literature and it is  
279 difficult to actually conclude from these studies that specialization towards one or a few  
280 plants species is the main pathway towards the formation of new phytophagous insect species.  
281 The pattern of “*host conservatism*” is in agreement with a scenario in which insects have  
282 radiated onto a plant lineage but it could also suggest that host-plant shifts are not important  
283 promoters of speciation events.

284 A more direct estimation of the contribution of host-plant adaptation in the speciation  
285 process consists in inferring the frequency of host-plant shifts in relation to speciation events.  
286 If adaptation to different ranges of host-plants drives reproductive isolation and speciation, it  
287 follows that insect sister species should partition host-plant resources: i.e. they should show  
288 no or little overlap in the plant species they use ( Nyman *et al.* 2010).

289 To investigate factors driving speciation in a genus of bark beetles (*Aphanarthrum*),  
290 Jordal & Hewitt ( 2004) simply compared host use of **sister species\*** and estimated that only  
291 two out of twelve cladogenetic events could be associated with host shifts. Nyman *et al.*  
292 (2010) used a phylogeny of sawflies belonging to the Nematinae (Hymenoptera) and  
293 reconstructed the evolution of their ecological niches (defined as the combination of feeding  
294 habits and host-plant families). They showed that the number of niche shifts represented at the  
295 most 60% of the number of speciation events. They also demonstrated that the probability that  
296 sister species overlapped in their niche decreased with time since the speciation event,  
297 suggesting that more recently diverged species have more chance of sharing host-plant  
298 species and thus have probably not differentiated via host shifts. Joussein *et al.* (2013)

299 adopted a similar approach on a genus of conifer-feeding aphids (Hemiptera). Species in this  
300 genus generally feed on one or few species and ecological niches were defined as a  
301 combination of “plant organ x host-plant species”. They showed that the number of niche  
302 shifts observed only represented 20% of the speciation events and was lower than expected if  
303 the niches were randomized onto the phylogeny; suggesting that ecological speciation was not  
304 the main process behind the diversification of this aphid lineage. Recently Winkler *et al.*  
305 (2018) showed that species splits associated with niche differentiation (host-plant species  
306 and/or type of plant tissue attacked) were less numerous than geographic shifts throughout the  
307 phylogeny of a genus of tropical fruit-flies (*Blepharoneura*). To quantify niche overlap at  
308 cladogenetic events, Nakadai & Kawatika (2016) used an approach that resembles *Disparity*  
309 *Through Time* studies (Harmon *et al.* 2003). They computed a dissimilarity index that  
310 calculates the difference in host use across the different nodes of the phylogeny and tested  
311 whether closely related species share a more similar range of host-plant than expected by  
312 chance. They show that changes in host-plant use are concentrated at the root of the tree and  
313 play a minor role in recent speciation events.

314 Linnen *et al.* (2010) adopted yet a different approach to investigate the role of host  
315 shifts in speciation. They suggested that if host-shifts triggered speciation events, the  
316 evolution of host association should follow a speciation model of evolution, in which  
317 changes in host use occur during speciation events and its probability is not related to branch  
318 length. They thus compared the likelihood of a speciation vs a gradual model of evolution  
319 on a phylogeny of *Neodiprion* (Hymenoptera) and demonstrated that the speciation model  
320 was more likely, implying that host shifts accompany speciation events.

321 Hence, the studies that estimated niche differentiation at speciation events gave mixed  
322 support for scenarios where specialization onto different sets of host-plants is the main  
323 speciation process. It is nevertheless surprising that such studies have not been conducted on  
324 more study systems. This is perhaps due to the fact that they require a precise knowledge of  
325 the range of host-plants used by each insect species.

### 326 II.2.2) Host-breadth evolution

327 In order to test the predictions of macroevolutionary scenarios and investigate the role  
328 of specialization in insect species formation, phylogenetic studies have also investigated how  
329 host breadth is distributed throughout the evolutionary history of insect groups.

330 According to the “*Oscillation hypothesis*”, host breadth should vary a lot along the  
331 phylogeny of insects and the character state “generalist” should be transient (Nylin *et al.*



332 2014); i.e. the phylogenetic reconstruction of this character should show many transitions  
333 between specialists and generalists. Kelley & Farrell (1998), using ancestral character state  
334 reconstructions, have shown that host-breaths were indeed labile in *Dendroctonus* beetles and  
335 that specialists could evolve towards generalists. Several studies have then estimated the rates  
336 of transition between specialists and generalists. Using the phylogenies of fifteen insect  
337 genera from various orders, Nosil & Mooers (2005) estimated that the transition rates toward  
338 specialization exceed the transition rates toward generalization and that specialization was not  
339 a dead-end. More recently, Simonsen *et al.* (2010) reported repeated broadenings of diet in a  
340 genus of butterflies but did not quantify the phylogenetic signal of host breadth. Janz *et al.*  
341 (2001) and Nylin *et al.* (2014) have demonstrated the lability of host breadths in Nymphalids  
342 using indicators of phylogenetic signal and Wang *et al.* (2017) also showed that this character  
343 was highly labile in moths.

