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

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10   **Keyword:** coevolution, herbivory; host-plant specialization, phylogeny, speciation.

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.

Introduction

The idea according to which new species arise through adaptation to different ecological niches constitutes the core of Darwin's work. This process is now termed ecological speciation and its study has become an intense field of research in evolutionary biology (Nosil, Crespi, Sandoval 2002; Rundle, Nosil 2005; Schluter 2009; Nosil 2012). **Phytophagous insects***[1] have always been at the forefront of these investigations (Drès, Mallet 2002; Funk, Filchak, Feder 2002; Matsubayashi, Ohshima, Nosil 2010; Elias et al. 2012; Forbes et al. 2017). The hypothesis of ecological speciation resulting from divergent selection exerted by host-plants was put forward a long time ago to explain the formation of new species of insects (Brues 1924). This scenario has been explored on several study systems. One text-book example of host-plant driven incipient speciation is the apple maggot (*Rhagoletis pomonella* complex) in which the evolution of new feeding preferences on the recently introduced domesticated apple (*Malus pumila*) has supposedly led to the emergence of specialized host races (Bush 1975; Berlocher 2000; Powell et al. 2014). Stick insects, leaf beetles (Nosil et al. 2012; Rundle et al. 2000), butterflies (McBride, Singer 2010), and the pea aphid also stand out as model systems in the study of host-driven speciation (Via, Bouck, Skillman 2000; Caillaud, Via 2000; Peccoud et al. 2009; Smadja et al. 2012). In all these examples, the speciation scenario hypothesizes that: 1) the restricted utilization of distinct sets of host-plant species by insect populations is the result of adaptive trade-offs; 2) hybrids with intermediate phenotypes (in terms of traits involved in **host-plant adaptation***) fare poorly on parental host-plants and are selected against and therefore, gene flow between populations is reduced; 3) gene flow can further be reduced through the evolution of assortative mating, especially when host-plants also represent mating sites. In support of this scenario, many studies show the existence of genetically differentiated host races in insect species. Some studies have quantified selection against hybrids (McBride, Singer 2010; Gow, Peichel, Taylor 2007) and some studies have uncovered genomic regions that determine host-plant preference and performance on alternative hosts (Egan, Nosil, Funk 2008; Smadja et al. 2012).

The role of host-plant-mediated speciation in the diversification of insects is also largely emphasized in the literature on large-scale patterns of insect diversity: macroevolutionary perspectives on phytophagous insect evolution have attributed their extraordinary diversification to selective responses to their host-plants (Ehrlich, Raven 1964; Yokoyama 1995; Winkler, Mitter 2008; Janz 2011). However, these macroevolutionary scenarios are often presented in the literature as narratives for specific insect lineages commenting on a phylogenetic reconstruction of

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[1] See glossary

62 the history of host-plant associations. Many phylogenetic studies still fail to clearly formulate
63 hypotheses and predictions about the speciation processes that underlie the observed patterns and
64 the role played by host-plant adaptation in those. The reason might be that the macroevolutionary
65 patterns that arise when **host-plant specialization*** is the driver of speciation events are not
66 always clear. There is no review on what to expect and how to formally test these predictions.

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

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

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

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

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

I Macroevolutionary scenarios of phytophagous insect diversification

91

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

93   More than 50 years ago, Ehrlich & Raven (1964) put forward a macroevolutionary

94   scenario that inspired most of the current research on plant-feeding insect diversification: it is

95   known as "***Escape and radiate***" (Thompson 1989). They hypothesized that when insects acquire

96   the ability to circumvent the chemical defenses of a plant group, it promotes their rapid

97   diversification by ecological release, *i.e.* the availability of novel resources and reduction in direct

98   competition. Insects undergo an **adaptive radiation***. In this scenario, adaptation towards host-

99   plants is the driving force of insect species formation. The "*Escape and radiate*" scenario also

100 hypothesizes that, in response to phytophagous insect predation, plants acquire novel chemical

101 defenses which allow them in turn to diversify very rapidly (Marquis et al. 2016). Ehrlich &

102 Raven' s seminal study suffers from several shortcomings that have been pinpointed before (Janz

103 2011). First, although the authors frame their theory within the concept of adaptive radiation, they

104 do not explicitly lay out any speciation mechanisms for the partners of the interaction. Following

105 their scenario, a trade-off in resource use and specialization towards specific host-plants is

106 necessary to explain the formation of numerous insect species (*i.e.,* species radiation) after the

107 capture of a new host-plant lineage. Such a trade-off is not mentioned in the original paper (Janz

108 2011). In addition, as underlined by contemporary researchers of Ehrlich and Raven's, it is

109 difficult to conceive how the selection pressures exerted by insects on plant defences can drive

110 plant speciation (Jermy 1976; Jermy 1984). Plant traits that reduce phytophagous insect attacks are

111 rarely linked with reproductive isolation between plant populations (but see Marquis et al. 2016;

112 Maron, Agrawal & Schemske, 2019 for a review of scenarios of herbivore-induced speciation in

113 plants) and the evidence for bursts of speciation in plants following the evolution of chemical

114 defence is scant (Futuyma, Agrawal 2009). However this study has been and remains a great

115 source of inspiration for studies on the diversification of plant-insect associations. This is probably

116 because it is one of the first studies that attempts to explain how microevolutionary processes

117 (host-plant adaptation) translate into macroevolutionary patterns (radiation onto newly acquired

118 plant lineages). Several predictions that can be tested on phylogenetic trees have been derived

119 from the *Escape & Radiate* scenario (Table 1).

120   In the years following its publication, *"Escape and radiate"* was often interpreted as

121 generating **cospeciation*** patterns; however it is now recognized that it rather predicts the

122 sequential speciation of insects onto an already diversified plant lineage (Janz 2011; Suchan,

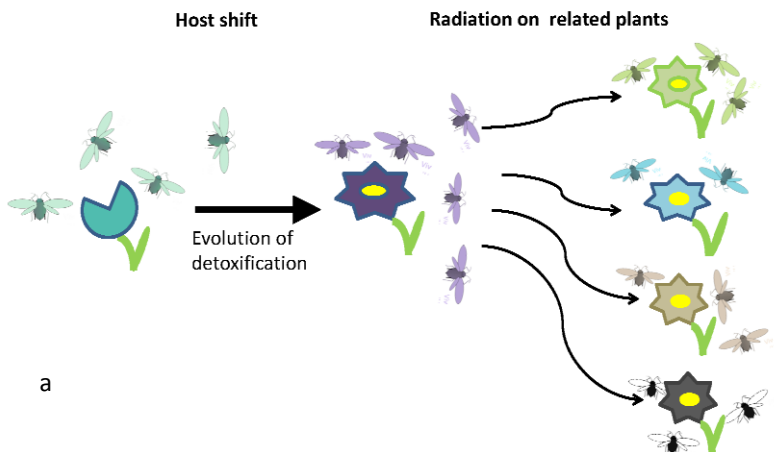
123 Alvarez 2015). According to this prediction: 1) the reconstruction of the history of host-plant

124 associations on the phylogenetic trees of insects should reveal **host-plant conservatism***, *i.e.* the

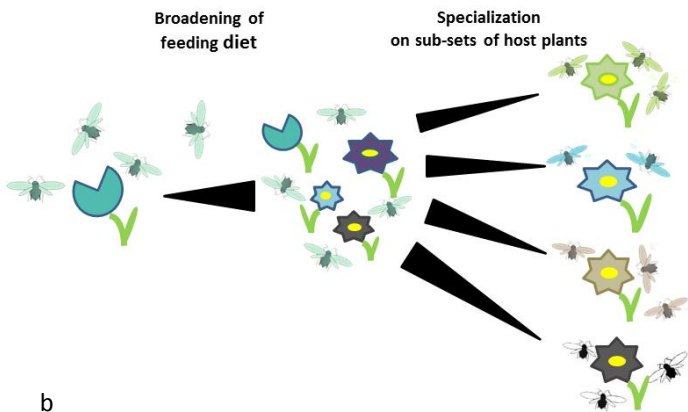
125 use of related plant species by related insects (Winkler, Mitter 2008); 2) the phylogenies of

126 herbivorous insects and their host-plants should be more congruent than expected by chance and

Escape and Radiate (Erlich & Raven 1964)

a

127

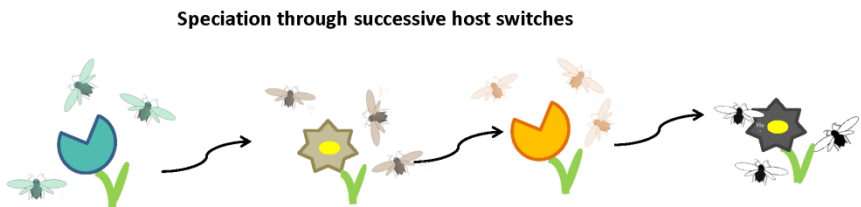
Oscillation hypothesis (Janz & Nylin 2008)

b

128

Musical chairs (Hardy & Otto 2014)

129

c

130

131   Figure 1: Schematic illustrations of the macroevolutionary scenarios of phytophagous insect
132   diversification.

133   the diversification of the insects should lag behind that of their host-plants; this is called sequential
134   evolution (Jermy 1984) or "*host tracking*". Nevertheless, when the association between insects
135   and their host plants is species-specific, a pattern of cospeciation can be expected through simple
136   co-vicariance: geographic barriers affect the differentiation of populations of interacting lineages
137   in a similar way and cause simultaneous speciation events (Althoff et al. 2012; Brookes et al.
138   2015; Martínez-Aquino 2016). In these cases, it is geographic isolation and not natural selection
139   that initiates the reproductive isolation of insect populations and subsequent speciation. However,
140   the specificity of the insects and host-adapted traits enhance the probability of shared vicariant
141   events.

