

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.

31 **Introduction**

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

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;

¹ See glossary

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

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

93 **I Macroevolutionary scenarios of phytophagous insect diversification**

94 **I.1) *Escape and radiate* (Figure 1 a)**

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

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

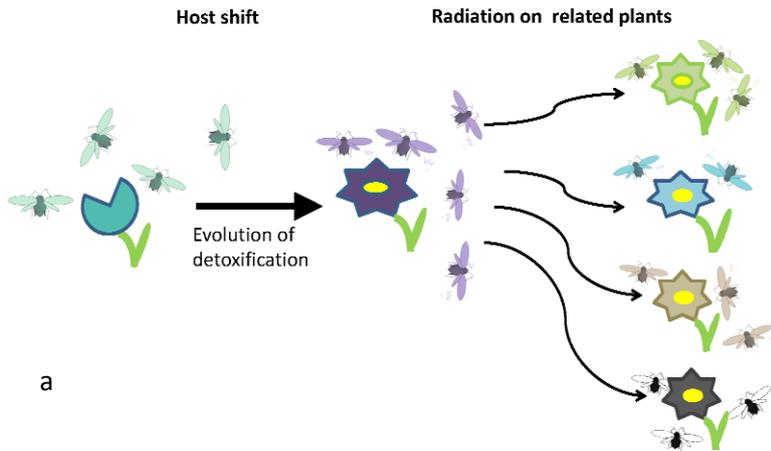
128 herbivorous insects and their host-plants should be more congruent than expected by chance and
129 the diversification of the insects should lag behind that of their host-plants; this is called sequential
130 evolution (Jermy 1984) or “*host tracking*”. Nevertheless, when the association between insects
131 and their host plants is species-specific, a pattern of cospeciation can be expected through simple
132 co-vicariance: geographic barriers affect the differentiation of populations of interacting lineages
133 in a similar way and cause simultaneous speciation events (Althoff et al. 2012; Brookes et al.
134 2015; Martínez-Aquino 2016). In these cases, it is geographic isolation and not natural selection
135 that initiates the reproductive isolation of insect populations and subsequent speciation. However,
136 the specificity of the insects and host-adapted traits enhance the probability of shared vicariant
137 events.

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

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

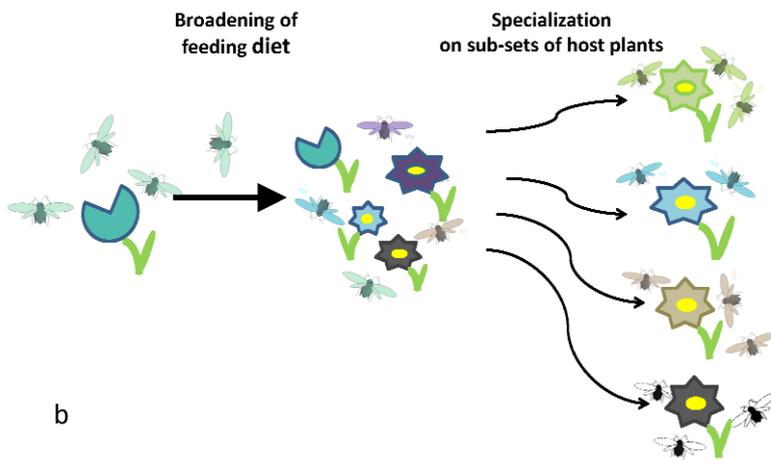
146 The “*Escape and radiate*” scenario was revisited more than a decade ago by Janz and
147 collaborators (Janz, Nylin, Wahlberg 2006; Janz, Nylin 2008; Nylin, Janz 2009). Using butterflies
148 as study systems, they stated that expansions in diet breadth followed by specialisation onto new
149 host-plant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

Escape and Radiate (Erich & Raven 1964)



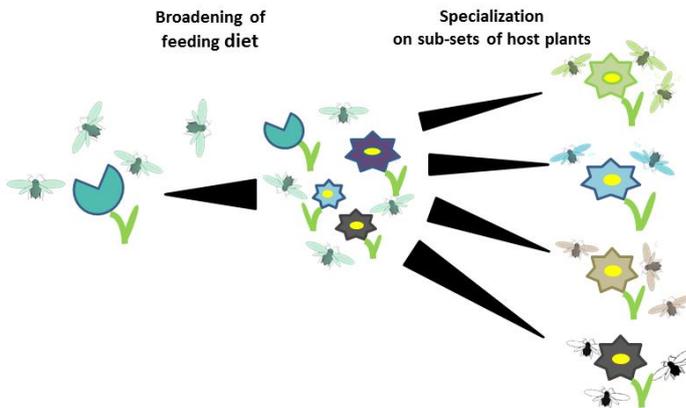
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Oscillation hypothesis (Janz & Nylin 2008)



162

Oscillation hypothesis (Janz & Nylin 2008)



163

Musical chairs (Hardy & Otto 2014)

Speciation through successive host switches



164

165

c

166 | Figure 1: Schematic illustrations of the macroevolutionary scenarios of phytophagous insect
167 diversification.

168

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

171 Most of the predictions from the *Escape and Radiate* scenario are valid under the
172 ~~“Oscillation hypothesis. However, the latter hypothesis”~~ yields several new predictions (Table
173 1):

174 - **generalist*** diets should be “transient and repeatedly disappear in favour of specialization
175 onto a limited set of related plants” (Nylin, Slove, Janz 2014);

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

177 - the amplitude of the oscillation determines the number of potential host-plant species;
178 therefore, insect clades with the most diverse host-use (the highest number of host-plant species)
179 are expected to be more speciose than clades using ~~less-fewer~~ host species (Janz, Nylin, Wahlberg
180 2006); and ~~along the same lines~~ insect clades that encompass species that exhibit large host
181 breadths should have higher ~~diversification-speciation~~ rates (Weingartner, Wahlberg, Nylin 2006;
182 Hardy, Otto 2014).

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

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

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

189 ~~As opposed to the Oscillation hypothesis, Hardy and Otto (2014) have proposed an~~
190 ~~alternative scenario in which recently put forward a scenario where~~ speciation in herbivorous
191 insects is driven ~~by host-switching rather than transitions in diet breadth by specialisation onto~~
192 ~~newly captured host plants without any transitions in diet breadth: insects speciate by successive~~
193 ~~switches to new host plants.~~ The authors named their scenario “***the Musical Chairs***” (Hardy, Otto
194 2014). ~~In this scenario, phytophagous insects speciate by the sequential capture of new host-~~
195 ~~plants and therefore the speciation of a plant-feeding insect lineage is merely driven by the number~~
196 ~~of plants it can colonize. Host-driven speciation remains at the centre of this hypothesis They~~
197 ~~explicitly state that specialization onto a few host plant species explains species diversification in~~
198 ~~phytophagous insect.~~

199 The “*musical chairs*” hypothesis yields several predictions that differentiate it from the
200 ~~“Oscillation hypothesis” previous macroevolutionary scenarios~~ (Table 1):

201 ~~- contrary to the *Escape and Radiate* hypothesis, the capture of a new host plant lineage~~
202 ~~does not initiate a radiation;—speciation rates~~
203 ~~- should be higher in lineages showing no conservatism in host-plant associations (Hardy &~~
204 ~~Otto 2014);~~
205 ~~- contrary to the *oscillation hypothesis*, gains of new hosts are not associated with host~~
206 ~~breath expansion (Hardy 2017), host breadth contraction is not associated with cladogenetic~~
207 ~~events (Hardy, Otto 2014) and overall there should be a negative correlation between host-plant~~
208 ~~breadth and speciation rates (Hardy, Otto 2014);~~
209 ~~- host breadth contraction is not associated with cladogenetic events (Hardy & Otto 2014);~~
210 ~~- speciation rates are higher in insect lineages that exhibit **lability*** in host-plant~~
211 ~~associations.~~
212 ~~—lineages showing many transitions from generalist to specialist feeding diets should not~~
213 ~~be more speciose than lineages that only encompass specialist species (Hardy & Otto 2014).~~
214 ~~The lack of connection between host breath contraction and speciation events and the~~
215 ~~negative association between host-breadth and speciation rates clearly differentiate the *Musical*~~
216 ~~*chairs* from the *Oscillation hypothesis*. However, several authors have pointed out that ~~it will be~~~~
217 ~~~~difficult to tell apart the “*Musical Chairs*” from “the *Oscillation Hypothesis*”.~~ ~~If generalism~~~~
218 ~~~~generalist feeding diets are indeed ephemeral as expected when specialization towards host-~~~~
219 ~~plants is adaptive, it will be difficult to reconstruct its history accurately on phylogenetic trees~~
220 ~~(Hardy, Peterson, Normark 2016; Janz et al. 2016). Consequently, the relationships between host-~~
221 ~~range size and speciation rates will be difficult to explore and the set of predictions that~~
222 ~~differentiate the *musical chairs* from the *oscillation hypothesis* will not always be testable.~~
223 Phylogenetic comparative methods (Pennell, Harmon 2013) including increasingly
224 sophisticated diversification models (Rabosky 2006; Stadler 2013; Stadler, Bokma 2013;
225 Rabosky, Goldberg 2015; Beaulieu, O’Meara 2016; O’Meara, Beaulieu 2016) can now be
226 deployed to reconstruct ancestral character states, investigate the diversification dynamics of
227 insect lineages and test whether shifts in diversification rates are associated with transitions in
228 character states. Below we review how these methods have been used to investigate the evolution
229 of plant/insects associations and test the predictions of host-driven speciation scenarios.