344 These patterns suggest that changes in host breadths are recurrent in the evolutionary  
345 history of insect lineages and are therefore compatible with the *Oscillation* hypothesis. In  
346 order to test whether these changes are linked with the colonization of new hosts (favouring  
347 subsequent specialization and speciation), Janz *et al.* (2001) inferred the number of gains and  
348 losses of host plants throughout the history of Nymphalini. They found that gains exceeded  
349 losses and suggested that these were the result of repeated range expansions. However Hardy  
350 (2017) recently reanalysed the same dataset using different models of evolution of host use  
351 and inferred equal numbers of gains and losses of plants throughout the phylogeny of  
352 Nymphalini. He concluded that in this insect group host shifts and speciation events do not  
353 necessarily result from host range expansions and contractions. May be another way to  
354 investigate the link between ‘host-breadth changes’ and ‘capture of new hosts’ would be to  
355 investigate correlated evolution of these two characters. In any case, the recent debates around  
356 the *oscillation* hypothesis (its predictions and how to test them) clearly demonstrates that  
357 ancestral character state reconstructions and statistical tests based on these reconstructions are  
358 very sensitive to model choices and character coding strategies and should always be  
359 interpreted with care, even when very specific predictions are verified.



### 360 II.2.3) Evolution of host-plant adapted traits

361 Many studies that aimed at finding support for the coevolutionary arm race  
362 hypothesized by the *Escape and Radiate* scenario have investigated the evolution of  
363 detoxification mechanisms in insect lineages and how they correlate with changes in host  
364 associations. Becerra (1997; 2003) reconstructed the evolution of detoxification mechanisms

365 and plant defence in a genus of Chrysomelidae and their associated host plants (Burseraceae),  
366 and showed synchronous evolution of defences and counter defences that agree with a  
367 scenario of host-plant driven radiation in these insects. Similarly, in a review on the  
368 interaction between the chemically-defended *Heliconius* butterflies and their *Passiflora* host-  
369 plants, de Castro *et al.* (2018) highlighted a large variety of anti-herbivory adaptations in the  
370 plants (including chemical defences, trichomes, fake eggs or herbivore damages, interaction  
371 with ants) and counter-adaptations in the butterflies that support a long history of coevolution.

372 Also in agreement with the *Escape and Radiate* theory, Wahlberg (2001) using  
373 ancestral character states reconstruction on a phylogeny of Melitaeini (Lepidoptera) showed  
374 that host switches occurred between plants with similar defences, rather than closely related  
375 plants (i.e. host-plant use was more influenced by chemistry than by plant taxonomy). Endara  
376 *et al.* (2017) showed opportunistic host switches to plants with similar defences in a genus of  
377 butterfly. They suggested that herbivores "choose" host-plants based on their own defensive  
378 traits. The authors conclude that disruptive selection is not a driver of speciation in this case.  
379 Many other studies looked at the diversification dynamics of genes involved in plant  
380 detoxification and how it correlates with changes in host-plant associations. Wheat *et al.*  
381 (2007) showed that the evolution of a detoxification mechanism, a nitrile-specifier protein  
382 (NSP) in Pieridae matches the distribution of glucosinolate in their host-plants. Edger *et al.*  
383 (2015) further investigated arm races between Brassicales and butterflies (Pieridae) and  
384 showed that repeated evolution of nitrile-specifier proteins were associated with bursts of  
385 diversification over the past 80 Myr in Pieridae. Calla *et al.* (2017) examined the cytochrome  
386 P450 monooxygenase (CYP) gene superfamily diversification in the genomes of seven  
387 Lepidoptera species varying in host breadth. They showed that its dynamics (duplication and  
388 losses) was correlated with the ability to metabolise defences. Bramer *et al.* (2015) analysed  
389 the ability to sequester toxic cardenolides throughout the phylogeny of the hemipteran  
390 subfamily Lygaeinae and suggested that it was acquired in response to selection by  
391 cardenolide-producing Apocynaceae host-plants.