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

149   **I.2) The *'Oscillation Hypothesis'* (Figure 1b)**

150   The "*Escape and radiate*" scenario was revisited more than a decade ago by Janz and
151   collaborators (Janz, Nylin, Wahlberg 2006; Janz, Nylin 2008; Nylin, Janz 2009). Using butterflies
152   as study systems, they stated that expansions in diet breadth followed by specialisation onto new
153   host-plant species constantly fuel the diversification of phytophagous insects. This has been
154   termed the '***Oscillation Hypothesis***' (Janz & Nylin 2008). It stipulates that transitions towards a
155   generalist diet generally open up a new adaptive zone, which favours the capture of new host-
156   plants. In this scenario, expansions in diet are enabled by the phenotypic plasticity of insects with
157   respect to host-plants (Nylin, Janz 2009). Population fragmentation and their specialisation onto
158   newly captured host-plants then lead to the formation of new species. Hence this scenario
159   explicitly predicts that species formation results from insect populations evolving towards the
160   utilization of a restricted set of host-plants. Nevertheless, it suggests that this specialization
161   process is often a consequence of the geographic isolation of generalist insect populations in areas
162   inhabited by different host-plant species (Janz, Nylin, Wahlberg 2006). Therefore the "*Oscillation
163   hypothesis*" does not necessarily postulate that natural selection is the main driving force of
164   species formation. However, subsequent papers quoting this scenario emphasize the central role of
165   host-plant specialisation (Hardy, Otto 2014; Nakadai 2017; Wang et al. 2017).

166   Most of the predictions from the *Escape and Radiate* scenario are valid under the

167   *Oscillation* hypothesis. However, the latter yields several new predictions (Table 1):

168   - **generalist*** diets should be "transient and repeatedly disappear in favour of specialization

169   onto a limited set of related plants" (Nylin, Slove, Janz 2014);

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

171   - the amplitude of the oscillation determines the number of potential host-plant species,

172   therefore, insect clades with the most diverse host-use (the highest number of host-plant species)

173   are expected to be more speciose than clades using fewer host species (Janz, Nylin, Wahlberg

174   2006) and insect clades that encompass species that exhibit large host breadths should have higher

175   speciation rates (Weingartner, Wahlberg, Nylin 2006; Hardy, Otto 2014);

176   - shifts from a generalist diet to a specialist one should be associated with an acceleration

177   of speciation rates; in other words, patterns of diversification should follow a model where

178   cladogenetic events are associated with host breadth reduction (Hardy, Otto 2014);

179   - generalists have larger geographic ranges as they are able to colonize more habitats and

180   can expand more easily (Slove, Janz 2011).

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

182   As opposed to the *Oscillation* hypothesis, Hardy and Otto (2014) proposed an alternative

183   scenario in which speciation in herbivorous insects is driven by host-switching rather than

184   transitions in diet breadth. The authors named their scenario *"**the Musical Chairs**"* (Hardy, Otto

185   2014). In this scenario, phytophagous insects speciate by the sequential capture of new host-plants

186   and therefore speciton in a plant-feeding insect lineage is merely driven by the number of plants it

187   can colonize. Host-driven speciation remains at the centre of this hypothesis.

188   The "*musical chairs*" hypothesis yields several predictions that differentiate it from the

189   previous macroevolutionary scenarios (Table 1):

190   - contrary to the *Escape* and *Radiate* hypothesis, the capture of a new host plant lineage

191   does not initiate a radiation;

192   - contrary to the *Oscillation hypothesis*, gains of new hosts are not associated with host

193   breath expansion (Hardy 2017), host breadth contraction is not associated with cladogenetic events

194   (Hardy, Otto 2014) and overall there should be a negative correlation between host-plant breadth

195   and speciation rates (Hardy, Otto 2014);

196   - speciation rates are higher in insect lineages that exhibit **lability*** in host-plant associations.

197   Table 1: Predictions from host-plant driven speciation scenarios: the first column indicates the evolutionary hypotheses tested and the headers
198   of the other columns indicate phylogenetic comparative approaches used for testing them.
199

Macroevolutionary scenarios	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 *et al.* 2010)	Predominance of specialists over generalists (Janz *et al.* 2001, Winkler & Mitter 2008)	- herbivorous insects are more diverse than their non-herbivorous relatives (Mitter *et al.* 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)
Escape and radiate	Phylogenetic 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 *et al.* 2007: Fordyce 2010)
Oscillation	Potentially phylogenetic tracking following the capture of a new host-plant lineage	Conservatism of host-plants following the capture of a new plant lineage.	- lability in host breadth (Janz *et al.* 2001, Janz & Nylin 2008) - gains of new host lineages are preceded by host breadth expansion (Janz *et al.* 2001) - positive correlation between diet breadth and geographic range (Slove & Janz 2011) - speciation events associated with shifts from generalist to specialist (Hardy, Otto 2014)	- clades including generalist species are more speciose than clades with only specialists (Weingartner, Wahlberg, Nylin 2006) - speciation rates higher in lineages with labile host breadth (Hardy, Otto 2014)
Musical chairs	No prediction	Less conservatism of host plant in more speciose lineages (Hardy, Otto 2014)	Host breadth is not labile (Hardy & Otto 2014; Hardy 2017)	- negative association between speciation rates and host breadth (Hardy, Otto 2014) - speciation rates positively correlate with host switching rates (Hardy, Otto 2014)

200   The lack of connection between host breath contraction and speciation events and the

201   negative association between host-breadth and speciation rates clearly differentiate the

202   *Musical chairs* from the *Oscillation hypothesis*. However, several authors have pointed out

203   that if generalist feeding diets are indeed ephemeral as expected when specialization towards

204   host-plants is adaptive, it will be difficult to reconstruct its history accurately on phylogenetic

205   trees (Hardy, Peterson, Normark 2016; Janz et al. 2016). Consequently, the relationships

206   between host breath and speciation rates will be difficult to explore and the set of predictions

207   that differentiate the *Musical chairs* from the *Oscillation hypothesis* will not always be

208   testable.

209   Phylogenetic comparative methods (Pennell, Harmon 2013) including increasingly

210   sophisticated diversification models (Rabosky 2006; Stadler 2013; Stadler, Bokma 2013;

211   Rabosky, Goldberg 2015; Beaulieu, O'Meara 2016; O'Meara, Beaulieu 2016) can now be

212   deployed to reconstruct ancestral character states, investigate the diversification dynamics of

213   insect lineages and test whether shifts in diversification rates are associated with transitions in

214   character states. Below we review how these methods have been used to investigate the

215   evolution of plant/insect associations and test the predictions of host-driven speciation

216   scenarios.

II Phylogenetic approaches for testing ecological speciation scenarios

II.1) Comparing the phylogenies of plants and insects

219   Several phylogenetic studies have compared the phylogenies of herbivorous insect and

220   their host-plants. Some have investigated cospeciation using dedicated tools such as tree

221   reconciliation analyses (Page 1994; Conow et al. 2010) and distance-based methods for tree

222   comparisons (Legendre, Desdevises, Bazin 2002). These tools statistically test the null

223   hypothesis that the phylogenies of insects and their associated plants are more congruent than

224   expected by chance and that speciation events are simultaneous. As stated above, this is only

225   expected in very specific plant/insect interactions. As predicted by early taxonomic studies

226   (Ramirez 1974; Wiebes 1979), cospeciation has been evidenced in figs and their

227   phytophagous pollinating wasps but the degree of phylogenetic congruency observed varies

228   according to taxonomic groups (see review by de Vienne et al. 2013 on cospeciation studies

229   and Cruaud et al. 2012). Reciprocal adaptations of plants and insects (*i.e,* **coevolution***) have

230   been unravelled in this study system (Jousselin, Rasplus, Kjellberg 2003; Weiblen 2004).

231   However, it is not known whether the cospeciation patterns observed are the sole result of this

232   coevolution, i.e. whether reciprocal selection exerted by both partners has driven the

233   reproductive isolation of interacting populations (Althoff, Segraves, Johnson 2014; Hembry,

234   Yoder, Goodman 2014) or whether matching speciation events have arisen through co-

235   vicariance. In the other iconic model system for the study of plant/insect **coevolutionary**

236   **diversification***, the *Yucca*–Yucca moth interaction (Pellmyr 2003), moth phylogenies

237   parallel parts of the evolutionary history of their hosts. Some studies suggest that this pattern

238   is the result of coevolution (Godsoe et al. 2009) while others hint towards co-vicariance

239   (Althoff et al. 2012). In both *Yucca*-moths and fig wasps the fact that the phytophagous

240   insects are specific pollinators of their host-plants and breed inside them necessarily links the

241   reproductive success of the two partners and increases the likelihood of concomitant

242   speciation events. Therefore host-plant adapted traits are certainly pivotal in the speciation

243   process of these insects.