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

<u>Macroevolutionary scenarios</u>	Insect and host tree comparison	Evolution of host associations	Evolution of host breadth	Insect diversification dynamics
Speciation driven by host-plant specialization	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)
<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 <u>labiality in</u> host breadth (Janz <i>et al.</i> 2001, Janz & Nylin 2008) - gains of new host lineages <u>are</u> preceded by host breadth expansion (Janz <i>et al.</i> 2001) - host breadth larger in species with large geographic range <u>positive correlation between diet breadth and geographic range</u> (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, Wahlberg, Nylin 2006) - speciation rates higher in lineages showing high labiality in host breadth (Hardy, Otto 2014)
<i>Musical chairs</i>	No prediction	Less conservatism of host plant <u>High labiality in more speciose lineages</u> breadth (Hardy, Otto	Few transitions in <u>Host breadth is not labile</u> - (Hardy & Otto 2014; Hardy 2017)	- no positive <u>negative</u> association between speciation rates and host breadth labiality (Hardy, Otto 2014) - speciation rates positively correlated <u>correlate</u>

		2014)		with ability in host associations <u>switching rates</u> (Hardy, Otto 2014)
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232 II Phylogenetic approaches for testing ecological speciation scenarios

233 II.1) Comparing the phylogenies of plants and insects

234 Many ~~Several~~ phylogenetic studies have compared the phylogenies of herbivorous insect and
235 their host-plants ~~and~~. ~~Some~~ have investigated cospeciation ~~and host tracking patterns~~. ~~They~~
236 ~~using have used dedicated~~ tools such as tree reconciliation analyses ([Page 1994](#); [Conow et al.](#)
237 [2010](#)) and distance-based methods for tree comparisons ([Legendre, Desdevises, Bazin 2002](#)).
238 ~~These tools statistically test the null hypothesis that the phylogenies of insects and their~~
239 ~~associated plants are more congruent than expected by chance and that speciation events are~~
240 ~~simultaneous. As stated above, this is only expected in species specific plant/insect~~
241 ~~interactions. A pattern of cospeciation~~ As predicted by early taxonomic studies ([Ramirez](#)
242 [1974](#); [Wiebes 1979](#)), cospeciation has been evidenced in figs and their phytophagous
243 ~~pollinating wasps found between figs and their phytophagous pollinating wasps but the degree~~
244 ~~of phylogenetic congruency observed varies according to taxonomic groups (see review by de~~
245 [Vienne, 2013 on cospeciation studies and](#) —[Cruaud, 2012](#)) ~~as predicted by early taxonomic~~
246 ~~studies on this biological system (Ramirez 1974; Wiebes 1979), but also between figs and~~
247 ~~some of the non-pollinating galling wasps that are highly specific to their hosts (Jousselin et~~
248 ~~al. 2008)~~. Reciprocal adaptations of plants and insects (i.e. **coevolution***) have been
249 unravelled in this study system ([Jousselin, Rasplus, Kjellberg 2003](#); [Weiblen 2004](#)). However,
250 it is not known whether the cospeciation patterns observed are the sole result of this
251 coevolution (i.e. whether reciprocal selection exerted by both partners) has driven the
252 reproductive isolation of interacting populations ([Althoff, Segraves, Johnson 2014](#); [Hembry,](#)
253 [Yoder, Goodman 2014](#)) or whether matching speciation events have arisen through co-
254 vicariance. In the other iconic model system for the study of plant/insect **coevolutionary**
255 **diversification***, the *Yucca*–*Yucca* moth interaction ([Pellmyr 2003](#)), ~~pollinating and non-~~
256 ~~pollinating the~~ moths phylogenetic histories parallel some parts of the evolutionary history of
257 their hosts. Some studies suggest that these patterns are the results of coevolution ([Godsoe et](#)
258 [al. 2009](#)) while others hint towards co-vicariance ([Althoff et al. 2012](#)) ~~{Kawakita, 2004~~
259 ~~#1058}~~.

260 In both interactions, the fact that the phytophagous insects are specific pollinators of their
261 host-plants and breed inside them necessarily links the reproductive success of the two
262 partners and increases the likelihood of concomitant speciation events. Therefore host-plant
263 adapted traits are certainly pivotal in the speciation process of these insects.

264 ~~Several studies~~ Studies that have have unravelled a pattern of investigated
265 **phylogenetic tracking*** between phytophagous insects and their host-plants (*e.g.* ~~suggesting~~

266 ~~that phytophagous insects in different orders (Coleoptera, Lepidoptera, Hemiptera) have~~
267 ~~speciated by switching and specialising onto different subsets of a newly captured plant~~
268 ~~lineage, have shown that insects rarely partly mimicking~~ their host-plant phylogenies. ~~All these~~
269 ~~studies give credit to the *Escape and Radiate* scenario.~~ ((see review by de Vienne, 2013 ,
270 Winkler, 2008 #; a third of the 20 studies reported in these two reviews found partial patterns
271 of congruence between insects and host plant phylogenies) (Suchan, 2015 #3814}). In many
272 plant/insect interactions, a simple observation of the patterns of distribution of host plants in
273 the insect phylogeny can actually rule out

274 ~~In many case studies, the phylogenies of plants and insect groups were not~~
275 ~~simultaneously available or the patterns of host associations precluded any possibility of~~
276 ~~cospeciation or phylogenetic tracking and studies on plant-insect interactions have moved~~
277 ~~away from cospeciation studies such.~~

278 ~~The~~ In order to test for successive burst of diversification in plants and insects, many
279 ~~authors~~ authors have ~~then~~ thus simply compared the timing of divergence of plants and
280 associated insects (e. g. Gómez-Zurita, 2007; Leppanen, 2012 ; Brandle et al. 2005; Lopez-
281 Vaamonde et al. 2006; Pena, Wahlberg 2008; McKenna et al. 2009; Stone et al. 2009;
282 Kergoat et al. 2011; Segar et al. 2012; McLeish, Miller, Mound 2013; Wahlberg, Wheat, Pena
283 2013; Kergoat et al. 2015; Veà, Grimaldi 2016). Most of these studies suggest delayed (~~but~~
284 ~~sometimes rapid~~) colonization of already diversified groups of plants by insect groups at
285 different temporal scales. They are generally based on mere qualitative comparisons of dates
286 of divergence obtained from fossil calibrated phylogenies of both plants and insects, but can
287 also include thorough statistical comparisons of dates obtained through phylogenetic methods
288 (Loss-Oliveira, Aguiar, Schrago 2012; McLeish, Miller, Mound 2013). They are generally
289 framed as supporting the *Escape and radiate* theory. However these studies do not give any
290 information on the speciation process behind the diversification of the insect lineages studied;
291 they merely indicate the timing of host plant colonization. The comparison of the
292 **diversification dynamics*** of both herbivorous insects and their host-plants provide a more
293 direct test of host-driven speciation hypotheses: under host-driven adaptive radiation insects
294 diversification dynamic is expected to roughly follow the diversification of its host-plant
295 lineage. These can be investigated through diversification analyses (Kergoat et al. 2018) (see
296 II. 3.2); but can also include the comparison of the fossil records of both insects and plants
297 (Labandeira, 1994 ; Labandeira, 2013). In general, the studies of fossil assemblage are

298 decoupled from phylogenetic studies of plant-/insect associations. We advocate for more
299 combined analyses fossil and phylogenetic evidence..

300

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

302 II.2.1) Evolution of host associations

303 Phylogenetic inferences are now widely used to reconstruct the evolutionary
304 trajectories of phenotypic traits throughout the diversification of a lineage. Most phylogenetic
305 studies of phytophagous insects map the history of host association onto the resulting trees at
306 different taxonomic levels (i.e. host plant order, family, genus depending on the level of host
307 specialization of the insect clade studied, multistate characters are used when species are
308 polyphagous). These reconstructions ~~often~~ generally show some level of host conservatism*
309 ~~(see Winkler & Mitter 2008 for a review)~~. These assertions stem from mere observations of
310 the reconstructions but numerous studies ~~now~~ include statistical tests. These include the
311 permutation tail probability test (PTP, Faith, Cranston 1991 ~~e. g. Kelley and Farrell 1998~~), or
312 some index of phylogenetic signal such as ~~the lambda (λ) of~~ (Pagel 1999) lambda (λ) (~~see~~see
313 (Winkler, Mitter 2008) for a review and for instance Leppanen et al. 2012; Wilson et al.
314 2012) ~~for statistical evidence of host conservatism on respectively: sawflies, leaf mining~~
315 ~~moths and geometrid moths~~ for more recent studies).

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

327 A more direct estimation of the contribution of host-plant adaptation in the speciation
328 process consists in inferring the frequency of host-plant shifts in relation to speciation events.
329 If adaptation to different ranges of host-plants drives reproductive isolation and speciation, it
330 follows that insect **sister species*** should partition host-plant resources: i.e. they should show
331 no or little overlap in the plant species they use (Jermy).