392 Reconstruction of the history of plant defences were also conducted on plant  
393 phylogenies. For instance, Livshultz *et al.* (2018) reconstructed the evolution of cardenolide  
394 production in Apocynaceae and suggested that it could have evolved in response to  
395 herbivorous insect predation. On the other hand, Agrawal *et al.* (2009), reconstructed the  
396 history of plant defences in North American milkweed species (*Asclepias*, Apocynaceae) and  
397 showed that less investment in cardenolide production correlates with an increase in  
398 speciation rates. This does not follow the predictions of "*Escape and Radiate*" and rather



399 suggest that investment in costly defences might have impeded diversification in this plant  
400 group.

401 In contrast to detoxification mechanisms, traits (and underlying genes) involved in  
402 host recognition and host-plant choice (chemosensory traits) have been less studied in a  
403 phylogenetic context. However their evolutionary dynamic probably plays as important a role  
404 as adaptations to plant defences in phytophagous insect speciation (Smadja & Butlin 2009).  
405 Matsuo (2008) showed that an odour binding protein in 27 **Drosophila** species can evolve  
406 relatively fast in closely related species through gene duplications and losses, and proposed  
407 that this dynamic could explain the evolution of host preferences in this species complex.  
408 Sánchez-Gracia *et al.* (2009) and Vieira & Rozas (2011) conducted a comparative genomic  
409 analysis of odour binding protein and chemosensory proteins from the genomes of several  
410 Arthropoda species (mainly **Drosophila**). They showed a high number of gains and losses of  
411 genes, pseudogenes, and independent origins of gene subfamilies. This dynamic if analysed in  
412 relation to host choices and host breadth in a phylogenetic context could explain some host  
413 shifts and subsequent speciation events.

414 Focusing on behavioural traits of insects, Molnar *et al.* (2018) analysed the antennal  
415 responses of 12 gall midge species to a wide range of host-plant-related volatiles and showed  
416 that species with similar response shared host-plants. They therefore suggested that  
417 modification of olfaction is associated with host-shifts and speciation in this system.

418 Finally deciphering the evolutionary dynamics of genes involved in mate recognition  
419 and their link with host association could also inform us on the role of host-plants in the  
420 speciation of insects that feed (and often mate) on them. For instance, Schwander *et al.* (2013)  
421 showed that cuticular hydrocarbon profiles involved in mate choices vary among *Timema*  
422 species (Coleoptera), and that most evolutionary change in hydrocarbon profiles occurs in  
423 association with host-plant shifts and speciation events in this genus of phytophagous insects.  
424 This study shows that physiological traits involved in reproductive isolation can be associated  
425 with host plant differentiation on a macroevolutionary time scale.

426 In summary, many studies have investigated the evolution of detoxification  
427 mechanisms in butterflies and found support for *Escape and Radiate*. More studies  
428 investigating changes in traits involved in host recognition throughout the diversification of  
429 insects are **need** in order to determine which traits underlie host-plant associations and  
430 whether their evolution accompany speciation events (see Perspectives).

## 431 **II. 3) Studying how host-plants use impact the diversification dynamics of herbivorous** 432 **insects**

433 Methods for testing diversification dynamics have expanded over the last decade.  
434 Testing for the existence of temporal bursts of diversification was once restricted to analyses  
435 of groups with comprehensive fossil records. Diversification dynamics can now be studied  
436 through comprehensive phylogenies (Goswami *et al.* 2016). Given the breadth of available  
437 methods, theoretically, nearly all hypotheses can be put to test.

### 438 II.3.1) Are phytophagous insects more diversified than their related counterparts?

439 Studies that posit that host-plant adaptation favours phytophagous insect  
440 diversification predict that those are much more diversified than non-phytophagous insects.  
441 However this assertion deserves to be statistically tested. The first studies addressing this  
442 question (Farrell & Mitter 1990; Farrell & Mitter 1998; Mitter *et al.* 1988), compared the  
443 diversity (number of species) of phytophagous vs related non-phytophagous clades in beetles.  
444 They all suggested that herbivorous clades are more diverse than their non-phytophagous  
445 sister clades. However, Hunt *et al.* (2007) and then Rainford *et al.* (2015), using more  
446 comprehensive beetle phylogenies, and also adopting a sister clade comparison, did not find a  
447 significant increase in species richness in phytophagous clades. In their phylogeny of the  
448 beetle family Erotylidae, Leschen & Buckley (2007) mapped the evolution of species number  
449 within clades (as a two-state character: 0/1) and did not detect any significant correlation  
450 between species richness and phytophagy (using Bayesian tests of character correlation).  
451 McKenna *et al.* (2015) tested for temporal variation in diversification rates (using MEDUSA  
452 Alfaro *et al.* 2009) on a global phylogeny of Coleoptera and showed that those underwent  
453 several accelerations of diversification rates; some seemed to be associated with the evolution  
454 of phytophagy while others were not.