244   Studies that have investigated **phylogenetic tracking*** between phytophagous insects

245   and their host-plants have shown that insects rarely mimic their host-plant phylogenies (see

246   reviews by Winkler, Mitter 2008; de Vienne et al. 2013 and Hsu et al. 2018 for an example of

247   a recent study); a third of the 20 studies reported in these studies found partial patterns of

248   congruence between insects and host plant phylogenies. In many plant/insect interactions, a

249   simple observation of the patterns of distribution of host plants in the insect phylogeny can

250   actually rule out cospeciation or phylogenetic tracking and studies on plant-insect interactions

251   have moved away from cospeciation studies.

252   In order to test for successive burst of diversification in plants and insects, many

253   authors have thus simply compared the timing of divergence of plants and associated insects

254   (*e. g*., Brandle et al. 2005; Lopez-Vaamonde et al. 2006; Gómez-Zurita et al. 2007; Pena,

255   Wahlberg 2008; McKenna et al. 2009; Stone et al. 2009; Kergoat et al. 2011; Leppanen et al.

256   2012; Segar et al. 2012; McLeish, Miller, Mound 2013; Wahlberg, Wheat, Pena 2013;

257   Kergoat et al. 2015; Vea, Grimaldi 2016; Winter et al. 2017). Most of these studies suggest

258   delayed colonization of already diversified groups of plants by insects groups at different

259   temporal scales. They are generally based on mere qualitative comparisons of dates of

260   divergence obtained from fossil calibrated phylogenies of both plants and associated insects,

261   but can also include thorough statistical comparisons of dates obtained through phylogenetic

262   methods (Loss-Oliveira, Aguiar, Schrago 2012; McLeish, Miller, Mound 2013). They are

263   often framed as supporting the *Escape and radiate* theory. However these studies do not give

264   any information on the speciation process behind the diversification of the insect lineages

265   studied, they merely indicate the timing of host plant colonization. The comparison of the

266   **diversification dynamics**[*] of both herbivorous insects and their host-plants provide a more

267   direct test of host-driven speciation hypotheses: under host-driven adaptive radiation, insect

268   diversification dynamic is expected to roughly follow the diversification of its host-plant

269   lineage. This can be investigated through diversification analyses (see II. 3.2) but can also

270   include the comparison of the fossil records of both insects and plants (Labandeira et al. 1994;

271   Labandeira, Currano 2013). In general, the studies of fossil assemblage are decoupled from

272   phylogenetic studies of plant/insect associations. We advocate for combining fossil and

273   phylogenetic evidence whenever possible.

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

275   <u>II.2.1) Evolution of host associations</u>

276   Phylogenetic inferences are widely used to reconstruct the evolutionary trajectories of

277   phenotypic traits throughout the diversification of a lineage. Most phylogenetic studies of

278   phytophagous insects map the history of host association onto the resulting trees –at different

279   taxonomic levels (host plant order, family, genus depending on the level of host specialization

280   of the insect clade studied and multistate characters are used when species are polyphagous).

281   These reconstructions generally suggest a pattern of **host conservatism***. This assertion stems

282   from mere observations of the reconstructions but numerous studies conduct statistical tests.

283   These include the permutation tail probability test (PTP, Faith, Cranston 1991) or some index

284   of phylogenetic signal such as Pagel' lambda (1999) (see Winkler, Mitter 2008 for a review

285   on host plant conservatism patterns and Leppanen et al. 2012; Wilson et al. 2012, Hernández-

286   Vera et al. 2019 for more recent examples).

287   Host conservatism is often interpreted as following the predictions of "*Escape and*

288   *Radiate"* and therefore evidence that speciation was promoted by host-plant specialization.

289   However, showing that related insects feed on related plants does not say much about the

290   process that has generated this pattern nor connects mechanistically host-plant use evolution

291   to speciation. The use of vague wording such as host-associations *favour* or *constrain*

292   speciation is commonly found when discussing host-conservatism in the literature and it is

293   difficult to conclude from these studies that specialization towards one or a few plants species

294   is the main pathway towards the formation of new phytophagous insect species. The pattern

295   of "*host conservatism*" is in agreement with a scenario in which insects have radiated onto a

296   plant lineage but it could also suggest that host-plant shifts are not important promoters of

297   speciation events.

298   A more direct estimation of the contribution of host-plant adaptation in the speciation

299   process consists in inferring the frequency of host-plant shifts in relation to speciation events.

300   If adaptation to different ranges of host-plants drives reproductive isolation and speciation, it

301   follows that insect **sister species*** should partition host-plant resources: i.e. they should show

302   no or little overlap in the plant species they use.

303   To test this hypothesis, early studies have conducted sister species comparisons of host

304   ranges and more recent studies have reconstructed the evolution of insect ecological niches

305   (defined as the combination of feeding habits and host-plant species or families) and

306   estimated the number of niche shifts associated with speciation events (Table 2.1).

307   Comparisons of alternative models of evolution of host-use have also been conducted. All

308   studies but one showed that the numbers of niche shifts observed generally represented less

309   than 50% of the speciation events and were generally lower than expected if the niches were

310   randomized onto the phylogeny. This suggests that ecological speciation is not the main

311   process behind the diversification of these lineages. Authors have also observed that host-use

312   differentiation occurred at the root of the trees and therefore concluded that it played a minor

313   role in recent speciation events (Table 2.1).

314   We must keep in mind that these methods may overlook many host shifts (shifts that

315   resulted in population extinction). Therefore, the studies that estimated niche differentiation at

316   speciation events probably present an overestimation of the impact of host shifts in speciation.

317   It is nevertheless surprising that such studies have not been conducted on more study systems.

318   This is likely due to the fact that they require a precise knowledge of the range of host-plants

319   used by each insect species.

320   <u>II.2.2) Host-breadth evolution</u>

321   In order to investigate the role of specialization in insect species formation,

322   phylogenetic studies have also investigated the distribution of host breadth throughout the

323   evolutionary history of insects groups.

324   According to the "*Oscillation hypothesis*", host breadth should vary along the

325   phylogeny of insects and the character state "generalist" should be transient; i.e. phylogenetic

326   reconstructions should show many transitions between specialists and generalists. Many

327   studies have indeed demonstrated the lability of host breadths (Table 2.2), which is

328   compatible with the *Oscillation* hypothesis but does not prove it.

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 synthetized 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	*Aphanartum* (25 spp.)	Jordal & M Hewitt 2004	Sister species comparison of host ranges	Ø	
	Nematinae (125 spp.)	Nyman *et al.* 2010	Investigate niche shifts at speciation nodes through ancestral state reconstruction	Ø	Geographic isolation is more important than host switching in speciation events
	Blepharoneura (49 spp.)	Winkler *et al.* 2018		Ø	
	Cinara (76 spp.)	Jousselin *et al.* 2013		Ø	
	Caloptilia (13 spp.)	Nakadai & Kawakita 2016	Niche dissimilarity index through time	Ø	
	Neodiprion (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	*Dendroctonus* (19 spp.)	Kelley & Farrell 1998	Phylogenetic signal of host breadth	√	Repeated broadening of host breadth
	Lymantrinae (55 genera)	Wang *et al.* 2017	Phylogenetic signal of host breadth and transition rates estimation	√	**Oscillation**
	Nymphalidae (551 spp.)	Nylin *et al.* 2014	Phylogenetic signal of host breadth and transition rates estimation	√	
	Nymphalini (31 spp.)	Janz *et al.* 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
	Boloria (37 spp.)	Simonsen *et al.* 2010	Visualization of reconstruction of host breadth	√	Repeated broadening of host breadth, **oscillation**
	Nymphalidae	Hamm & Fordyce 2016	Phylogenetic signal of host breadth	Ø	**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)	Ø	**Musical chairs**
	Nymphalini (31 spp.)	Janz *et al.* 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	Ø	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

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	Blepharidae (37 spp.)	Becerra 2003	Comparison of timing of acquisition of plant defenses and insect counter-defenses	√	Coevolutionary arm race
	Lygaeinae (20 spp.)	Bramer *et al.* 2015	Reconstruction of the ability to resist or sequester cardenolides	√	Adaptation of insects to host plant defenses
	Heliconius	de Castro *et al.* 2018	Review on correlated evolution of anti-herbivory adaptations in plants and counter-adaptations in *Heliconius*	√	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 *et al.* 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 *et al.* 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 *et al.* 1988	Sister groups comparison of phytophagous vs non phytophagous clades	√	Phytophagy promotes diversification
	1900 spp	Hunt *et al.* 2007	Sister groups comparison of phytophagous vs non phytophagousclades and estimation of diversification rates	Ø	Various types of niche shifts explain beetles diversification
	Erolytidae, 53 taxa	Leschen & Buckley 2007	Correlated evolution between species richness and phytophagy	Ø	
	367 spp, 172 families	McKenna *et al.* 2015	Infer shifts in diversification rates (MEDUSA)	√ & Ø	Some shifts associated with phytophagy others not
	31 insect orders	Wiens *et al.* 2015	Phylogenetic regression	√ & Ø	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**
	Adelpha (38 spp.)	Mullen *et al.* 2011	Test for shifts in diversification rates across the phylogeny (SymmeTREE)	√	One rate shift attributed to hots shift but also other ecological factors
	Adelpha & *Limenitis* (200 spp.)	Ebel *et al.* 2015	Test for shifts in diversification rates across the phylogeny (BAMM)		Shift to Rubiacea 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)	√ & Ø	Shift to Solanacea spurred diversification
	Hesperidae (290 genera)	Sahoo *et al.* 2017	Detection of shifts in diversification rates (LASER), BAMM, BiSSE (trait= feeding on monocotyledonss vs dicotyledons) & HiSSE	√	Several diversification shifts however could be associated with grassland expansion and geographic factors