332 To investigate factors driving speciation, ~~early studies have conducted in a genus of~~
333 ~~bark beetles (*Aphanarthrum*), Jordal & Hewitt (2004) simply compared host use of sister~~
334 ~~species comparisons of host ranges. More recent studies have and estimated that only two out~~
335 ~~of twelve cladogenetic events could be associated with host shifts. Nyman *et al.* (2010) used a~~
336 ~~phylogeny of sawflies belonging to the Nematinae (Hymenoptera) and reconstructed the~~
337 evolution of ~~their insects~~ ecological niches (defined as the combination of feeding habits and
338 host-plant ~~families species or families~~). ~~They showed that the and estimated the~~ number of
339 niche shifts ~~represented at the most 60% of the number of associated with~~ speciation events
340 ~~(Table 2. 1). Comparisons of alternative models of evolution of host-use have also been~~
341 ~~conducted. They also demonstrated that the probability that sister species overlapped in their~~
342 ~~niche decreased with time since the speciation event, suggesting that more recently diverged~~
343 ~~species have more chance of sharing host plant species and thus have probably not~~
344 ~~differentiated via host shifts. Jousselein *et al.* (2013) adopted a similar approach on a genus of~~
345 ~~conifer feeding aphids (Hemiptera). Species in this genus generally feed on one or few~~
346 ~~species and ecological niches were defined as a combination of “plant organ x host plant~~
347 ~~species”.~~ ~~They All studies but one~~ showed that the numbers of niche shifts observed ~~only~~
348 ~~generally~~ represented ~~less than 2050%~~ of the speciation events and ~~was were generally~~ lower
349 than expected if the niches were randomized onto the phylogeny. ~~This suggests that~~
350 ~~ecological speciation is not the main process behind the diversification of these lineages. ;~~
351 ~~Authors have also observed that host-use differentiation occurred at the root of the trees and~~
352 ~~therefore concluded that it played a minor role in recent speciation events, suggesting that~~
353 ~~ecological speciation was not the main process behind the diversification of this aphid~~
354 ~~lineage. Recently Winkler *et al.* (2018) showed that species splits associated with niche~~
355 ~~differentiation (host plant species and/or type of plant tissue attacked) were less numerous~~
356 ~~than geographic shifts throughout the phylogeny of a genus of tropical fruit flies~~
357 ~~(*Blepharoneura*). To quantify niche overlap at cladogenetic events, Nakadai & Kawatika (~~
358 ~~2016) used an approach that resemble *Disparity Through Time* studies (Harmon *et al.* 2003).~~
359 ~~They computed a dissimilarity index that calculates the difference in host use across the~~
360 ~~different nodes of the phylogeny and tested whether closely related species share a more~~
361 ~~similar range of host plant than expected by chance. They show that changes in host plant~~
362 ~~use are concentrated at the root of the tree and play a minor role in recent speciation events.~~

Table 2: Summary of studies testing the predictions of host-driven speciation scenarios using phylogenetic methods. Cospeciation studies and studies on host-plant conservatism are not included as they are already synthesized in respectively: de Vienne *et al.* 2013 and Winkler & Mitter 2008.

Predictions tested	Taxa	Reference	Approaches	Results	Conclusions
1) Partitioning of host plants at speciation events	 <i>Aphanartum</i> (25 spp.)	Jordal & M Hewitt 2004	Sister species comparison of host ranges	∅	} Geographic isolation is more important than host switching in speciation events
	 Nematinae (125 spp.)	Nyman <i>et al.</i> 2010	} Investigate niche shifts at speciation nodes through ancestral state reconstruction	∅	
	 <i>Blepharoneura</i> (49 spp.)	Winkler <i>et al.</i> 2018		∅	
	 <i>Cinara</i> (76 spp.)	Jousselin <i>et al.</i> 2013		∅	
	 <i>Caloptilia</i> (13 spp.)	Nakadai & Kawakita 2016	Niche dissimilarity index through time	∅	
	 <i>Neodiprion</i> (19 spp.)	Linnen & Farrell 2010	Comparisons of models of evolution of host use (speciational model vs gradual)	✓	Host shift (in allopatry) induces speciation
2) Host breadth is labile	 <i>Dendroctonus</i> (19 spp.)	Kelley & Farrell 1998	Phylogenetic signal of host breadth	✓	Repeated broadening of host breadth
	 Lymantrinae (55 genera)	Wang <i>et al.</i> 2017	Phylogenetic signal of host breadth and transition rates estimation	✓	} Oscillation
	 Nymphalidae (551 spp.)	Nylin <i>et al.</i> 2014	Phylogenetic signal of host breadth and transition rates estimation	✓	
	 Nymphalini (31 spp.)	Janz <i>et al.</i> 2001	Visualization of reconstruction of host breadth	✓	
	15 insect groups	Nosil & Mooers 2005	Estimation of transition rates in host breadth	✓	Specialization is not a dead-end
	 <i>Boloria</i> (37 spp.)	Simonsen <i>et al.</i> 2010	Visualization of reconstruction of host breadth	✓	Repeated broadening of host breadth, oscillation
	 Nymphalidae	Hamm & Fordyce 2016	Phylogenetic signal of host breadth	∅	No oscillation
3) Changes in host breadth spur diversification or speciation events are associated with shift away from polyphagy	 Papilionoidea (2573 spp.)	Hardy & Otto 2014	Use of BiSSEness to test whether change in host breadth is associated with speciation events (speciational model vs gradual model of evolution for host breadth)	∅	Musical chairs
	 Nymphalini (31 spp.)	Janz <i>et al.</i> 2001	Estimate whether polyphagy is ancestral, estimate gains of new host vs losses of hosts (if polyphagy drives speciation; gains should exceed losses)	✓	Oscillation
	 Nymphalini (172 spp.)	Hardy 2017	Use of DEC model to reconstruct the history of host use and estimate gains and losses of plants	∅	Speciation not associated with shift away from polyphagy, no oscillation
4) Detoxification mechanisms in insects evolve in response to plant association	 Blepharidae (23 spp.)	Becerra 1997	Comparison of insect phylogeny with chemical defense similarity dendrogram of host plants	✓	Coevolutionary arm race
	 Blepharidae (37 spp.)	Becerra 2003	Comparison of timing of acquisition of plant defenses and insect counter-defenses	✓	Coevolutionary arm race

		Blepharidae (37 spp.)	Becerra 2003	Comparison of timing of acquisition of plant defenses and insect counter-defenses	✓	Coevolutionary arm race
		Lygaeinae (20 spp.)	Bramer <i>et al.</i> 2015	Reconstruction of the ability to resist or sequester cardenolides	✓	Adaptation of insects to host plant defenses
		<i>Heliconius</i>	de Castro <i>et al.</i> 2018	Review on correlated evolution of anti-herbivory adaptations in plants and counter-adaptations in <i>Heliconius</i>	✓	Adaptation of insects to host plant defenses
		Melitaeini (77 spp.)	Wahlberg 2001	Reconstruction of host association on insects and the presence of glycosides in associated plants	✓	Insects switch to chemically similar plants
		174 taxa	Endara <i>et al.</i> 2017	Comparison of Lepidoptera assemblages associated with different plant species	✓	Similarity of assemblages on chemically similar plants; host association driven by similarity of plants
		Apocynaceae	Livshultz <i>et al.</i> 2018	Evolution of cardenolide production in plants	✓	Plant defenses evolve in response to herbivorous insect predation
5) Diversification rates in phytophagous insect clades > non phytophagous insects		13 families in various orders	Mitter <i>et al.</i> 1988	Sister groups comparison of phytophagous vs non phytophagous clades	✓	Phytophagy promotes diversification
		1900 spp	Hunt <i>et al.</i> 2007	Sister groups comparison of phytophagous vs non phytophagous clades and estimation of diversification rates	∅	} Various types of niche shifts explain beetles diversification
		Erolytidae, 53 taxa	Leschen & Buckley 2007	Correlated evolution between species richness and phytophagy	∅	
		367 spp, 172 families	McKenna <i>et al.</i> 2015	Infer shifts in diversification rates (MEDUSA)	✓ & ∅	Some shifts associated with phytophagy others not
		31 insect orders	Wiens <i>et al.</i> 2015	Phylogenetic regression	✓ & ∅	Different ecological factors prevail at different scales: phytophagy promotes diversification overall but not in all orders
6) Major host shifts spur diversification		Nymphalidae (54 genera)	Nylin & Wahlberg 2008	Estimation of diversification rates after two major host shifts	✓	Escape and radiate and/or Oscillation
		Butterflies (15 groups)	Fordyce 2010	Test for shifts in diversification rates across the phylogeny (LASER)	✓	Burst of diversification concomitant to some host shift, Escape and radiate
		<i>Adelpha</i> (38 spp.)	Mullen <i>et al.</i> 2011	Test for shifts in diversification rates across the phylogeny (SymmeTREE)	✓	One rate shift attributed to host shift but also other ecological factors
		<i>Adelpha</i> & <i>Limnitis</i> (200 spp.)	Ebel <i>et al.</i> 2015	Test for shifts in diversification rates across the phylogeny (BAMM)		Shift to Rubiaceae played a role in insect diversification
		Nymphalidae (398 genera)	Pena & Espeland 2015	Detection of shifts in diversification rates (MEDUSA & BiSSE with trait= feeding on a particular plant family)	✓ & ∅	Shift to Solanaceae spurred diversification
		Hesperiidae (290 genera)	Sahoo <i>et al.</i> 2017	Detection of shifts in diversification rates (LASER), BAMM, BiSSE (trait= feeding on monocotyledons vs dicotyledons) & HiSSE	✓	Several diversification shifts however could be associated with grassland expansion and geographic factors

7) Acquisition of detoxification mechanisms spur diversification in insects, new defenses spur diversification in plant		Pierinae (60 spp.)	Wheat <i>et al.</i> 2007	Distribution of a defense mechanism in insect and assessment of the glucosinolate in their host / comparison of rates of diversification in two sister clades with and without this defense	✓	Escape and Radiate
		Pieridae (96 spp.)/Brassicales	Edger <i>et al.</i> 2015	Distribution of a defense mechanism and estimation of shifts in diversification rates in plants and insects (MEDUSA)	✓	
		Asclepias	Agrawal <i>et al.</i> 2009	Comparison of various model of evolution for plant defences including a speciation model	✓	
8) Adaptive radiation pattern		<i>Erebia</i> (74 spp.)	Pena <i>et al.</i> 2015	Test for shifts in diversification rates (BAMM & DDD)	✓ & ∅	Density dependant model fits the data, diversification shifts not always significant depending on methods : acceleration of diversification associated to colonization of new area Constant rate of diversification, no adaptive radiation Constant rate of diversification, no adaptive radiation, diversification patterns mostly explained by geographical factors Inverse patterns of diversification in insects and associated plants ; host plant diversity alone does not explain insect diversification
		<i>Cinara</i> (92 spp.)	Meseguer <i>et al.</i> 2015	Test for shifts in diversification rates (TreePar)	∅	
		<i>Blepharoneura</i> (49 spp.)	Winkler <i>et al.</i> 2018	Test for shifts in diversification (LASER, DDD)	∅	
		Sesamiina (241 spp.)	Kergoat <i>et al.</i> 2018	Test for shifts in diversification through different methods (BAMM, *SSE)	∅	
9) Positive relationship between insect lineage diversity and their host plant diversity		115 spp.	Farrell & Mitter 1998	Sister-clade comparison of angiosperm vs non angiosperm feeding groups	✓	Host- driven speciation
		Nymphalidae (309 genera)	Janz <i>et al.</i> 2006	Sister clade comparisons	✓	
		Lymantrinae (55 genera)	Wang <i>et al.</i> 2017	Phylogenetic regression	✓	Oscillation hypothesis
		Coccidae (158 genera)	Lin <i>et al.</i> 2015	} Regression without phylogenetic correction	✓	
		Cecidomyiid (352 genera)	Joy & Crespi 2012		✓	