455 There are more informative tests than those that merely test whether one group  
456 contains more species or has diversified more rapidly than others. More recently Wiens *et al.*  
457 (2015) used *Phylogenetic Generalized Least Square Regressions* and comprehensive  
458 phylogenies within and **between** several insect orders and showed that the proportion of  
459 phytophagous insect species in a clade was positively correlated with diversification rates in  
460 several insect orders. But this relationship did not hold for Coleoptera, Hymenoptera and  
461 Orthoptera. Likelihood-based character state dependent diversification models (known as, the  
462 –SSE models, such as BiSSE, ClaSSE and QuaSSE for binary, multistate and quantitative  
463 traits, respectively FitzJohn 2010; Maddison & FitzJohn 2015; Maddison *et al.* 2007) can

464 specifically test whether transition in character states are associated with variations in  
465 speciation and extinction rates. These diversification models can be used to test whether the  
466 evolution of phytophagy has favoured diversification. However, they were not employed in  
467 Wiens *et al.* (2015) as a robust estimate of diversification parameters by these methods would  
468 require dense and random species sampling throughout the phylogeny. According to FitzJohn  
469 (2010) more than 15% of the species must be included in the phylogeny in order to conduct  
470 unbiased –SSE tests. The study was conducted at the order level and within each order the  
471 proportion of missing species was too high to apply –SSE methods.

472 From current studies using more comprehensive phylogenies and statistical tests, it is  
473 thus yet not completely clear whether phytophagy increases diversification rates in insects in  
474 comparison to other life habits. The availability of more comprehensive phylogenies will  
475 allow testing this hypothesis on more insect orders using character state dependent  
476 diversification models. Nevertheless; a caveat of these diversification models is that they may  
477 overlook more complex models involving many unmeasured and co-distributed traits  
478 (especially when few transitions in feeding habits are observed). The HiSSE model (Beaulieu  
479 & O’Meara 2016) which models hidden characters that might influence diversification might  
480 help untangling these confounding factors.

### 481 II.3.2) Testing for adaptive radiation

482 Diversification analyses can also be applied to test whether the capture of new host-  
483 plants has favoured adaptive radiations. Under such a scenario, the diversification curve of  
484 phytophagous insect clades should exhibit early bursts of speciation upon the capture of new  
485 groups of host-plants. Eventually, the lineages are expected to fill the newly found niche  
486 space and the diversification curves should reach a plateau.

487 There are several studies that have observed acceleration in diversification rates in  
488 insect lineages and have put forward ad-hoc narratives that attribute this acceleration to the  
489 capture of new host-plant lineages or detoxification mechanism. For instance, Wheat *et al*  
490 (2007) showed that the Pierinae clade that can detoxify glucosinolate in their host plants are  
491 more diversified than its sister clade. Mullen *et al.* (2011) have observed an increase in species  
492 richness in the butterfly genus *Adelpha* (Nymphalidae) and attributed this increase to adaptive  
493 divergence in response to host-plant diversity found within the neotropics (namely host-plant  
494 shift to Rubiaceae and other plant families). Ebel *et al.* (2015) revealed an increase in the rates  
495 of diversification on the phylogeny of the genus *Adelpha* and observed that those were  
496 concomitant to host shifts. Sahoo *et al.* (2017) revealed two accelerations in diversification in

497 skipper butterflies that they attributed to shifts from dicots to monocots at time where those  
498 diversified and expanded. Fordyce (2010) showed changed in diversification rates upon the  
499 capture of new plant lineages in several butterfly lineages and Edger *et al.* (2015) detected  
500 shifts in diversification rate associated with the colonization of new host-plants with new  
501 defences, though this was not statistically tested. Winkler *et al.* (2018) on the other hand,  
502 uncovered stable diversification rates and no decrease associated with overlap in host use  
503 throughout the phylogeny of the fly genus *Blepharoneura*, suggesting that this lineage did not  
504 undergo an adaptive radiation. Using BiSSE, Peña & Espeland (2015) found that a hostplant  
505 shift to Solanaceae was correlated with an increase in net diversification rates in *Ithomiini*  
506 butterflies (Nymphalidae). However, since only one shift to Solanaceae occurred in the  
507 Nymphalidae, this correlation should not be taken as evidence that hostplant shift has driven  
508 diversification of this butterfly tribe. Instead, the radiation of Ithomiini may be linked with  
509 geographical context in this study.