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	Symphita (164 spp.)	Nyman *et al.* 2019	Detection of shifts in diversification rates MEDUSA, BAMM, MuSSE (traits =feeding on angiosperms, gymnosperms, pteridophytes)	√ & Ø	No significant shifts associated with feeding on angiosperm, discuss confounding factors
7) Acquisition of detoxification mechanisms spur diversification in insects, new defenses spur diversification in plant	Pierinae (60 spp.)	Wheat *et al.* 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 *et al.* 2015	Distribution of of a defense mechanism and estimation of shifts in diversification rates in plants and insects (MEDUSA)	√	Complex coevolutionary arm race involving gene duplication in plants and associated with shift in diversification
	Asclepias	Agrawal *et al.* 2009	Comparison of various model of evolution for plant defences including a speciational model	√	Plant defenses are costly and can hinder diversification
8) Adaptive radiation pattern	*Erebia* (74 spp.)	Pena *et al.* 2015	Test for shifts in diversification rates (BAMM & DDD)	√ & Ø	Density dependant model fits the data, diversification shifts not always significant depending on methods : acceleration of diversification associated to colonization of new area
	Cinara (92 spp.)	Meseguer *et al.* 2015	Test for shifts in diversification rates (TreePar)	Ø	Constant rate of diversification, no adaptive radiation
	Blepharoneura (49 spp.)	Winkler *et al.* 2018	Test for shifts in diversification (LASER, DDD)	Ø	Constant rate of diversification, no adaptive radiation, diversification patterns mostly explained by geographical factors
	Sesamiina (241 spp.)	Kergoat *et al.* 2018	Test for shifts in diversification through different methods (BAMM, *SSE)	Ø	Inverse patterns of diversification in insects and associated plants ; host plant diversity alone does not explain insect diversification
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 *et al.* 2006	Sister clade comparisons	√	**Oscillation hypothesis**
	Lymantrinae (55 genera)	Wang *et al.* 2017	Phylogenetic regression	√	
	Coccidae (158 genera)	Lin *et al.* 2015	Regression without phylogenetic correction	√	Host- driven speciation
	Cecidomyiid (352 genera)	Joy & Crespi 2012		√	

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10) Clades including generalists speciate faster than clades with only specialists; diversification rates are positively correlated with host breadth		*Nymphalis* & *Polygonia* (20 spp.)	Weingartner *et al.* 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)	Ø	**No oscillation, Musical chairs**
		Nymphalidae	Hamm & Fordyce 2015 Hamm & Fordyce 2016		Ø	Host breadth dynamics does not drive diversification
		Coccidea	Hardy *et al.* 2016	⎭	√	Specialization by drift
		Nymphalini (172 spp.)	Hardy 2017	Phylogenetic independant contrasts (proportion of generalists vs number of species in a genus)	Ø	**No oscillation**
		Sesamiina (241 spp.)	Kergoat *et al.* 2018	Evaluate whether shifts in diversification rates follow shifts in host breadth (BAMM and others)	Ø	**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, Ø prediction not verified

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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335

336   In order to test whether these changes are linked with speciation, some studies have
337   investigated how gains and losses of new hosts along the phylogenetic history of lineage
338   relate to the number of speciation events (Table 2.3).

339   Maybe another way to investigate the link between 'host-breadth changes' and 'gains
340   of new hosts' without using diversification analyses would be to test for the correlated
341   evolution of these two characters; i.e. explore how often the gain of new hosts is associated
342   with a transition from specialist to generalist.

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

344   Several studies that aimed at finding support for the coevolutionary arm race
345   hypothesized by the *Escape and Radiate* scenario have investigated the evolution of
346   detoxification mechanisms in insect lineages and have shown that they correlate with changes
347   in their host plant defences (Table 2.4). Studies that show that host switches occurred between
348   plants with similar defenses, rather than closely related plants generally conclude to
349   coevolutionary arm race between insects and associated plants. However some of these
350   studies argue in favour of a scenario in which herbivores simply "choose" host-plants based
351   on their own defensive traits. Host switches underlie insect species differentiation but this
352   differentiation is not the product of coevolutionary interactions.

353   Reconstructions of the history of plant defences were also conducted on plant
354   phylogenies. However direct tests of acceleration of diversification upon the acquisition of
355   new defence mechanisms sometimes contradict the '*Escape and Radiate*'' prediction and
356   suggests that investment in costly defences can impede plant diversification (Table 2.4).

357   In contrast to detoxification mechanisms, traits involved in host recognition and host-
358   plant choice (chemosensory traits) have been less studied in a phylogenetic context. However
359   their evolution probably plays as important a role as adaptations to plant defences in
360   phytophagous insect speciation (Smadja, Butlin 2009). Matsuo (2008) showed that an odour
361   binding protein can evolve relatively fast in closely related *Drosophila* species through gene
362   duplications and losses, and proposed that this dynamic could explain the evolution of host
363   preferences in this species complex. Comparative analyses of odour binding proteins and
364   chemosensory proteins from the genomes of several Arthropoda species (Sánchez-Gracia,
365   Vieira, Rozas 2009; Vieira, Rozas 2011) revealed a high number of gains and losses of genes,
366   pseudogenes, and independent origins of gene subfamilies. This dynamic, if analysed in
367   relation to host choices and host breadth in a phylogenetic context, could explain some host
368   shifts and subsequent speciation events. Finally, deciphering the evolutionary dynamics of

369   genes involved in mate recognition and their link with host association could also inform us

370   on the role of host-plants in the speciation of insects that feed (and often mate) on them. For

371   instance, Schwander et al. (2013) showed that cuticular hydrocarbon profiles involved in mate

372   choices vary among *Timema* species (Phasmatodea), and that most evolutionary changes in

373   hydrocarbon profiles occur in association with host-plant shifts and speciation events in this

374   genus of phytophagous insects.

375   In summary, many studies have investigated the evolution of detoxification

376   mechanisms in insects, framing their hypotheses within the ***Escape and Radiate*** theory.

377   Studies investigating changes in traits involved in host recognition throughout the

378   diversification of insects are rare and they are generally not framed within host-plant driven

379   scenarios. Such studies are needed in order to determine which traits underlie host-plant

380   associations and whether their evolution drives speciation events (see Perspectives).

381   **II. 3) Studying how host-plant uses impact the diversification dynamics of herbivorous**

382   **insects**

383   Methods for testing diversification dynamics have expanded over the last decade.

384   Testing for the existence of temporal bursts of diversification was once restricted to analyses

385   of groups with comprehensive fossil records. Diversification dynamics can now be studied

386   through comprehensive phylogenies (Goswami, Mannion, Benton 2016). Given the breadth of

387   available methods, theoretically, nearly all hypotheses can be put to test.

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

389   Studies that posit that host-plant adaptation favours phytophagous insect

390   diversification predict that those are much more diversified than non-phytophagous insects.

391   However this assertion deserves to be statistically tested. The first study addressing this

392   question suggested that herbivorous clades contain more species than their non-phytophagous

393   sister clades (Table 2.5). However, comprehensive phylogenies associated with recent

394   comparative methods suggest that several types of niche shifts beside phytophagy can explain

395   insect species richness. Studies within insect orders have mostly been addresses within

396   Coleoptera –as they are by far the most diverse order, but more in-depth analyses of other

397   orders would also be insightful.

398   To our knowledge likelihood-based character state dependent diversification models

399   (known as, the *SSE models, such as BiSSE, ClaSSE and QuaSSE for binary, multistate and

400   quantitative traits, respectively Maddison, Midford, Otto 2007; FitzJohn 2010; Maddison,

401   FitzJohn 2015), which test whether transition in character states are associated with variations

402   in speciation and extinction rates, have not been yet used to test the role of phytophagy in
403   insect diversification. A robust estimate of diversification parameters by these methods
404   requires dense and random species sampling throughout the phylogeny (more than 15% of the
405   species must be included in the phylogeny in order to conduct unbiased tests; FitzJohn 2010).
406   Therefore *SSE tests await the availability of comprehensive phylogenies in more insect
407   orders. Nevertheless, a caveat of these diversification models is that they may overlook more
408   complex models involving many unmeasured and co-distributed traits. In particular, for
409   phytophagy, other traits that can drive shifts in diversification may cause a spurious detection
410   of increased diversification rates in phytophagous insects if these trait's states partly correlate
411   with phytophagy, or may instead erase any signal due to phytophagy. The HiSSE model
412   (Beaulieu, O'Meara 2016) which models hidden characters that influence diversification
413   might help untangling these confounding factors.

414   <u>II.3.2) Testing for adaptive radiation</u>

415   Diversification analyses can also be applied to test whether the capture of new host-
416   plants has favoured adaptive radiations. Under such a scenario, the diversification curve of
417   phytophagous insect clades should exhibit early bursts of speciation upon the capture of new
418   groups of host-plants. Insect lineages are eventually expected to fill the newly found niche
419   space and the diversification curves should reach a plateau.