10) Clades including generalists speciate faster than clades with only specialists; diversification rates are positively correlated with host breadth		<i>Nymphalis</i> & <i>Polygonia</i> (20 spp.)	Weingartner <i>et al.</i> 2006	Sister clade comparison of species richness between clades with only specialist and clades that encompass species with large host breadth	✓	Broadening of host range: plasticity facilitates the capture of new hosts and subsequent ecological speciation
		Nymphalidae (54 genera)	Nylin & Wahlberg 2008	Estimation of diversification rates	✓	Clades experiencing higher rates of diversification experience a polyphagous state: oscillation
		Papilionoidea (2573 spp.)	Hardy & Otto 2014	} Test for shifts in diversification through different *SSE methods (trait= host breadth)	∅	No oscillation, Musical chairs
		Nymphalidae	Hamm & Fordyce 2015		∅	Host breadth dynamics does not drive diversification
		Coccidea	Hamm & Fordyce 2016		✓	Specialization by drift
		Nymphalini (172 spp.)	Hardy 2017		Phylogenetic independent contrasts (proportion of generalists vs number of species in a genus)	∅
		Sesamiina (241 spp.)	Kergoat <i>et al.</i> 2018	Evaluate whether shifts in diversification rates follow shifts in host breadth (BAMM and others)	∅	Oscillation might not be detectable at this scale
11) Diversification rates of clades with labile host association > diversification rates of clades with conservatism in host association		Papilionoidea (2573 spp.)	Hardy & Otto 2014	Use of *SSE to test whether speciation rates vary between lineages, correlation between host switching rates and diversification rates	✓	Musical chairs

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 Coleoptera ,  Lepidoptera,  Hemiptera,  Diptera,  Hymenoptera
 ✓ Prediction verified, ∅ prediction not verified

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DEC (Ree, Smith 2008); Laser (Rabosky 2006); Medusa (Alfaro *et al.* 2009) , BiSSE (Maddison, Midford, Otto 2007), BAMM (Rabosky *et al.* 2014), DDD (Etienne *et al.* 2012), HiSSE (Beaulieu, O'Meara 2016), SymmeTREE (Chan, Moore 2002)

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

Hence, the studies that estimated niche differentiation at speciation events gave mixed support for scenarios where specialization onto different sets of host-plants is the main speciation process (Table 2.1). We must also keep in mind that these methods probably overlook many host shifts (shifts that resulted in population extinction do not leave any trace on phylogenetic trees) and therefore, these studies probably represent an overestimation of the impact of host shifts in speciation. It is nevertheless surprising that such studies have not been conducted on more study systems. This is perhaps likely due to the fact that they require a precise knowledge of the range of host-plants used by each insect species.

II.2.2) Host-breadth evolution

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

According to the “*Oscillation hypothesis*”, host breadth should vary a lot along the phylogeny of insects and the character state “generalist” should be transient (~~Nylin *et al.* 2014~~); i.e. the phylogenetic reconstruction of this character should show many transitions between specialists and generalists. ~~Kelley & Farrell (1998), using ancestral character state reconstructions, have shown that host breadths were indeed labile in *Dendroctonus* beetles and that specialists could evolve towards generalists. Several studies have then estimated the rates of transition between specialists and generalists. Using the phylogenies of fifteen insect genera from various orders, Nosil & Mooers (2005) estimated that the transition rates toward specialization exceed the transition rates toward generalization and that specialization was not a dead-end. More recently, Simonsen *et al.* (2010) reported repeated broadenings of diet in a genus of butterflies but did not quantify the phylogenetic signal of host breadth. Janz *et al.* (2001) and Nylin *et al.* (2014) have~~ Many studies have indeed demonstrated the lability of host breadths (Table 2.2), which in Nymphalids using indicators of phylogenetic signal and

402 ~~Wang *et al.* (2017) also showed that this character was highly labile in moths. is compatible~~
403 ~~with the *Oscillation* hypothesis but does not necessarily prove it.~~

404 ~~These patterns suggest that changes in host breadths are recurrent in the evolutionary~~
405 ~~history of insect lineages and are therefore compatible with the *Oscillation* hypothesis. In~~
406 ~~order to test whether these changes are linked with the colonization of new hosts (favouring~~
407 ~~subsequent specialization and speciation, some studies have investigated how gains and losses~~
408 ~~of new hosts along the phylogenetic history of lineage relate) to the number of speciation~~
409 ~~events -obtaining alternative results on Nymphalidae{Hardy, 2017 #4976} (Table 2.3). Janz~~
410 ~~*et al.* (2001) inferred the number of gains and losses of host plants throughout the history of~~
411 ~~Nymphalini. They found that gains exceeded losses and suggested that these were the result of~~
412 ~~repeated range expansions. However Hardy (2017) recently reanalysed the same dataset using~~
413 ~~different models of evolution of host use and inferred equal numbers of gains and losses of~~
414 ~~plants throughout the phylogeny of Nymphalini. He concluded that in this insect group host~~
415 ~~shifts and speciation events do not necessarily result from host range expansions and~~
416 ~~contractions. May-be another way to investigate the link between ‘host-breadth changes’ and~~
417 ~~‘capture gains of new hosts’ without using diversification analyses would be to investigate~~
418 ~~test for the correlated evolution of these two characters; i.e. explore how often the gains of~~
419 ~~new hosts is associated with a transition from specialist to generalists. In any case, the recent~~
420 ~~debates around the *oscillation* hypothesis (its predictions and how to test them) clearly~~
421 ~~demonstrates that ancestral character state reconstructions and statistical tests based on these~~
422 ~~reconstructions are very sensitive to model choices and character coding strategies and should~~
423 ~~always be interpreted with care, even when very specific predictions are verified.~~

424 II.2.3) Evolution of host-plant adapted traits traits involved in host-plant choice

425 ~~Many Several studies that aimed at finding support for the coevolutionary arm race~~
426 ~~hypothesized by the *Escape and Radiate* scenario have investigated the evolution of~~
427 ~~detoxification mechanisms in insect lineages and how they showed that they correlate with~~
428 ~~changes in their host plant associations defences (Table 2.4). Studies that show that host~~
429 ~~switches occurred between plants with similar defenses, rather than closely related plants~~
430 ~~generally fit their results with the *Escape and radiate* hypothesis and Becerra (1997; 2003)~~
431 ~~reconstructed the evolution of detoxification mechanisms and plant defence in a genus of~~
432 ~~Chrysomelidae and their associated host plants (Burseraceae), and showed synchronous~~
433 ~~evolution of defences and counter defences that agree with a scenario of host plant driven~~
434 ~~radiation in these insects. Similarly, in a review on the interaction between the chemically-~~

435 defended *Heliconius* butterflies and their *Passiflora* host plants, de
436 Castro *et al.* (2018) highlighted a large variety of anti herbivory adaptations in the plants
437 (including chemical defences, trichomes, fake eggs or herbivore damages, interaction with
438 ants) and counter adaptations in the butterflies that support a long history of coevolution.
439 conclude to coevolutionary arm race between insects and associated plants.

440 Also in agreement with the *Escape and Radiate* theory, Wahlberg (2001) using
441 ancestral character states reconstruction on a phylogeny of Melitaeini (Lepidoptera) showed
442 that host switches occurred between plants with similar defences, rather than closely related
443 plants (i.e. host plant use was more influenced by chemistry than by plant taxonomy). Endara
444 *et al.* (2017) showed opportunistic host switches to plants with similar defences in a genus of
445 butterfly. They However some of these studies argue in favour of a scenario in which
446 suggested that herbivores simply "choose" host-plants based on their own defensive traits.
447 The authors conclude that disruptive selection is not a driver of speciation in this case. Many
448 other studies looked at the diversification dynamics of genes involved in plant detoxification
449 and how it correlates with changes in host plant associations. Wheat *et al.* (2007) showed that
450 the evolution of a detoxification mechanism, a nitrile specifier protein (NSP) in Pieridae
451 matches the distribution of glucosinolate in their host plants. Edger *et al.* (2015) further
452 investigated arm races between Brassicales and butterflies (Pieridae) and showed that
453 repeated evolution of nitrile specifier proteins were associated with bursts of diversification
454 over the past 80 Myr in Pieridae. Calla *et al.* (2017) examined the cytochrome P450
455 monooxygenase (CYP) gene superfamily diversification in the genomes of seven Lepidoptera
456 species varying in host breadth. They showed that its dynamics (duplication and losses) was
457 correlated with the ability to metabolise defences. Bramer *et al.* (2015) analysed the ability to
458 sequester toxic cardenolides throughout the phylogeny of the hemipteran subfamily
459 Lygaeinae and suggested that it was acquired in response to selection by cardenolide-
460 producing Apocynaceae host plants. Host switches underlie insect species differentiation but
461 this differentiation is not the product of coevolutionary interactions.