510 While several studies have uncovered acceleration in diversification rates upon the  
511 capture of new host-plant lineages, only a handful have investigated whether the number of  
512 species reaches a plateau after an initial burst of diversification. Meseguer *et al.* (2015)  
513 studied the diversification dynamic of a conifer-feeding aphid genus. They revealed an  
514 accelerated rate upon the capture of conifers but no saturation as expected under a scenario of  
515 adaptive radiation. The use of density-dependent models of diversification would be better  
516 suited to test whether rates of diversification decrease through time during evolutionary  
517 radiations (Etienne *et al.* 2012; Rabosky & Lovette 2008). But these tests can only be applied  
518 to lineages in which the number of species in each subclade is well known. Peña *et al.* (2015)  
519 used such diversity-dependent birth-death models to infer speciation, extinction rates and  
520 carrying capacity on a phylogenetic tree of the butterfly genus *Erebia* and showed that the  
521 diversification dynamics was consistent with a model of adaptive radiation. Kergoat *et al.*  
522 (2018) compared the diversification dynamics of Sesamiina stemborer moths and their  
523 associated grasses. The initial burst of diversification observed in moths suggests that their  
524 emergence might have been favoured by the diversification of their host-plants. A decline in  
525 speciation rates was then inferred in these insects using Diversity-dependent birth-death  
526 models. However, their host-plants continued to thrive. This challenges the “adaptive  
527 radiation scenario” and suggests that these moth diversification patterns cannot solely be  
528 explained **but** the availability of suitable host-plants (Kergoat *et al.* 2018).

529

530 II.3.3) Correlating host breadth with diversification dynamic

531 Advocates of the *Oscillation hypothesis* suggest that clades showing a higher diversity  
532 of host-use (using more host-plant species altogether) should be more diverse than their sister  
533 clade (Janz *et al.* 2006), and this prediction has been verified in butterflies. Janz *et al.* (2006)  
534 and Nylin & Wahlberg (2008) found a positive relationship between species diversity of  
535 butterflies and species diversity of host-plant taxa in several genera of Nymphalidae, through  
536 a sister clade comparisons of number of species. Joy & Crespi (2012) and Lin *et al.* (2015)  
537 found a similar result in respectively gall-inducing flies and Coccidae. Wang *et al.* (2017)  
538 used a sister clade comparisons and PGLS to demonstrate a similar trend in moths.

539 Although these results support a model where the diversity of phytophagous insects is  
540 sustained by the diversity of the hosts they use, they could fit both a model of *Oscillation* and  
541 the *Musical chairs* hypothesis. The latter indeed predicts that lineages including specialist  
542 species that often switch between hosts, use a large number of host-plants. To tell apart the  
543 *Oscillation* from the *Musical chairs*, it is actually more informative to test how host breadth  
544 variations affect insect diversification dynamics. According to the *Oscillation* hypothesis,  
545 clades including generalist species should be more speciose than clades including only  
546 specialists. Weingartner *et al.* (2006) tested this prediction in *Polygonia* butterflies  
547 (Nymphalidae) through sister clade analyses and showed that clades using a broader host-  
548 plant range are more species-rich than their sister group that encompass species that only use  
549 the ancestral hosts (here, urticalean rosids), in agreement with the *Oscillation* scenario.

550 More finely tuned analyses, such as trait-dependant diversification models (BiSSE and  
551 QuaSSE models) have been used on the phylogenies of Papilionidaea and the tribe  
552 *Heliconiini* by Hardy and Otto (2014). In this paper, where the *Musical chairs* hypothesis  
553 **hwas** put forward, the authors showed that: 1) speciation rates decreased with host breadth  
554 (i.e. monophagous species diversified faster than polyphagous species); 2) changes in host  
555 breadth were not associated with cladogenetic events; 3) rates of host switching were  
556 positively associated with diversification rates. All these results were in agreement with the  
557 *Musical chair* hypothesis. Still on Nymphalidae, (Hamm & Fordyce 2015) found that host  
558 breadth characteristics were phylogenetically conserved which does not fit the predictions of  
559 the *Oscillation hypothesis* about the lability of host-breadth and also found that speciation  
560 rates did not increase with host-breadth expansion, in agreement with the *Musical chair*  
561 scenario.

562 By contrast, Hardy *et al.* (2016) showed on a Coccidea phylogeny that host breadth  
563 (measured as the number of host-plant families) was positively correlated to speciation rates.  
564 As  $-SSE$  models are known to generate false positives (Bouchenak-Khelladi *et al.*

565 2015; Rabosky & Goldberg 2015; Davis *et al.* 2013), they conducted the analysis on a set of  
566 randomized trees in order to test whether the constrained diversification model (i.e. the model  
567 in which evolutionary transitions in character states associated with shifts in extinction  
568 and/or speciation rates) is also chosen in these analyses. The authors did not frame their study  
569 within the *Oscillation vs Musical chairs* controversy, but if we refer to the paper of Hardy &  
570 Otto (2014), these results fit with some of the predictions of the *Oscillation hypothesis*.