420   Several studies have investigated acceleration in speciation rates in insect lineages
421   upon the capture of new host-plant lineages (Table 2.6) or detoxification mechanism (Table
422   2.7). These studies have mainly been conducted in butterflies. Studies have rarely included
423   trait-dependent diversification models and when they did, they often relied on a few
424   colonization events that were also correlated with important geographical changes, making it
425   difficult to conclude on the causal effect of the sole host shifts (Table 2.6).

426   Among studies testing adaptive radiation patterns (Table 2.8), few have investigated
427   whether the number of species reached a plateau after an initial burst of speciation. This is
428   better addressed using density-dependent models of diversification (DDD) that test whether
429   rates of speciation decrease once the number of species supposedly reach the carrying
430   capacity of the novel ecological niche (Rabosky, Lovette 2008; Etienne et al. 2012). But these
431   tests can only be applied to lineages in which the number of species in each subclade is well
432   known. In any case, studies generally provided weak support for adaptive radiation scenarios
433   (Table 2.8). They all suggested that diversification patterns cannot solely be explained by the

434   availability of suitable host-plants and suggested that abiotic factors such as geography and

435   temperature should be taken into account in diversification scenarios.

436   II.3.3) Correlating host breadth with diversification dynamic

437   Advocates of the *Oscillation hypothesis* suggest that clades showing a higher diversity

438   of host-use (using more host-plant species altogether) should be more diverse than their sister

439   clade (Janz, Nylin, Wahlberg 2006), and this prediction has been verified in butterflies,

440   Coccidae and some gall inducing flies (Table 2.9).

441   Although these results support a model where the diversity of phytophagous insects is

442   sustained by the diversity of the hosts they use; they could fit both a model of *Oscillation* and

443   the *Musical chairs* hypothesis. To tell apart the *Oscillation* from the *Musical chairs*, it is more

444   informative to test how host breadth variations affect insect diversification dynamics.

445   According to the *Oscillation* hypothesis, clades including generalist species should be more

446   speciose than clades including only specialists. Early papers have used fairly basic methods

447   such as 'sister clade analyses" to test this prediction while more recent investigations have

448   adopted trait-dependant diversification models (Table 2.10). These studies provided mixed

449   support for *Oscillation* scenarios. Furthermore, even when a specific prediction was met, the

450   authors could not always reach a firm conclusion: as previously mentioned, the transient

451   nature of the generalist feeding diet under host-driven speciation scenarios complicates

452   predictions. The negative or positive relationship observed between host breadth dynamics

453   and diversification can always be obscured by the rapid evolution of host breadth (Nylin, Janz

454   2009; Janz et al. 2016). The way host breadth is measured (binary vs continuous) is also

455   known to affect the results (Hamm, Fordyce 2015) and it has been long recognized that

456   categorizing species into either specialist or generalist can be somewhat subjective (Janz,

457   Nyblom, Nylin 2001). Furthermore, although the musical chair yields specific predictions,

458   those are mainly rebuttals of the "*Oscillation*" predictions (but see Table 2.11). Yet, rejecting

459   an "*Oscillation*" scenario does not instantly mean that a "*Musical chairs*" scenario is at play.

460   Hence despite the existence of sophisticated methods and comprehensive phylogenies, the

461   prevalence of these scenarios in insects is still debated.

462   Another caveat of these studies lies in the distinction between speciation and

463   extinction rates. Indeed, if specialization towards host plants can accelerate speciation it can

464   also increase extinction risks when host plants are not highly abundant. Consequently,

465   predicting exactly how changes in host-plant breadth affect diversification rates is difficult.

466   Finally diversification methods such as *SSE models are known to generate false positives

467   (Davis, Midford, Maddison 2013; Bouchenak-Khelladi et al. 2015; Rabosky, Goldberg 2015),

468   and can thus inflate the role of host plants and host breadth in diversification when those are

469   investigated. It is therefore, highly recommended to conduct the analyses on a set of

470   randomized trees in order to test whether the constrained diversification model (i.e. the model

471   in which evolutionary transitions in character states are associated with shifts in extinction

472   and/or speciation rates) is also chosen in these analyses (as in Hardy, Peterson, Normark

473   2016).

474   Moving away from methodological issues, our survey also underlines that many

475   studies that explore macroevolutionary scenarios have been conducted on Lepidoptera. In

476   order to have a better understanding the role of host-plant shifts in insect diversification, it

477   seems necessary to test the predictions of macroevolutionary scenarios on more insect groups.

478   Aphids (Hemiptera) could be good candidates for such investigation. Their range of host-

479   plants is well documented (Blackman, Eastop 2006; Holman 2009). Although most aphids are

480   host-specific, some species are polyphagous. Some species are even only polyphagous during

481   part of their life-cycle. This temporary broadening of diet has already been suggested to

482   facilitate the capture of new host-plants (Moran 1992) and subsequent speciation onto these

483   new lineages. These life-cycle transitions could have thus favoured aphid diversification

484   (Moran 1992; Jousselin, Genson, Coeur d'Acier 2010). This scenario actually fits the

485   *Oscillation hypothesis* and should be investigated. Other Hemiptera which host plant

486   repertoire is well known such as Coccidae (Garcia-Morales et al. 2016) and psyllids (Ouvrard

487   et al. 2015) could also be used to test the predictions on the role of host breadth evolution in

488   macroevolutionary scenarios. The limitation for these groups for now lies in the availability of

489   robust and comprehensive phylogenies.

III Perspectives

491   As seen throughout this review, phylogenetic comparative methods provide the

492   template to test hypotheses on the role of host plant association in the speciation of

493   phytophagous insects. While those methods have undoubtedly advanced the field significantly

494   since "the *Escape and Radiate*" paper, one must keep in mind that phylogenetic comparative

495   methods often constitute mere correlations. Significant associations between character

496   changes and cladogenetic events might arise as a consequence of speciation itself when post-

497   speciational character changes occur. Furthermore, comparisons of models of evolution such

498   as those used in trait-dependent diversification analyses often rely on trees that encompass

499   few transitions in character states and are therefore not always robust (see Beaulieu,

500   Donoghue 2013). In such analyses, the "best model" is not necessarily the true model and
501   significant *P* values should not be interpreted as strong evidence for an evolutionary scenario.
502   Finally, all these methods are sensitive to sampling biases and those need to be carefully taken
503   into consideration.

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

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

513   Geography and ecology are always closely intertwined in speciation scenarios. There have
514   been several studies that have investigated geographic range expansion in herbivorous insects
515   (Becerra, Venable 1999; Slove, Janz 2011); climate induced host shifts (see Winkler, Mitter,
516   Scheffer 2009; Nyman et al. 2012 for reviews and recent studies since then Sanchez-Guillen
517   et al. 2016; Lisa De-Silva et al. 2017; Owen et al. 2017; Pitteloud et al. 2017; Sahoo et al.
518   2017) and climate driven diversification dynamics (Kergoat et al. 2018, Letsch et al. 2018).
519   All these studies suggest that abiotic factors are entangled with host-plants changes in species
520   diversification scenarios. However there are few studies that explicitly test the predictions of
521   speciation through geographic isolation (Barraclough, Vogler 2000) and whether these events
522   systematically accompany host shifts or sustain most speciation events (but see Jordal &
523   Hewitt 2004; Jousselin et al. 2013; Doorenweerd, van Nieukerken, Menken 2015; Hardy,
524   Peterson, Normark 2016). Such analyses are important if we want to tell whether adaptations
525   to new host plants represent post-speciational changes following geographic isolation rather
526   than the main driver of speciation events. Cospeciation methods that take into account the
527   biogeographic history of interacting lineages (Berry et al. 2018) could also be used to
528   investigate whether host shifts are associated with dispersal events in systems where host
529   plant and insect phylogenies show congruent patterns.

III.2) Unravelling traits involved in the interaction and their underlying genes, and integrating this information in phylogenetic studies

532   Interactions between insects and their host-plant are ultimately mediated by traits, such
533   as host-plant defences and the capacity of circumventing plants defences, but also host-plant
534   cues and the capacity for herbivores to detect those cues. Characterizing such traits, their
535   genetic determinism and looking at their evolutionary trajectory would greatly advance our
536   understanding of the diversification of insects (*e. g.*, de Castro et al. 2018). Testing whether
537   different trait states are associated with different speciation rates can be performed using
538   *SSE methods (*e. g.*, as in Onstein et al. 2017 for a trait related to frugivory in palm trees). In
539   addition, methods that test whether patterns of trait evolution conform to a model accounting
540   for interactions mediated by those traits are currently being developed (Manceau, Lambert,
541   Morlon 2016; Drury et al. 2017), and they could inform on the processes underlying herbivore
542   diversification. However, targeting traits involved in plant-insect interactions may be
543   challenging. Pivotal traits are difficult to identify, they include chemical, behavioral and
544   metabolic traits and when they are properly characterized they are often multigenic.