462 Reconstruction of the history of plant defences defences were was also conducted on
463 plant phylogenies. For instance, Livshultz *et al.* (2018) reconstructed the evolution of
464 cardenolide production in Apocynaceae and suggested that it could have evolved in response
465 to herbivorous insect predation. On the other hand, Agrawal *et al.* (2009), reconstructed the
466 history of plant defences in North American milkweed species (*Asclepias*, Apocynaceae) and
467 showed that less investment in cardenolide production correlates with an increase in
468 speciation rates. This does not follow the predictions of "*Escape and Radiate*" and However

469 direct tests of acceleration of diversification upon the acquisition of new defense mechanisms
470 rather sometimes contradict the ‘Escape and Radiate’ prediction and suggests that investment
471 in costly defences might have can impeded plant diversification in this plant group.

472 In contrast to detoxification mechanisms, traits ~~(and underlying genes)~~ involved in
473 host recognition and host-plant choice (chemosensory traits) have been less studied in a
474 phylogenetic context. However their evolutionary dynamic probably plays as important a role
475 as adaptations to plant defences in phytophagous insect speciation (Smadja, Butlin 2009).
476 (Matsuo 2008) showed that an odour binding protein in 27 *Drosophila* species can evolve
477 relatively fast in closely related species through gene duplications and losses, and proposed
478 that this dynamic could explain the evolution of host preferences in this species complex.
479 ~~Sánchez-Gracia et al. (2009) and Vieira & Rozas (2011) conducted a c~~Comparative genomic
480 ~~analysis-analyses~~ of odour binding protein and chemosensory proteins from the genomes of
481 several Arthropoda species ~~(mainly Drosophila)~~. ((Sánchez-Gracia, Vieira, Rozas 2009;
482 Vieira, Rozas 2011) conducted ~~They showed~~revealed a high number of gains and losses of
483 genes, pseudogenes, and independent origins of gene subfamilies. This dynamic, if analysed
484 in relation to host choices and host breadth in a phylogenetic context, could explain some host
485 shifts and subsequent speciation events. ~~Focusing on behavioural traits of insects, Molnar et al.~~
486 ~~(2018) analysed the antennal responses of 12 gall midge species to a wide range of host plant~~
487 ~~related volatiles and showed that species with similar response shared host plants~~. Finally,
488 deciphering the evolutionary dynamics of genes involved in mate recognition and their link
489 with host association could also inform us on the role of host-plants in the speciation of
490 insects that feed (and often mate) on them. For instance, (Schwander et al. 2013) showed that
491 cuticular hydrocarbon profiles involved in mate choices vary among *Timema* species
492 ~~(ColeopteraPhasmatodea)~~, and that most evolutionary changes in hydrocarbon profiles occurs
493 in association with host-plant shifts and speciation events in this genus of phytophagous
494 insects. ~~This study shows that physiological traits involved in reproductive isolation can be~~
495 ~~associated with host plant differentiation on a macroevolutionary time scale.~~

496 In summary, many studies have investigated the evolution of detoxification
497 mechanisms in insects butterflies and found support for framing their hypotheses within the
498 Escape and Radiate theory. ~~More s~~Studies investigating changes in traits involved in host
499 recognition throughout the diversification of insects are rare and they are generally not framed
500 within host-plant driven scenarios. ~~These~~Such studies are needed in order to determine which
501 traits underlie host-plant associations and whether their evolution ~~accompany~~ drives
502 speciation events (see Perspectives).

503 **II. 3) Studying how host-plants use impact the diversification dynamics of herbivorous** 504 **insects**

505 Methods for testing diversification dynamics have expanded over the last decade.
506 Testing for the existence of temporal bursts of diversification was once restricted to analyses
507 of groups with comprehensive fossil records. Diversification dynamics can now be studied
508 through comprehensive phylogenies (Goswami, Mannion, Benton 2016). Given the breadth of
509 available methods, theoretically, nearly all hypotheses can be put to test.

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

511 Studies that posit that host-plant adaptation favours phytophagous insect
512 diversification predict that those are much more diversified than non-phytophagous insects.
513 However this assertion deserves to be statistically tested. The first ~~studies~~ study addressing
514 this question (~~Farrell & Mitter 1990; Farrell & Mitter 1998; Mitter *et al.* 1988~~), ~~compared the~~
515 ~~diversity (number of species) of phytophagous vs related non-phytophagous clades in beetles.~~
516 ~~They all~~ suggested that herbivorous clades ~~are more diverse~~ contain more species than their
517 non-phytophagous sister clades (Table 2. 5). However, ~~Hunt *et al.* (2007) and then Rainford *et*~~
518 ~~*al.* (2015), using more comprehensive beetle phylogenies associated with up to date recent~~
519 ~~comparative methods, and also adopting a sister clade comparison, did not find a significant~~
520 ~~increase in species richness in phytophagous clades. In their phylogeny of the beetle family~~
521 ~~Erotylidae, Leschen & Buckley (2007) mapped the evolution of species number within clades~~
522 ~~(as a two-state character: 0/1) and did not detect any significant correlation between species~~
523 ~~richness and phytophagy (using Bayesian tests of character correlation). McKenna *et al.*~~
524 ~~(2015) tested for temporal variation in diversification rates (using MEDUSA Alfaro *et al.*~~
525 ~~2009) on a global phylogeny of Coleoptera and showed that those underwent several~~
526 ~~accelerations of diversification rates; some seemed to be associated with the evolution of~~
527 ~~phytophagy while others were not~~ suggest that several types of niche shifts beside phytophagy
528 can explain insects species richness.

529 ~~There are more informative tests than those that merely test whether one group contains more~~
530 ~~species or has diversified more rapidly than others. More recently Wiens *et al.* (2015) used~~
531 ~~Phylogenetic Generalized Least Square Regressions and comprehensive phylogenies within~~
532 ~~and between several insect orders and showed that the proportion of phytophagous insect~~
533 ~~species in a clade was positively correlated with diversification rates in several insect orders.~~
534 ~~But this relationship did not hold for Coleoptera, Hymenoptera and Orthoptera. Studies within~~

535 ~~insect orders have mostly been addresses within Coleoptera –as they are by far the most~~
536 ~~diverse order but more in–depth analyses of other orders would actually also be useinsightful.~~
537 ~~To our knowledge Likelihoodlikelihood~~-based character state dependent diversification
538 models (known as, the ~~–*~~SSE models, such as BiSSE, ClaSSE and QuaSSE for binary,
539 multistate and quantitative traits, respectively (Maddison, Midford, Otto 2007; FitzJohn 2010;
540 Maddison, FitzJohn 2015), ~~which can specificallythat~~ test whether transition in character
541 states are associated with variations in speciation and extinction rates. ~~These diversification~~
542 ~~models can be used to test whether the evolution of phytophagy has favoured diversification.~~
543 ~~However, they werehave~~ not ~~been yet used~~ ~~employed in Wiens et al. (2015)~~ to test the role of
544 ~~phytophagy in insect diversification.~~ A robust estimate of diversification parameters by these
545 methods ~~would actually~~ requires dense and random species sampling throughout the
546 phylogeny. ~~(aAccording to (FitzJohn 2010) more than 15% of the species must be included in~~
547 ~~the phylogeny in order to conduct unbiased –*SSE tests).~~ ~~The study was conducted at the~~
548 ~~order level and within each order the proportion of missing species was too high to apply –~~
549 ~~SSE methods.~~
550 ~~From current studies using more comprehensive phylogenies and statistical tests, it is thus yet~~
551 ~~not completely clear whether phytophagy increases diversification rates in insects in~~
552 ~~comparison to other life habits.~~ ~~Therefore character state dependent diversification models~~
553 ~~awaits t~~The availability of more comprehensive phylogenies ~~will allow testing this hypothesis~~
554 ~~on in~~ more insect orders ~~using character state dependent diversification models.~~ Nevertheless;
555 a caveat of these diversification models is that they may overlook more complex models
556 involving many unmeasured and co-distributed traits ~~(especially when few transitions in~~
557 ~~feeding habits are observed).~~ ~~In particular, for phytophagy, other traits that may drive shifts in~~
558 ~~diversification may cause a spurious detection of increased diversification rates in~~
559 ~~phytophagous insects if this trait’s states partly correlate with phytophagy states, or may~~
560 ~~instead erase any signal due to phytophagy.~~ The HiSSE model (Beaulieu, O’Meara 2016)
561 which models hidden characters that ~~might~~ influence diversification might help untangling
562 these confounding factors.

563 II.3.2) Testing for adaptive radiation

564 Diversification analyses can also be applied to test whether the capture of new host-
565 plants has favoured adaptive radiations. Under such a scenario, the diversification curve of
566 phytophagous insect clades should exhibit early bursts of speciation upon the capture of new

567 groups of host-plants. ~~Eventually, Insect~~the lineages are eventually expected to fill the newly
568 found niche space and the diversification curves should reach a plateau.