571 As already mentioned, there are debates on the influence of host breadth variation on  
572 diversification dynamics (Hamm & Fordyce 2015; Janz *et al.* 2016; Hamm & Fordyce 2016;  
573 Wang *et al.* 2017). The transient nature of the generalist feeding diet under host-driven  
574 speciation scenarios makes it difficult to derive clear predictions (Janz *et al.* 2016).  
575 Furthermore, if specialization towards host plants can accelerate speciation rates it can also  
576 increase extinction risks when plants are not highly abundant. Although diversification  
577 methods can potentially differentiate extinction rates from speciation rates (Morlon 2014),  
578 predicting exactly how changes in host-plant breadth affects diversification dynamics remains  
579 difficult.

580 Finally, many studies have been conducted on butterflies. In order to have a better  
581 understanding of how phytophagous insects capture new host-plants and whether it influences  
582 their diversification dynamics, it seems necessary to test the predictions of macroevolutionary  
583 scenarios on other insect groups. Aphids could be good candidates for such investigation.  
584 Their range of host-plants is very well documented (Blackman & Eastop 2006; Holman  
585 2009). Although most aphids are host-specific, there are some polyphagous species. Some  
586 species are even only polyphagous during the asexual part of their life-cycle (Jousselin *et al.*  
587 2010; Moran 1992; Hardy *et al.* 2015). This temporary broadening of diet has already been  
588 suggested to facilitate the capture of new host-plants (Moran 1992) and subsequent  
589 specialization and speciation on these new hosts. These life-cycle transitions could have  
590 thus favoured the diversification on this group (Jousselin *et al.* 2010; Moran 1992). This  
591 scenario fits the *Oscillation hypothesis* and should be tested on a robust and comprehensive  
592 aphid phylogeny. Other insect groups for which host plant repertoire are well known such as  
593 Coccidae (Garcia-Morales *et al.* 2016) and Psyllids (Ouvrard *et al.* 2015) could also be used  
594 to test the predictions of macroevolutionary scenarios.

595 In summary, diversification analyses have been widely applied to phytophagous  
596 insects. These methods were fairly basic in early papers but they have been refined throughout  
597 the years and their use allowed reframing hypotheses on the role of host-plant specialization

598 on insect speciation. Recent results brought mixed evidence for phytophagy as an accelerator  
599 of diversification. Trait-dependent diversification analyses supported alternative scenarios  
600 involving oscillation in diet breadths as a driver of host-plants shifts and speciation, and from  
601 our review, it is likely that different scenarios will prevail in different lineages and even  
602 probably in the same lineage at different time scales.

603

### 604 III Perspectives

605 As seen throughout this review, phylogenetic comparative methods provide the  
606 template to test hypotheses on the role of host plant association in the speciation of  
607 phytophagous insects. While those methods have undoubtedly advanced the field significantly  
608 since “the *Escape and Radiate*” paper, readers must keep in mind that phylogenetic  
609 comparative methods often rely on mere correlations. Significant associations between  
610 character changes and the cladogenetic events might arise as a consequence of speciation  
611 itself when post-speciational character changes occur. Furthermore, comparisons of models of  
612 evolution such as those used in trait-dependent diversification analyses often rely on trees that  
613 encompass few transitions in character states and are therefore not always robust. In such  
614 analyses, the “best model” is not necessarily the true model and significant *P* values should  
615 not be interpreted as strong evidence for an evolutionary scenario. Finally, all these methods  
616 are very sensitive to sampling biases and those need to be carefully taken into consideration.

617 In addition to using the approaches focused on host plant associations and diet breadth  
618 cited throughout this review, one way to further investigate hypotheses of speciation driven  
619 by associations with host-plants would be to integrate a variety of data in a phylogenetic  
620 context. Below we outline three potential directions for future research: 1) disentangling the  
621 role of plant-insect interaction from that of co-variates, such as geography and climate; 2)  
622 combining phylogenetic analyses with interaction network approaches including other  
623 partners, at various ecological scales (from community-scale to global scale); and 3) studying  
624 traits and genes underlying the association.