545   Perhaps a promising direction for future research is the implementation of a hybrid
546   genomic approach that combines transcriptomics, phylogenomics, comparative analyses and
547   population genomics (see Nevado et al. 2016). In such approaches, full transcriptomes of
548   species from a target clade (for instance, a clade of phytophagous insect) are generated. These
549   transcriptomes are used to generate a phylogeny, where diversification and character
550   evolution tests can be performed (*i.e.* test for diversity-dependent diversification, shifts in
551   diversification following host-plant shift). Then, genes under selection can be detected from
552   transcriptomic data using population genetics statistics, and can be matched to existing
553   databases (e. g., Lepbase for Lepidoptera, Challis *et al.* 2016) for identification purpose.
554   Additionally, genes that are down or upregulated can also been detected by classical tests of
555   differential expression and identified, and the association of genes under selection, either via
556   different sequence or expression pattern, with species diversity can be tested. One of the
557   limits of this approach lies in the availability of specimens (transcriptomic data need to be
558   obtained from fresh or suitably preserved tissues; biological replicates are needed), those
559   might be difficult to obtain throughout an entire phylogenetic tree. The availability and
560   quality of the reference gene database to match genes with putative functions might also limit
561   the applications of this approach.

562

563   **III.3) Combining phylogenetic with interaction network approaches, at various**
564   **ecological scales**

565   Herbivores and the plants they feed on form interaction networks, and as such the
566   structures of the networks can be characterized by several parameters, such as modularity (the
567   propensity of a group of species to interact with a similar set of partners) and nestedness (the
568   propensity of specialist species to interact with generalist species and vice-versa).
569   Antagonistic interaction networks, such as plant-herbivore networks, tend to be highly
570   modular (Thébault, Fontaine 2010). A recent study combining interaction network with
571   phylogenetic approaches on simulated and real datasets predicted that the *Escape and radiate*
572   scenario should produce a modular network structure, whereas the *Oscillations* scenario
573   should produce a more nested structure (Braga et al. 2018). When applied to real data (two
574   butterfly families, Nymphalidae and Pieridae), this approach revealed that host-plant butterfly
575   networks tend to be both modular and nested, which the authors interpret as being the result of
576   a complex pattern of diversification, involving both episodes of radiation on new hosts
577   (producing modules containing closely related species) and occasional shifts to other host
578   lineages, producing both nestedness within modules and connections between modules.
579   Additionally, phylogenetic and network approaches could be expanded to encompass other
580   interacting partners (*e. g.,* Ives, Godfray 2006; Elias, Fontaine, van Veen 2013). Indeed,
581   insect-host-plant communities can be seen as ecosystems where biotic interactions, such as
582   parasitism and mutualism also take place (Forister et al. 2012). These partners can indirectly
583   influence the interaction between plants and their herbivores: *e.g*., direct competition (Jermy
584   1988) apparent competition between herbivores, stemming from shared natural enemies (Holt
585   1977), and vice-versa (*e. g.,* when herbivory elicits anti-herbivore defences mediated by
586   herbivore enemies, Fatouros et al. 2008). Multitrophic interactions probably explain many
587   diversification patterns in herbivorous insects (Singer, Stireman 2005)
588   Finally, such approaches could be applied both at a large scale (*e. g*., Braga et al.
589   2018), to embrace global patterns of diversification and interaction, or at the community level
590   (Ives, Godfray 2006; Elias, Fontaine, van Veen 2013), where interactions actually occur, and
591   where fine-scale processes (*e. g*., host-plant shift at the species or the population level) can be
592   unveiled.

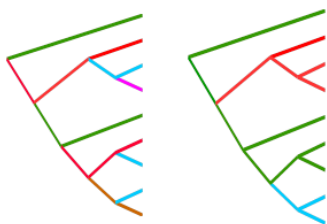
Conclusions

594   Many phylogenetic studies of plant-insect associations now include formal tests of
595   macroevolutionary scenarios involving host-driven speciation. In an attempt to summarize the
596   literature on this topic, we show that the predictions of host-plant driven speciation are not
597   straightforward and can vary depending on studies. We advocate a standardization of these

predictions to facilitate cross study analyses. Furthermore, it is also recognized that different scenarios can leave the same phylogenetic signature (Janz *et al.* 2016) and that depending on the analytical approaches undertaken to test the predictions laid out in Table 1, conclusions can vary (Table 2). Unfortunately this means that the interpretations of phylogenetic inferences can remain somewhat subjective. But these shortcomings should not cloud the progresses that have been made in the field. Phylogenetic comparative analyses help framing hypotheses and clarify some of the narratives for the diversification of phytophagous insects. In order to move towards a standardization of phylogenetic approaches, we propose here a list (non-exhaustive) of relatively simple tests that could be applied to an insect phylogeny that includes robust data on host plant association to test some of the non-controversial predictions of host-driven speciation scenarios (Fig. 2). The limitations of these approaches (sampling biases, false positives) have been described throughout this review.

Finally, this survey of the literature shows that: 1) the simple assumption that phytophagy has accelerated insect diversification is not always sustained by meta-analyses; 2) the expectation that sister lineage will use different ranges of host plants is not often tested, and, when it is, the predictions of a host-driven speciation scenarios are not always met. We then underline that the results of phylogenetic comparative methods cannot be interpreted as hard evidence as they remain mere correlations. In the end, a full understanding of the processes explaining the diversification of phytophagous insects will require the integration of phylogenies with other data sources and analytical methods.

To conclude, if the last two decades have seen the rise of molecular phylogenies and the development of analytical methods that include ecological data, this should not mask the need for thorough curation of the data used before applying any phylogenetic comparative analyses. Qualifying host associations of insect species necessitates field work and advanced taxonomy, as mistakes can seriously impact the results of macroevolutionary studies. Functional studies aimed at deciphering host-plant adapted traits in insects (and in particular traits implied in host choice) and characterizing genes that underlie these traits are also needed to integrate this data in a phylogenetic context and link microevolutionary processes with macroevolutionary scenarios.

a) Host-plant range history

Range 1
Range 2
Range 3
Range 4

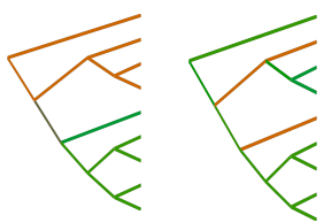
H1: Speciation driven by host shifts

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 ≈ 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.

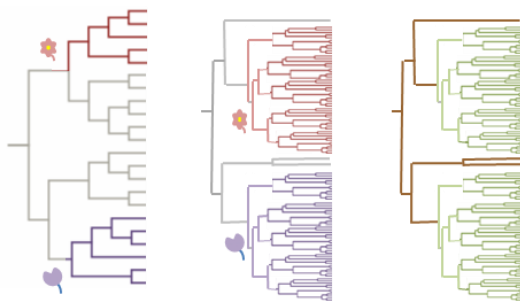
b) Host breadth history

specialist
generalist

H1: No oscillation   H2: Oscillation

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

Under H1 : host breadth exhibits a phylogenetic signal.

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

c) Diversification analyses

Range 1
Range 2
Range 3

specialist
generalist

H1: No adaptive radiation

H2: Adaptive radiation driven by host shifts (Escape and radiate)

H3: Adaptive radiation driven by shifts in diet breath (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 rates.

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 rates increase following shift away from polyphagy.

627

628   Figure 2: Suggestions of phylogenetic comparative methods that can be deployed to test some of the prediction of host-driven speciation scenarios: a) tests that rely on the reconstruction of
629   host-plant range evolution; b) tests that rely on the reconstruction of host-breadth; c) diversification analyses that rely on reconstruction of both these characters. H1, H2, H3 are alternative
630   scenarios and are each time represented by a schematic phylogenetic reconstruction.

Glossary:

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

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

Coevolutionary diversification: when diversification patterns arise from coevolution.

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

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

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

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

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

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

Phylogenetic conservatism: tendency for closely related species to be more similar than expected under Brownian motion evolution.

Phylogenetic tracking: it occurs when a host-dependent species (here a phytophagous insect) diversifies and utilizes niches created by the speciation its hosts (here host-plants), this leads to parallel phylogenetic trees but no temporal congruence of speciation events.

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

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

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

Conflict of interest disclosure

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

References

Agrawal, AA, M Fishbein, R Halitschke, AP Hastings, DL Rabosky, S Rasmann. 2009. Evidence for adaptive radiation from a phylogenetic study of plant defenses. Proceedings of the National Academy of Sciences of the United States of America 106:18067-18072.

Alfaro, ME, F Santini, C Brock, H Alamillo, A Dornburg, DL Rabosky, G Carnevale, LJ Harmon. 2009. Nine exceptional radiations plus high turnover explain species diversity in jawed vertebrates. Proceedings of the National Academy of Sciences of the United States of America 106:13410-13414.

Althoff, DM, KA Segraves, MTJ Johnson. 2014. Testing for coevolutionary diversification: linking pattern with process. Trends in Ecology & Evolution 29:82-89.

Althoff, DM, KA Segraves, CI Smith, J Leebens-Mack, O Pellmyr. 2012. Geographic isolation trumps coevolution as a driver of yucca and yucca moth diversification. Molecular Phylogenetics and Evolution 62:898-906.

Barraclough, TG, AP Vogler. 2000. Detecting the geographical pattern of speciation from species-level phylogenies. American Naturalist 155:419-434.

Beaulieu, JM, MJ Donoghue. 2013. Fruit evolution and diversification in campanulid angiosperms. Evolution 67:3132-3144.

Beaulieu, JM, BC O'Meara. 2016. Detecting Hidden Diversification Shifts in Models of Trait-Dependent Speciation and Extinction. Systematic Biology 65:583-601.