569 ~~There are s~~Several studies ~~that~~ have ~~observed~~ investigated acceleration in
570 ~~diversification~~ speciation rates in insect lineages and ~~have put forward ad-hoc narratives that~~
571 ~~attribute this acceleration~~ se rates to upon the capture of new host-plant lineages (Table 2. 6) or
572 detoxification mechanism (Table 2. 7). ~~These studies have mainly been conducted in~~
573 butterflies. While most studies have observed shifts in speciation rates in insects upon host
574 plant acquisition For instance, ~~Wheat et al (2007) showed that the Pierinae clade that can~~
575 ~~detoxify glucosinolate in their host plants are more diversified than its sister clade. Mullen et~~
576 ~~al. (2011) have observed an increase in species richness in the butterfly genus Adelpha~~
577 ~~(Nymphalidae) and attributed this increase to adaptive divergence in response to host plant~~
578 ~~diversity found within the neotropics (namely host-plant shift to Rubiaceae and other plant~~
579 ~~families). Ebel et al. (2015) revealed an increase in the rates of diversification on the~~
580 ~~phylogeny of the genus Adelpha and observed that those were concomitant to host shifts.~~
581 ~~Sahoo et al. (2017) revealed two accelerations in diversification in skipper butterflies that~~
582 ~~they attributed to shifts from dicots to monocots at time where those diversified and~~
583 ~~expanded.~~ these results seem to be sensitive to the models used. Studies have also rarely
584 included trait-dependent diversification models and when they did, they often relied on single
585 or few colonization events that were also correlated with ~~important geographical changes,~~
586 making it difficult to conclude on the causal effect of the sole host shift (Table 2.6). ~~Fordyce~~
587 ~~(2010) showed changed in diversification rates upon the capture of new plant lineages in~~
588 ~~several butterfly lineages and Edger et al. (2015) detected shifts in diversification rate~~
589 ~~associated with the colonization of new host plants with new defences, though this was not~~
590 ~~statistically tested. Winkler et al. (2018) on the other hand, uncovered stable diversification~~
591 ~~rates and no decrease associated with overlap in host use throughout the phylogeny of the fly~~
592 ~~genus Blepharoneura, suggesting that this lineage did not undergo an adaptive~~
593 ~~radiation. Using BiSSE, Peña & Espeland (2015) found that a hostplant shift to Solanaceae~~
594 ~~was correlated with an increase in net diversification rates in Ithomiini butterflies~~
595 ~~(Nymphalidae). However, since only one shift to Solanaceae occurred in the Nymphalidae,~~
596 ~~this correlation should not be taken as evidence that hostplant shift has driven diversification~~
597 ~~of this butterfly tribe. Instead, the radiation of Ithomiini may be linked with geographical~~
598 ~~context in this study.~~

599 ~~While several studies have uncovered acceleration in diversification rates upon the~~
600 ~~capture of new host plant lineages~~ Among ~~these~~ studies addressing investigating adaptive

601 radiation patterns (Table 2.8), ~~only a handful full~~ have investigated whether the number of
602 species ~~reaches reached~~ a plateau after an initial burst of ~~diversification speciation~~. ~~Meseguier~~
603 ~~et al. (2015) studied the diversification dynamic of a conifer feeding aphid genus. They~~
604 ~~revealed an accelerated rate upon the capture of conifers but no saturation as expected under a~~
605 ~~scenario of adaptive radiation. This is better addressed using~~ The use of density-dependent
606 models of diversification (DDD) would be better suited to that test whether rates of
607 ~~diversification speciation~~ decrease ~~through time during evolutionary radiations~~ once the
608 number of species supposedly reach the carrying capacity of the novel ecological niche
609 (Rabosky, Lovette 2008; Etienne et al. 2012). But these tests can only be applied to lineages
610 in which the number of species in each subclade is well known. ~~Peña et al. (2015) used such~~
611 ~~diversity dependent birth death models to infer speciation, extinction rates and carrying~~
612 ~~capacity on a phylogenetic tree of the butterfly genus Erebia and showed that the~~
613 ~~diversification dynamics was consistent with a model of adaptive radiation. In any case,~~
614 ~~studies generally provided weak support for adaptive radiation scenarios (Table 2.8). They all~~
615 ~~suggested that~~ Kergoat et al. (2018) compared the diversification dynamics of Sesamiina
616 stemborer moths and their associated grasses. The initial burst of diversification observed in
617 moths suggests that their emergence might have been favoured by the diversification of their
618 host plants. A decline in speciation rates was then inferred in these insects using Diversity-
619 dependent birth death models. However, their host plants continued to thrive. This challenges
620 the “adaptive radiation scenario” and suggests that these moth diversification patterns cannot
621 solely be explained but by the availability of suitable host-plants and insisted that abiotic
622 factors such as geography and temperature should be taken into account in diversification
623 scenarios. (Kergoat et al. 2018).

624

625 II.3.3) Correlating host breadth with diversification dynamic

626 Advocates of the *Oscillation hypothesis* suggest that clades showing a higher diversity
627 of host-use (using more host-plant species altogether) should be more diverse than their sister
628 clade (Janz, Nylin, Wahlberg 2006), and this prediction has been verified in butterflies,
629 Coccidae and some gall inducing flies (Table 2.9). ~~Janz et al. (2006) and Nylin & Wahlberg~~
630 ~~(2008) found a positive relationship between species diversity of butterflies and species~~
631 ~~diversity of host plant taxa in several genera of Nymphalidae, through a sister clade~~
632 ~~comparisons of number of species. Joy & Crespi (2012) and Lin et al. (2015) found a similar~~
633 ~~result in respectively gall inducing flies and Coccidae. Wang et al. (2017) used a sister clade~~
634 ~~comparisons and PGLS to demonstrate a similar trend in moths.~~

635 Although these results support a model where the diversity of phytophagous insects is
636 sustained by the diversity of the hosts they use, they could fit both a model of *Oscillation* and
637 the *Musical chairs* hypothesis. The latter indeed predicts that lineages including specialist
638 species that often switch between hosts; use a large number of host-plants. To tell apart the
639 *Oscillation* from the *Musical chairs*, it is actually more informative to test how host breadth
640 variations affect insect diversification dynamics. According to the *Oscillation* hypothesis,
641 clades including generalist species should be more speciose than clades including only
642 specialists. ~~In order to test this prediction, diversification analyses have been conducted on
643 various insect phylogenies. Early papers have used fairly basic methods such as ‘sister clade
644 analyses’ while Weingartner et al. (2006) tested this prediction in *Polytonia* butterflies
645 (Nymphalidae) through sister clade analyses and showed that clades using a broader host-
646 plant range are more species-rich than their sister group that encompass species that only use
647 the ancestral hosts (here, urticalean rosids), in agreement with the *Oscillation* scenario.~~

648 ~~More finely tuned analyses, such as more recent investigations have adopted trait-
649 dependant diversification models (BiSSE and QuaSSE models)(Table 2.10) have been used
650 on the phylogenies of Papilionidae and the tribe *Heliconiini* by Hardy and Otto (2014). In
651 this paper, where the *Musical chairs* hypothesis was put forward, the authors showed that: 1)
652 speciation rates decreased with host breadth (i.e. monophagous species diversified faster than
653 polyphagous species); 2) changes in host breadth were not associated with cladogenetic
654 events; 3) rates of host switching were positively associated with diversification rates. All
655 these results were in agreement with the *Musical chair* hypothesis. Still on Nymphalidae,
656 (Hamm & Fordyce 2015) found that host breadth characteristics were phylogenetically
657 conserved which does not fit the predictions of the *Oscillation hypothesis* about the lability of
658 host breadth and also found that speciation rates did not increase with host breadth expansion,
659 in agreement with the *Musical chair* scenario.~~

660 ~~By contrast, Hardy et al. (2016) showed on a Coccidea phylogeny that host breadth
661 (measured as the number of host plant families) was positively correlated to speciation rates.
662 As SSE models are known to generate false positives (Bouchenak Khelladi et al.
663 2015; Rabosky & Goldberg 2015; Davis et al. 2013), they conducted the analysis on a set of
664 randomized trees in order to test whether the constrained diversification model (i.e. the model
665 in which evolutionary transitions in character states are associated with shifts in extinction
666 and/or speciation rates) is also chosen in these analyses. The authors did not frame their study
667 within the *Oscillation vs Musical chairs* controversy, but if we refer to the paper of Hardy &
668 Otto (2014), these results fit with some of the predictions of the *Oscillation hypothesis*.~~

669 These studies provided support for alternative scenarios. But even when a specific
670 prediction was met, the authors could not always reach a firm conclusion. As already
671 previously mentioned, there are debates on the influence of host breadth variation on
672 diversification dynamics (Hamm & Fordyce 2015; Janz et al. 2016; Hamm & Fordyce 2016;
673 Wang et al. 2017). The transient nature of the generalist feeding diet under host-driven
674 speciation scenarios makes it difficult to derive clear predictions; The negative or positive
675 relationship observed between host breadth dynamics and diversification can always be
676 obscured by the rapid evolution of host breadth (Nylin, Janz 2009; Janz et al. 2016). The
677 way host breadth is measured (binary vs continuous) is also known to affect the results
678 (Hamm, 2015) and it has been long recognized that categorizing species into either specialist
679 or generalist can be difficult and somewhat subjective (Janz, 2001). Furthermore, although
680 the musical chair yields specific predictions, those are mainly rebuttals of the “Oscillation”
681 predictions (but see Table 2.11), but rejecting an “Oscillation” scenario does not instantly
682 mean that a “Musical chair” scenario is at play. Hence despite the existence of sophisticated
683 methods and comprehensive phylogenies, the prevalence of these scenarios in insects is still
684 debated.

685 Furthermore Another caveat of these studies lies in the distinction between speciation
686 and extinction rates. Indeed, if specialization towards host plants can accelerate speciation
687 rates it can also increase extinction risks when plants are not highly abundant. Although
688 diversification methods can potentially differentiate extinction rates from speciation rates
689 (Morlon 2014), Consequently, predicting exactly how changes in host-plant breadth affects
690 diversification dynamics remains difficult. Finally diversification methods such as *SSE
691 models are known to generate false positives (Bouchenak-Khelladi et al. 2015; Rabosky,
692 Goldberg 2015; Davis, Midford, Maddison 2013), and can thus inflate the role of host plant
693 and host breadth in diversification when those are investigated. It is therefore, highly
694 recommended to conduct the analyses on a set of randomized trees in order to test whether the
695 constrained diversification model (i.e. the model in which evolutionary transitions in character
696 states are associated with shifts in extinction and/or speciation rates) is also chosen in these
697 analyses (as done in (Hardy, 2016).