#### 625 III.1) Investigating the role of abiotic factors: geography and climate

626 Geography and ecology are always closely intertwined in speciation scenarios. There have  
627 been several studies that have investigated geographic range expansion in herbivorous insects  
628 (Becerra & Venable 1999; Slove & Janz 2011); climate induced host shifts (see Nyman *et al.*  
629 2012 for a review and recent studies since then Lisa De-Silva, 2017; Owen *et al.* 2017;  
630 Pitteloud *et al.* 2017; Sahoo *et al.* 2017; Sanchez-Guillen *et al.* 2016; Winkler *et al.* 2009) and

631 climate driven diversification dynamics (Kergoat *et al.* 2018). All these studies suggest that  
632 abiotic factors are entangled with host-plants changes in species diversification scenarios.  
633 However there are few studies that explicitly test the predictions of speciation through  
634 geographic isolation (Barraclough & Vogler 2000) and whether these events systematically  
635 accompany host shifts or sustain most speciation events (but see Jordal & Hewitt 2004;  
636 Jousselin *et al.* 2013; Doorenweerd *et al.* 2015; Hardy *et al.* 2016). Such analyses are  
637 important if we want to tell whether adaptations to new host plants represent post-speciational  
638 changes following geographic isolation rather than the main driver of speciation events.  
639 Cospeciation methods that take into account the biogeographic history of interacting lineages  
640 (Berry *et al.* 2018) could be also used to investigate whether host shifts are associated with  
641 dispersal events in systems where hosts plants and insects phylogenies show some congruent  
642 patterns.

643

### 644 **III.2) Combining phylogenetic with interaction network approaches, at various** 645 **ecological scales**

646 Herbivores and the plants they feed on form interaction networks, and as such the  
647 structures of the networks can be characterized by several parameters, such as modularity (the  
648 propensity of a group of species to interact with a similar set of partners) and nestedness (the  
649 propensity of specialist species to interact with generalist species and vice-versa).  
650 Antagonistic interaction networks, such as plant-herbivore networks, tend to be highly  
651 modular (Thébault & Fontaine 2010). A recent study combining interaction network with  
652 phylogenetic approaches on simulated and real datasets predicted that the *Escape and radiate*  
653 scenario should produce a modular network structure, whereas the *Oscillations* scenario  
654 should produce a more nested structure (Braga *et al.* 2018). When applied to real data (two  
655 butterfly families, Nymphalidae and Pieridae), this approach revealed that host-plant butterfly  
656 networks tend to be both modular and nested, which the authors interpret as being the result of  
657 a complex pattern of diversification, involving both episodes of radiation on new hosts  
658 (producing modules containing closely related species) and occasional shifts to other host  
659 lineages, producing both nestedness within modules and connections between modules.  
660 Additionally, phylogenetic and network approaches could be expanded to encompass other  
661 interacting partners (*e. g.* Elias *et al.* 2013, Ives & Godfray 2006) . Indeed, insect-host-plant  
662 communities can be seen as ecosystems where biotic interactions, such as parasitism and  
663 mutualism also take place (Forister *et al.* 2012). These other partners can indirectly influence

664 the interaction between plants and **there** herbivores: e. g., direct competition (Jermy 1988)  
665 apparent competition between herbivores, stemming from shared natural enemies, (Holt  
666 1977), and vice-versa (e. g., when herbivory elicits anti-herbivore defences mediated by  
667 herbivore enemies, (Fatouros *et al.* 2008)). Multitrophic interactions probably explain many  
668 diversification patterns in herbivorous insects (Singer & Stireman 2005)  
669 Finally, such approaches could be applied both at a large scale (e. g., Braga *et al.* 2018), to  
670 embrace global patterns of diversification and interaction, or at the community level (Elias *et*  
671 *al.* 2013, Ives & Godfray 2006), where interactions actually occur, and where fine-scale  
672 processes (e. g., host-plant shift at the species or the population level) can be unveiled.

### 673 **III.3) Unravelling traits involved in the interaction and their underlying genes, and** 674 **integrating this information in phylogenetic studies**

675 Interactions between insects and their host-plant are ultimately mediated by traits, such as  
676 host-plant defences and the capacity of circumventing plants defences, but also host-plant  
677 cues and the capacity for herbivores to detect those cues. Characterizing such traits, their  
678 genetic determinism and looking at their evolutionary trajectory would greatly advance our  
679 understanding of the diversification of insects (e. g., de Castro *et al.* 2018). In addition,  
680 methods that test whether patterns of trait evolution conform to a model accounting for  
681 interactions mediated by those traits are currently being developed (Manceau *et al.* 2016;  
682 Drury *et al.* 2017), and they could inform on the processes underlying herbivore  
683 diversification. However, targeting traits involved in plant-insect interaction may be  
684 challenging. Pivotal traits are difficult to identify, they include chemical, behavioral and  
685 metabolic traits and when they are properly characterized they are often multigenic.