Becerra, JX. 1997. Insects on plants: macroevolutionary chemical trends in host use. Science 276:253-256.

Becerra, JX. 2003. Synchronous coadaptation in an ancient case of herbivory. Proceedings of the National Academy of Sciences of the United States of America 100:12804-12807.

Becerra, JX, DL Venable. 1999. Macroevolution of insect-plant associations: the relevance of host biogeography to host affiliation. Proceedings of the National Academy of Sciences of the United States of America 96:12626-12631.

Berlocher, SH. 2000. Radiation and divergence in the *Rhagoletis pomonella* species group: inferences from allozymes. Evolution 54:543-557.

Blackman, RL, VF Eastop. 2006. Aphids on the World's Herbaceous Plants and Schrubs. London, UK: The Natural History Museum.

Bouchenak-Khelladi, Y, RE Onstein, YW Xing, O Schwery, HP Linder. 2015. On the complexity of triggering evolutionary radiations. New Phytologist 207:313-326.

Braga, MP, PR Guimarães, CW Wheat, S Nylin, N Janz. 2018. Unifying host-associated diversification processes using butterfly–plant networks. Nature Communications 9:5155.

Bramer, C, S Dobler, J Deckert, M Stemmer, G Petschenka. 2015. Na+/K+-ATPase resistance and cardenolide sequestration: basal adaptations to host plant toxins in the milkweed bugs (Hemiptera: Lygaeidae: Lygaeinae). Proceedings of the Royal Society B-Biological Sciences 282.

Brandle, M, S Knoll, S Eber, J Stadler, R Brandl. 2005. Flies on thistles: support for synchronous speciation? Biological Journal of the Linnean Society 84:775-783.

Brookes, DR, JP Hereward, LI Terry, GH Walter. 2015. Evolutionary dynamics of a cycad obligate pollination mutualism – Pattern and process in extant *Macrozamia* cycads and their specialist thrips pollinators. Molecular Phylogenetics and Evolution 93:83-93.

Brues, CT. 1924. The Specificity of Food-Plants in the Evolution of Phytophagous Insects. The American Naturalist 58:127-144.

Bush, GL. 1975. Sympatric Speciation in Phytophagous Parasitic Insects. In: PW Price, editor. Evolutionary Strategies of Parasitic Insects and Mites. Boston, MA: Springer US. p. 187-206.

Caillaud, MC, S Via. 2000. Specialized feeding behavior influences both ecological specialization and assortative mating in sympatric host races of pea aphids. American Naturalist 156:606-621.

Chan, KMA, BR Moore. 2002. Whole-tree methods for detecting differential diversification rates. Systematic Biology 51:855-865.

Conow, C, D Fielder, Y Ovadia, R Libeskind-Hadas. 2010. Jane: a new tool for the cophylogeny reconstruction problem. Algorithms for Molecular Biology 5.

Cruaud, A, N Ronsted, B Chantarasuwan, et al. 2012. An extreme case of plant-insect codiversification: figs and fig-pollinating wasps. Systematic Biology 61:1029-1047.

Davis, MP, PE Midford, W Maddison. 2013. Exploring power and parameter estimation of the BiSSE method for analyzing species diversification. BMC Evolutionary Biology 13:38.

de Castro, ÉCP, M Zagrobelny, MZ Cardoso, S Bak. 2018. The arms race between heliconiine butterflies and Passiflora plants – new insights on an ancient subject. Biological reviews 93:555-573.

de Vienne, DM, G Refregier, M Lopez-Villavicencio, A Tellier, ME Hood, T Giraud. 2013. Cospeciation vs host-shift speciation: methods for testing, evidence from natural associations and relation to coevolution. New Phytologist 198:347-385.

Doorenweerd, C, EJ van Nieukerken, SBJ Menken. 2015. A Global Phylogeny of Leafmining *Ectoedemia* Moths (Lepidoptera: Nepticulidae): Exploring Host Plant Family Shifts and Allopatry as Drivers of Speciation. Plos One 10.

731   Drès, M, J Mallet. 2002. Host races in plant-feeding insects and their importance in sympatric
732   speciation. Philosophical Transactions of the Royal Society of London Series B-Biological
733   Sciences 357:471-492.

734   Drury, JP, GF Grether, T Garland, Jr., H Morlon. 2017. An assessment of phylogenetic tools for
735   analyzing the interplay between interspecific interactions and phenotypic evolution.
736   Systematic Biology 67:413-427.

737   Ebel, ER, JM DaCosta, MD Sorenson, RI Hill, AD Briscoe, KR Willmott, SP Mullen. 2015. Rapid
738   diversification associated with ecological specialization in Neotropical *Adelpha* butterflies.
739   Molecular Ecology 24:2392-2405.

740   Edger, PP, HM Heidel-Fischer, M Bekaert, et al. 2015. The butterfly plant arms-race escalated by gene
741   and genome duplications. Proceedings of the National Academy of Sciences of the United
742   States of America 112:8362-8366.

743   Egan, SP, P Nosil, DJ Funk. 2008. Selection and genomic differentiation during ecological speciation:
744   Isolating the contributions of host association via a comparative genome scan of
745   Neochlamisus bebbianae leaf beetles. Evolution 62:1162-1181.

746   Ehrlich, PR, PH Raven. 1964. Butterflies and plants: a study in coevolution. Evolution 18:586-608.

747   Elias, M, R Faria, Z Gompert, A Hendry. 2012. Factors Influencing Progress toward Ecological
748   Speciation. International Journal of Ecology 2012:7.

749   Elias, M, C Fontaine, FJF van Veen. 2013. Evolutionary history and ecological processes shape a local
750   multilevel antagonistic network. Current Biology 23:1355-1359.

751   Endara, MJ, PD Coley, G Ghabash, JA Nicholls, KG Dexter, DA Donoso, GN Stone, RT Pennington,
752   TA Kursar. 2017. Coevolutionary arms race versus host defense chase in a tropical herbivore-
753   plant system. Proceedings of the National Academy of Sciences of the United States of
754   America 114:E7499-E7505.

755   Etienne, RS, B Haegeman, T Stadler, T Aze, N Pearson Paul, A Purvis, B Phillimore Albert. 2012.
756   Diversity-dependence brings molecular phylogenies closer to agreement with the fossil record.
757   Proceedings of the Royal Society B: Biological Sciences 279:1300-1309.

758   Faith, DP, PS Cranston. 1991. Could a cladogram this short have arisen by chance alone? : on
759   permutation for cladistic structure. Cladistics 7:1-28.

760   Farrell, BD, C Mitter. 1998. The timing of insect/plant diversification: might *Tetraopes* (Coleoptera:
761   Cerambycidae) and *Asclepias* (Asclepiadaceae) have co- evolved? Biological Journal of the
762   Linnean Society 63:553-577.

763   Fatouros, NE, C Broekgaarden, G Bukovinszkine'Kiss, JJA van Loon, R Mumm, ME Huigens, M
764   Dicke, M Hilker. 2008. Male-derived butterfly anti-aphrodisiac mediates induced indirect
765   plant defense. Proceedings of the National Academy of Sciences 105:10033-10038.

766   FitzJohn, RG. 2010. Quantitative Traits and Diversification. Systematic Biology 59:619-633.

767   Forbes, AA, SN Devine, AC Hippee, ES Tvedte, AKG Ward, HA Widmayer, CJ Wilson. 2017.
768   Revisiting the particular role of host shifts in initiating insect speciation. Evolution 71:1126-
769   1137.

Fordyce, JA. 2010. Host shifts and evolutionary radiations of butterflies. Proceedings of the Royal Society B: Biological Sciences 277:3735-3743.

Forister, ML, LA Dyer, MS Singer, JO Stireman, JT Lill. 2012. Revisiting the evolution of ecological specialization, with emphasis on insect-plant interactions. Ecology 93:981-991.

Funk, DJ, KE Filchak, JL Feder. 2002. Herbivorous insects: model systems for the comparative study of speciation ecology. Genetica 116:251-267.

Futuyma, DJ, AA Agrawal. 2009. Macroevolution and the biological diversity of plants and herbivores. Proceedings of the National Academy of Sciences 106:18054-18061.

Godsoe, W, E Strand, CI Smith, JB Yoder, TC Esque, O Pellmyr. 2009. Divergence in an obligate mutualism is not explained by divergent climatic factors. New Phytologist 183:589-599.

Gómez-Zurita, J, T Hunt, F Kopliku, AP Vogler. 2007. Recalibrated tree of leaf beetles (Chrysomelidae) indicates independent diversification of angiosperms and their insect herbivores. Plos One 2:e360.

Goswami, A, PD Mannion, MJ Benton. 2016. Radiation and extinction: investigating clade dynamics in deep time. Biological Journal of the Linnean Society 118:6-12.

Gow, JL, CL Peichel, EB Taylor. 2007. Ecological selection against hybrids in natural populations of sympatric threespine sticklebacks. Journal of Evolutionary Biology 20:2173-2180.

Hamm, CA, JA Fordyce. 2015. Patterns of host plant utilization and diversification in the brush-footed butterflies. Evolution 69:589-601.

Hamm, CA, JA Fordyce. 2016. Greater host breadth still not associated with increased diversification rate in the Nymphalidae-A response to Janz et al. Evolution 70:1156-1160.