698 In summary, diversification analyses have been widely applied to phytophagous
699 insects. These methods were fairly basic in early papers but they have been refined throughout
700 the years and their use allowed reframing hypotheses on the role of host plant specialization
701 on insect speciation. Recent results brought mixed evidence for phytophagy as an accelerator

702 ~~of diversification. Trait dependant diversification analyses supported alternative scenarios~~
703 ~~involving oscillation in diet breadths as a driver of host plants shifts and speciation, and from~~
704 ~~our review, it is likely that different scenarios will prevail in different lineages and even~~
705 ~~probably in the same lineage at different time scales.~~

706 ~~Finally~~ Moving away from methodological issues, our survey also underlines that ,
707 many studies that explore macroevolutionary scenarios have been conducted on
708 ~~butterflies~~ Lepidoptera. In order to have a better understanding ~~of how phytophagous insects~~
709 ~~capture new host plants and whether it influence~~ the role of host-plant shifts in insects their
710 diversification dynamics, it seems necessary to test the predictions of macroevolutionary
711 scenarios on other insect groups. Aphids (Hemiptera) could be good candidates for such
712 investigation. Their range of host-plants is very well documented (Blackman, Eastop 2006;
713 Holman 2009). Although most aphids are host-specific, there are some polyphagous species.
714 Some species are even only polyphagous during ~~the asexual~~ part of their life-cycle (Moran
715 1992; Joussein, Genson, Coeur d'Acier 2010; Hardy, Peterson, von Dohlen 2015). This
716 temporary broadening of diet has already been suggested to facilitate the capture of new host-
717 plants (Moran 1992) and subsequent ~~specialization and~~ speciation onto these new hosts. These
718 life-cycle ~~y~~ transitions could have thus favoured the diversification on this ~~group~~ clade
719 (Moran 1992; Joussein, Genson, Coeur d'Acier 2010). This scenario fits the *Oscillation*
720 ~~hypothesis and should be tested on a robust and comprehensive aphid phylogeny~~. Other ~~insect~~
721 Hemipteragroups ~~for~~ which host plant repertoire ~~are is~~ well known such as Coccidae (Garcia-
722 Morales *et al.* 2016) and Psyllids-psyllids (Ouvrard *et al.* 2015) could also be used to test the
723 predictions ~~of on the role of host breadth evolution in~~ macroevolutionary scenarios. The
724 limitation lies in the availability of robust and comprehensive phylogenies for these groups.

725 ~~In summary, diversification analyses have been widely applied to phytophagous~~
726 ~~insects. These methods were fairly basic in early papers but they have been refined throughout~~
727 ~~the years and their use allowed reframing hypotheses on the role of host plant specialization~~
728 ~~on insect speciation. Recent results brought mixed evidence for phytophagy as an accelerator~~
729 ~~of diversification. Trait dependant diversification analyses supported alternative scenarios~~
730 ~~involving oscillation in diet breadths as a driver of host plants shifts and speciation, and from~~
731 ~~our review, it is likely that different scenarios will prevail in different lineages and even~~
732 ~~probably in the same lineage at different time scales.~~

733

734 **III Perspectives**

735 As seen throughout this review, phylogenetic comparative methods provide the
736 template to test hypotheses on the role of host plant association in the speciation of
737 phytophagous insects. While those methods have undoubtedly advanced the field significantly
738 since “the *Escape and Radiate*” paper, readers must keep in mind that phylogenetic
739 comparative methods often rely on mere correlations. Significant associations between
740 character changes and the cladogenetic events might arise as a consequence of speciation
741 itself when post-speciational character changes occur. Furthermore, comparisons of models of
742 evolution such as those used in trait-dependent diversification analyses often rely on trees that
743 encompass few transitions in character states and are therefore not always robust (see
744 {Beaulieu, 2013 #5053}). In such analyses, the “best model” is not necessarily the true model
745 and significant *P* values should not be interpreted as strong evidence for an evolutionary
746 scenario. Finally, all these methods are very-sensitive to sampling biases and those need to be
747 carefully taken into consideration.

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

758 **III.1) Investigating the role of abiotic factors: geography and climate**

759 Geography and ecology are always closely intertwined in speciation scenarios. There have
760 been several studies that have investigated geographic range expansion in herbivorous insects
761 (Becerra, Venable 1999; Slove, Janz 2011); climate induced host shifts (see (Winkler, Mitter,
762 Scheffer 2009; Nyman et al. 2012 for a review and recent studies since then {Lisa De-Silva,
763 2017 #4641; Sanchez-Guillen et al. 2016; Lisa De-Silva et al. 2017; Owen et al. 2017;
764 Pitteloud et al. 2017; Sahoo et al. 2017) and climate driven diversification dynamics (Kergoat
765 et al. 2018). All these studies suggest that abiotic factors are entangled with host-plants
766 changes in species diversification scenarios. However there are few studies that explicitly test
767 the predictions of speciation through geographic isolation (Barraclough, Vogler 2000) and

768 whether these events systematically accompany host shifts or sustain most speciation events
769 (but see Jordal & Hewitt 2004; Jousselin et al. 2013; Doorenweerd, van Nieuwerkerken, Menken
770 2015; Hardy, Peterson, Normark 2016). Such analyses are important if we want to tell
771 whether adaptations to new host plants represent post-speciational changes following
772 geographic isolation rather than the main driver of speciation events. Cospeciation methods
773 that take into account the biogeographic history of interacting lineages (Berry *et al.* 2018)
774 could be also used to investigate whether host shifts are associated with dispersal events in
775 systems where hosts plants and insects phylogenies show some congruent patterns.

776

777 ~~III_[M1].2) Combining phylogenetic with interaction network approaches, at various~~ 778 ~~ecological scales~~

779 ~~Herbivores and the plants they feed on form interaction networks, and as such the~~
780 ~~structures of the networks can be characterized by several parameters, such as modularity (the~~
781 ~~propensity of a group of species to interact with a similar set of partners) and nestedness (the~~
782 ~~propensity of specialist species to interact with generalist species and vice-versa).~~
783 ~~Antagonistic interaction networks, such as plant herbivore networks, tend to be highly~~
784 ~~modular (Thébault & Fontaine 2010). A recent study combining interaction network with~~
785 ~~phylogenetic approaches on simulated and real datasets predicted that the *Escape and radiate*~~
786 ~~scenario should produce a modular network structure, whereas the *Oscillations* scenario~~
787 ~~should produce a more nested structure (Braga *et al.* 2018). When applied to real data (two~~
788 ~~butterfly families, Nymphalidae and Pieridae), this approach revealed that host plant butterfly~~
789 ~~networks tend to be both modular and nested, which the authors interpret as being the result of~~
790 ~~a complex pattern of diversification, involving both episodes of radiation on new hosts~~
791 ~~(producing modules containing closely related species) and occasional shifts to other host~~
792 ~~lineages, producing both nestedness within modules and connections between modules.~~

793 ~~Additionally, phylogenetic and network approaches could be expanded to encompass other~~
794 ~~interacting partners (*e. g.* Elias *et al.* 2013, Ives & Godfray 2006). Indeed, insect host plant~~
795 ~~communities can be seen as ecosystems where biotic interactions, such as parasitism and~~
796 ~~mutualism also take place (Forister *et al.* 2012). These other partners can indirectly influence~~
797 ~~the interaction between plants and there herbivores: *e. g.*, direct competition (Jermy 1988)~~
798 ~~apparent competition between herbivores, stemming from shared natural enemies, (Holt~~
799 ~~1977), and vice versa (*e. g.*, when herbivory elicits anti herbivore defences mediated by~~

800 ~~herbivore enemies, (Fatouros *et al.* 2008)). Multitrophic interactions probably explain many~~
801 ~~diversification patterns in herbivorous insects (Singer & Stireman 2005)~~
802 ~~Finally, such approaches could be applied both at a large scale (e. g., Braga *et al.* 2018), to~~
803 ~~embrace global patterns of diversification and interaction, or at the community level (Elias *et*~~
804 ~~*al.* 2013, Ives & Godfray 2006), where interactions actually occur, and where fine-scale~~
805 ~~processes (e. g., host plant shift at the species or the population level) can be unveiled.~~

806 **III.32) Unravelling traits involved in the interaction and their underlying genes, and** 807 **integrating this information in phylogenetic studies**

808 Interactions between insects and their host-plant are ultimately mediated by traits, such as
809 host-plant defences and the capacity of circumventing plants defences, but also host-plant
810 cues and the capacity for herbivores to detect those cues. Characterizing such traits, their
811 genetic determinism and looking at their evolutionary trajectory would greatly advance our
812 understanding of the diversification of insects (e. g., (de Castro *et al.* 2018). [Testing whether](#)
813 [different trait states are associated with different speciation rates can be performed using](#)
814 [*SSE methods \(e. g., as in Onstein, 2017 for a trait related to frugivory in palm trees\)](#). In
815 addition, methods that test whether patterns of trait evolution conform to a model accounting
816 for interactions mediated by those traits are currently being developed (Manceau, Lambert,
817 Morlon 2016) (Drury *et al.* 2017), and they could inform on the processes underlying
818 herbivore diversification. However, targeting traits involved in plant-insect interactions may
819 be challenging. Pivotal traits are difficult to identify, they include chemical, behavioral and
820 metabolic traits and when they are properly characterized they are often multigenic.