686 Perhaps a promising direction for future research is the implementation of a hybrid  
687 genomic approach that combines transcriptomics, phylogenomics, comparative analyses and  
688 population genomics (see Nevado *et al.* 2016 for an example on plants). In such approaches,  
689 full transcriptomes of species from a target clade (for instance, a clade of phytophagous  
690 insect) are generated. These transcriptomes (or other sequence data) are used to generate a  
691 phylogeny, where classical diversification and character evolution tests can be performed  
692 (evolution of characters, test for diversity-dependent diversification, shifts in diversification  
693 following host-plant shift). Then, genes under selection can be detected from transcriptomic  
694 data using population genetics statistics, and can be matched to existing databases (e. g.,  
695 Lepbase for Lepidoptera, Challis *et al.* 2016) for identification purpose. Additionally, genes  
696 that are down or upregulated can also been detected by classical tests of differential

697 expression and identified, and the association of genes under selection, either via different  
698 sequence or expression pattern, with species diversity can be tested. The main limits of this  
699 approach lie in the availability of specimens (transcriptomic data need to be obtained from  
700 fresh or suitably preserved tissues; biological replicates are needed), and the quality of the  
701 reference gene database to match genes with putative functions.

702

## 703 **Conclusions**

704 Many phylogenetic studies of plant-insect associations now include formal tests of  
705 macroevolutionary scenarios involving host-driven speciation. In an attempt to summarize the  
706 literature on this topic, we show that the predictions of host-plant driven speciation are not  
707 straightforward and can vary depending on studies. We advocate a standardization of these  
708 predictions to facilitate cross study analyses. Furthermore, it is also recognized that different  
709 scenarios can leave the same phylogenetic signature (Janz *et al.* 2016) and that depending on  
710 the analytical approaches undertaken to test the predictions laid out in Table 1, conclusions  
711 can vary (Hardy *et al.* 2017). Unfortunately this means that the interpretations of phylogenetic  
712 inferences can remain somewhat subjective. But these shortcomings should not obscure the  
713 progresses that have been made in the field. Phylogenetic comparative analyses help framing  
714 hypotheses and clarify some of the narratives used to explain the diversification of  
715 phytophagous insects. Finally, this survey of the literature shows that: 1) the simple  
716 assumption that phytophagy has accelerated insect diversification is not always sustained by  
717 meta-analyses; 2) the expectation that sister lineage will use different ranges of host plants is  
718 not often tested, and, when it is, the predictions of a host-driven speciation scenarios are not  
719 always met. We then underline that the results of phylogenetic comparative methods cannot  
720 be interpreted as hard evidence as they remain mere correlations. In the end, a full  
721 understanding of the processes explaining the diversification of phytophagous insects will  
722 require the integration of phylogenies with other data sources and analytical methods. We  
723 propose here a few perspectives to integrate such data and investigate host-driven speciation  
724 scenarios on a macroevolutionary time scale.

725 Finally, if the last two decades have seen the rise of molecular phylogenies and the  
726 development of analytical methods that include ecological data, this should not obscure the  
727 fact that **this** data needs to be thoroughly cured before any phylogenetic comparative analyses.  
728 Qualifying host associations of insect species necessitates field work and advanced taxonomy,  
729 as mistakes can seriously impact the results of macroevolutionary studies. Functional studies

730 aimed at deciphering host-plant adapted traits in insects (and in particular traits implied in  
731 host choice) and characterizing genes that underlie these traits are also needed to integrate **this**  
732 data in a phylogenetic context and link microevolutionary processes with macroevolutionary  
733 scenarios.

734 **Glossary:**

735 **Adaptive radiation:** the evolution of ecological and phenotypic diversity within a rapidly  
736 multiplying lineage. It occurs when natural selection drives divergence of an ancestral species  
737 into descendants that exploit different ecological niches.

738

739 **Coevolution:** reciprocal evolutionary changes occurring in two or more species that result  
740 from reciprocal selective pressures exerted by the interacting partners.

741 **Coevolutionary diversification:** when diversification patterns arise from coevolution.

742 **Cospeciation:** simultaneous speciation events in lineages involved in long-term interspecific  
743 associations which result in congruent phylogenies

744 **Diversification dynamic:** rates of species formation and extinction through time.

745 **Ecological specialization:** when species limit themselves to a restricted set of resources  
746 (diet- habitat-niches), as a result of evolutionary trade-offs.

747 **Generalists:** species that use a wide niche.

748 **Host-plant adaptation:** heritable trait that confers a selective advantage on a particular host-  
749 plant.

750 **Specialists:** species that use a narrow niche.

751 **Phytophagous insect:** an insect that feeds on any plant organ during whole or part of its life  
752 cycle, it excludes pollinators feeding on nectar and pollen but include pollinators that feed on  
753 developing seeds (*i.e.* seminiphagous insects).

754 **Sister species/ sister clades:** the closest relatives of another given unit (species/ clade) in a  
755 phylogenetic tree.

756

757 **Conflict of interest disclosure**

758           The authors of this preprint declare that they have no financial conflict of interest with  
759 the content of this article."

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