821 Perhaps a promising direction for future research is the implementation of a hybrid
822 genomic approach that combines transcriptomics, phylogenomics, comparative analyses and
823 population genomics (see (Nevado *et al.* 2016). In such approaches, full transcriptomes of
824 species from a target clade (for instance, a clade of phytophagous insect) are generated. These
825 transcriptomes (or other sequence data) are used to generate a phylogeny, where classical
826 diversification and character evolution tests can be performed (evolution of characters, test for
827 diversity-dependent diversification, shifts in diversification following host-plant shift). Then,
828 genes under selection can be detected from transcriptomic data using population genetics
829 statistics, and can be matched to existing databases (e. g., Lepbase for Lepidoptera, Challis *et*
830 *al.* 2016) for identification purpose. Additionally, genes that are down or upregulated can also
831 been detected by classical tests of differential expression and identified, and the association of
832 genes under selection, either via different sequence or expression pattern, with species

833 | diversity can be tested. ~~The main~~One of the limits of this approach lies in the availability of
834 | specimens (transcriptomic data need to be obtained from fresh or suitably preserved tissues;
835 | biological replicates are needed), ~~and the~~those might be difficult to obtain throughout an entire
836 | phylogenetic tree. ~~and the~~The availability and quality of the reference gene database to match
837 | genes with putative functions might also limit the applications of this approach. -

838 | III.3) Combining phylogenetic with interaction network approaches, at various 839 | ecological scales

840 | Herbivores and the plants they feed on form interaction networks, and as such the
841 | structures of the networks can be characterized by several parameters, such as modularity (the
842 | propensity of a group of species to interact with a similar set of partners) and nestedness (the
843 | propensity of specialist species to interact with generalist species and vice-versa).
844 | Antagonistic interaction networks, such as plant-herbivore networks, tend to be highly
845 | modular (Thébault, Fontaine 2010). A recent study combining interaction network with
846 | phylogenetic approaches on simulated and real datasets predicted that the *Escape and radiate*
847 | scenario should produce a modular network structure, whereas the *Oscillations* scenario
848 | should produce a more nested structure (Braga et al. 2018). When applied to real data (two
849 | butterfly families, Nymphalidae and Pieridae), this approach revealed that host-plant butterfly
850 | networks tend to be both modular and nested, which the authors interpret as being the result of
851 | a complex pattern of diversification, involving both episodes of radiation on new hosts
852 | (producing modules containing closely related species) and occasional shifts to other host
853 | lineages, producing both nestedness within modules and connections between modules.

854 | Additionally, phylogenetic and network approaches could be expanded to encompass other
855 | interacting partners (e. g. (Elias, Fontaine, van Veen 2013), (Ives, Godfray 2006) . Indeed,
856 | insect-host-plant communities can be seen as ecosystems where biotic interactions, such as
857 | parasitism and mutualism also take place (Forister et al. 2012). These other partners can
858 | indirectly influence the interaction between plants and their herbivores: e. g., direct
859 | competition (Jermy 1988) apparent competition between herbivores, stemming from shared
860 | natural enemies, (Holt 1977), and vice-versa (e. g., when herbivory elicits anti-herbivore
861 | defences mediated by herbivore enemies, (Fatouros et al. 2008)). Multitrophic interactions
862 | probably explain many diversification patterns in herbivorous insects (Singer, Stireman 2005)
863 | Finally, such approaches could be applied both at a large scale (e. g., Braga et al. 2018), to
864 | embrace global patterns of diversification and interaction, or at the community level (Elias,
865 | Fontaine, van Veen 2013), (Ives, Godfray 2006), where interactions actually occur, and where

866 | fine-scale processes (e. g., host-plant shift at the species or the population level) can be
867 | unveiled.

868

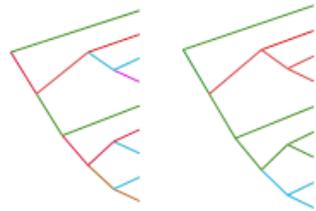
869 | **Conclusions**

870 | Many phylogenetic studies of plant-insect associations now include formal tests of
871 | macroevolutionary scenarios involving host-driven speciation. In an attempt to summarize the
872 | literature on this topic, we show that the predictions of host-plant driven speciation are not
873 | straightforward and can vary depending on studies. We advocate a standardization of these
874 | predictions to facilitate cross study analyses. Furthermore, it is also recognized that different
875 | scenarios can leave the same phylogenetic signature (Janz *et al.* 2016) and that depending on
876 | the analytical approaches undertaken to test the predictions laid out in Table 1, conclusions
877 | can vary (Hardy *et al.* 2017). Unfortunately this means that the interpretations of phylogenetic
878 | inferences can remain somewhat subjective. But these shortcomings should not obscure the
879 | progresses that have been made in the field. Phylogenetic comparative analyses help framing
880 | hypotheses and clarify some of the narratives used to explain the diversification of
881 | phytophagous insects. In order to move towards a standardization of phylogenetic approaches,
882 | we propose here a (non-exhaustive) list of relatively simple tests that could be applied to an
883 | insect phylogeny that includes robust data on host plant association (Fig. 2). The limitations
884 | of these approaches (sampling biases, false positives) have been described throughout this
885 | review. Finally, this survey of the literature shows that: 1) the simple assumption that
886 | phytophagy has accelerated insect diversification is not always sustained by meta-analyses; 2)
887 | the expectation that sister lineage will use different ranges of host plants is not often tested,
888 | and, when it is, the predictions of a host-driven speciation scenarios are not always met. We
889 | then underline that the results of phylogenetic comparative methods cannot be interpreted as
890 | hard evidence as they remain mere correlations. In the end, a full understanding of the
891 | processes explaining the diversification of phytophagous insects will require the integration of
892 | phylogenies with other data sources and analytical methods. ~~We propose here a few~~
893 | ~~perspectives to integrate such data and investigate host-driven speciation scenarios on a~~
894 | ~~macroevolutionary time-scale.~~

895 | Finally~~To conclude~~, if the last two decades have seen the rise of molecular
896 | phylogenies and the development of analytical methods that include ecological data, this
897 | should not obscure the fact that ~~these~~is data needs to be thoroughly curated before any

898 phylogenetic comparative analyses. Qualifying host associations of insect species necessitates
899 field work and advanced taxonomy, as mistakes can seriously impact the results of
900 macroevolutionary studies. Functional studies aimed at deciphering host-plant adapted traits
901 in insects (and in particular traits implied in host choice) and characterizing genes that
902 underlie these traits are also needed to integrate this data in a phylogenetic context and link
903 | microevolutionary processes with macroevolutionary scenarios.

a) Host-plant range history



— Range 1
— Range 2
— Range 3
— Range 4

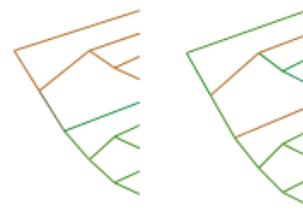
H1: Speciation driven by host shifts H2: Speciation not driven by host shift

Tests: evaluate the number of host shifts and compare models of evolution for host range .

Under H1: number of host shifts \approx number of speciation events > number expected when host use is randomized; host-plant range follows a speciational model of evolution.

Under H2: host plant range exhibits a phylogenetic signal.

b) Host breadth history



— specialist
— generalist

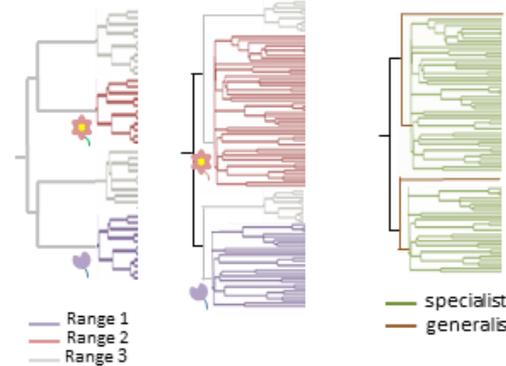
H1: No oscillation H2: Oscillation

Tests: evaluate phylogenetic signal and compare models of evolution for host breadth .

Under H1 : host breadth exhibits a phylogenetic signal.

Under H2 : host breadth follows a speciational model of evolution.

c) Diversification analyses



H1: No adaptive radiation H2: Adaptive radiation driven by host shifts (Escape and radiate) H3: Adaptive radiation driven by shifts in diet breadth (Oscillation)

Tests: use sister-clade analyses, PGLs, diversity dependant models of diversification or *SSE models to test the effect of host shift, host breadth and host plant lineage diversity on speciation.

Under H1: no significant shifts in speciation rates upon host shifts.

Under H2: significant shifts in speciation rates upon host shifts, number of insect species higher in species rich plant clades.

Under H3: speciation rate increase following shift away from polyphagy

905 Suggestions of phylogenetic comparative methods that can be deployed to test the prediction of host-driven speciation scenarios. a) Tests that rely on a robust
906 reconstruction of host-plant range evolution. b) Tests that rely a robust reconstruction of host-breadth. c) Diversification analyses that rely on reconstruction of
907 both these characters. H1, H2, H3 are alternative scenarios and are represented by a schematic phylogenetic reconstruction above.

908

909

910

911 **Glossary:**

912 **Adaptive radiation:** the evolution of ecological and phenotypic diversity within a rapidly
913 multiplying lineage (Schluter 2000). It occurs when natural selection drives divergence of an
914 ancestral species into descendants that exploit different ecological niches.

915

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

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

919 **Cospeciation:** simultaneous speciation events in lineages involved in long-term interspecific
920 associations which result in congruent phylogenies and temporal congruence of speciation
921 events

922

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

924 **Ecological specialization:** when species are limited themselves to a restricted set of
925 resources (diet- habitat-niches), as a result of evolutionary trade-offs.

926 **Evolutionary lability:** tendency for a character to change frequently throughout evolution.

927 **Generalists:** species that use a wide niche (a wide range of host plants belonging to different
928 lineages in the particular case of phytophagous insects)-

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

931 **Phylogenetic conservatism (-);** tendency for closely related species to be more similar than
932 expected under Brownian motion evolution.

933

934 ~~**Specialists:** species that use a narrow niche;~~

935 **Phylogenetic tracking** occurs when a host-dependent species (here phytophagous insects)
936 diversifies to utilize niches created by the speciation its hosts (here host-plants), related

937 insects use related plants, this leads to parallel phylogenetic trees but no temporal congruence
938 of speciation events

939

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

943 Specialists: species that use a narrow niche (a restricted set of resources);

944

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

947

948 **Conflict of interest disclosure**

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

951 **References**

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