Hardy, NB. 2017. Do plant-eating insect lineages pass through phases of host-use generalism during speciation and host switching? Phylogenetic evidence. Evolution 71:2100-2109.

Hardy, NB, SP Otto. 2014. Specialization and generalization in the diversification of phytophagous insects: tests of the musical chairs and oscillation hypotheses. Proceedings of the Royal Society B-Biological Sciences 281.

Hardy, NB, DA Peterson, BB Normark. 2016. Nonadaptive radiation: Pervasive diet specialization by drift in scale insects? Evolution 70:2421-2428.

Hardy, NB, DA Peterson, CD von Dohlen. 2015. The evolution of life cycle complexity in aphids: Ecological optimization or historical constraint? Evolution 69:1423-1432.

Hembry, DH, JB Yoder, KR Goodman. 2014. Coevolution and the Diversification of Life. American Naturalist 184:425-438.

Hernández-Vera G, Toševski I, Caldara R, Emerson BC. 2019. Evolution of host plant use and diversification in a species complex of parasitic weevils (Coleoptera: Curculionidae). *PeerJ* **7:** e6625.

Holman, J. 2009. Host Plant Catalog of Aphids: Palaearctic Region. Springer, Dordrecht.

Holt, RD. 1977. Predation, apparent competition, and the structure of prey communities. Theoretical Population Biology 12:197-229.

Hunt, T, J Bergsten, Z Levkanicova, et al. 2007. A comprehensive phylogeny of beetles reveals the evolutionary origins of a superradiation. Science 318:1913-1916.

Hsu YH, Cocroft RB, Snyder RL, Lin CP. 2018. You stay, but I Hop: Host shifting near and far co-dominated the evolution of Enchenopa treehoppers. Ecology and Evolution 8: 1954-1965.

Ives, AR, HCJ Godfray. 2006. Phylogenetic analysis of trophic associations. American Naturalist 168:E1-E14.

Janz, N. 2011. Ehrlich and Raven revisited: mechanisms underlying codiversification of plants and enemies. In: DJ Futuyma, HB Shaffer, D Simberloff, editors. Annual Review of Ecology, Evolution, and Systematics. p. 71-89.

Janz, N, MP Braga, N Wahlberg, S Nylin. 2016. On oscillations and flutterings—A reply to Hamm and Fordyce. Evolution. 70:1150-1155.

Janz, N, K Nyblom, S Nylin. 2001. Evolutionary dynamics of host-plant specialization: A case study of the tribe Nymphalini. Evolution 55:783-796.

Janz, N, S Nylin. 2008. The oscillation hypothesis of host-plant range and speciation. In: D Tilman, editor. The evolutionary biology of herbivorous insects: specialization, speciation and radiation. University of california press p. 203-215.

Janz, N, S Nylin, N Wahlberg. 2006. Diversity begets diversity: host expansions and the diversification of plant-feeding insects. BMC Evolutionary Biology 6.

Jermy, T. 1976. Insect—Host-plant Relationship—Co-evolution or Sequential Evolution? The host-plant in relation to insect behaviour and reproduction: Springer. p. 109-113.

Jermy, T. 1984. Evolution of insect/ plant relationship. The American Naturalist 124:609-630.

Jordal, B, G M Hewitt. 2004. The Origin and Radiation of Macaronesian Beetles Breeding in *Euphorbia*: The Relative Importance of Multiple Data Partitions and Population Sampling. Systematic Biology 53:711-734.

Jousselin, E, A Cruaud, G Genson, F Chevenet, RG Foottit, AC d'acier. 2013. Is ecological speciation a major trend in aphids? Insights from a molecular phylogeny of the conifer-feeding genus *Cinara*. Frontiers in Zoology 10.

Jousselin, E, G Genson, A Coeur d'Acier. 2010. Evolutionary lability of a complex life cycle in the aphid genus *Brachycaudus*. BMC Evolutionary Biology 10.

Jousselin, E, JY Rasplus, F Kjellberg. 2003. Convergence and coevolution in a mutualism: Evidence from a molecular phylogeny of *Ficus*. Evolution 57:1255-1269.

Joy, JB, BJ Crespi. 2012. Island phytophagy: explaining the remarkable diversity of plant-feeding insects. Proceedings of the Royal Society B-Biological Sciences 279:3250-3255.

Kelley, ST, BD Farrell. 1998. Is specialization a dead end? The phylogeny of host use in *Dendroctonus* bark beetles (Scolytidae). Evolution 52:1731-1743.

Kergoat, GJ, FL Condamine, EFA Toussaint, C Capdevielle-Dulac, A-L Clamens, J Barbut, PZ Goldstein, B Le Ru. 2018. Opposite macroevolutionary responses to environmental changes in grasses and insects during the Neogene grassland expansion. Nature Communications 9:5089.

Kergoat, GJ, BP Le Ru, G Genson, C Cruaud, A Couloux, A Delobel. 2011. Phylogenetics, species boundaries and timing of resource tracking in a highly specialized group of seed beetles (Coleoptera: Chrysomelidae: Bruchinae). Molecular Phylogenetics and Evolution 59:746-760.

Kergoat, GJ, BP Le Ru, SE Sadeghi, M Tuda, CAM Reid, Z Gyorgy, G Genson, CS Ribeiro-Costa, A Delobel. 2015. Evolution of *Spermophagus* seed beetles (Coleoptera, Bruchinae, Amblycerini) indicates both synchronous and delayed colonizations of host plants. Molecular Phylogenetics and Evolution 89:91-103.

Labandeira, CC, ED Currano. 2013. The Fossil Record of Plant-Insect Dynamics. Annual Review of Earth and Planetary Sciences 41:287-311.

Labandeira, CC, DL Dilchet, DR Davis, DL Wagner. 1994. Ninety-seven million years of angiosperm-insect association: Paleobiological insights into the meaning of coevolution. Proceedings of the National Academy of Sciences of the United States of America 91:12278-12282.

Legendre, P, Y Desdevises, E Bazin. 2002. A statistical test for host parasite coevolution. Systematic Biology 51:217-234.

Leppanen, SA, E Altenhofer, AD Liston, T Nyman. 2012. Phylogenetics and evolution of host-plant use in leaf-mining sawflies (Hymenoptera: Tenthredinidae: Heterarthrinae). Molecular Phylogenetics and Evolution 64:331-341.

Leschen, RAB, TR Buckley. 2007. Multistate characters and diet shifts: Evolution of Erotylidae (Coleoptera). Systematic Biology 56:97-112.

Letsch H, Gottsberger B, Metzl C, Astrin J, Friedman ALL, McKenna DD, Fiedler K. 2018. Climate and host-plant associations shaped the evolution of ceutorhynch weevils throughout the Cenozoic. *Evolution* 72: 1815-1828.

Lin, Y-P, Dh Cook, Pj Gullan, Lg Cook. 2015. Does host-plant diversity explain species richness in insects? A test using Coccidae (Hemiptera). Ecological Entomology 40:299-306.

Linnen, CR, BD Farrell. 2010. A test of the sympatric host race formation hypothesis in *Neodiprion* (Hymenoptera: Diprionidae). Proceedings of the Royal Society B-Biological Sciences 277:3131-3138.

Lisa De-Silva, D, LL Mota, N Chazot, et al. 2017. North Andean origin and diversification of the largest ithomiine butterfly genus. Scientific Reports 7:45966.

Livshultz, T, E Kaltenegger, SCK Straub, K Weitemier, E Hirsch, K Koval, L Mema, A Liston. 2018. Evolution of pyrrolizidine alkaloid biosynthesis in Apocynaceae: revisiting the defence de-escalation hypothesis. The New phytologist 218:762-773.

881   Lopez-Vaamonde, C, N Wikstrom, C Labandeira, HCJ Godfray, SJ Goodman, JM Cook. 2006. Fossil-
882   calibrated molecular phylogenies reveal that leaf-mining moths radiated millions of years after
883   their host plants. Journal of Evolutionary Biology 19:1314-1326.

884   Loss-Oliveira, L, BO Aguiar, CG Schrago. 2012. Testing Synchrony in Historical Biogeography: The
885   Case of New World Primates and Hystricognathi Rodents. Evolutionary Bioinformatics
886   8:127-137.

887   Maddison, WP, RG FitzJohn. 2015. The unsolved challenge to phylogenetic correlation tests for
888   categorical characters. Systematic Biology 64:127-136.

889   Maddison, WP, PE Midford, SP Otto. 2007. Estimating a binary character's effect on speciation and
890   extinction. Systematic Biology 56:701-710.

891   Manceau, M, A Lambert, H Morlon. 2016. A unifying comparative phylogenetic framework including
892   traits coevolving across interacting lineages. Systematic Biology 66:551-568.

893   Marquis, RJ, D Salazar, C Baer, J Reinhardt, G Priest, K Barnett. 2016. Ode to Ehrlich and Raven or
894   how herbivorous insects might drive plant speciation. Ecology 97:2939-2951.

895   Maron JL, Agrawal AA, Schemske DW. 2019. Plant–herbivore coevolution and plant speciation.
896   *Ecology* 100: e02704.

897   Martínez-Aquino, A. 2016. Phylogenetic framework for coevolutionary studies: a compass for
898   exploring jungles of tangled trees. Current Zoology 62:393-403

899   Matsubayashi, KW, I Ohshima, P Nosil. 2010. Ecological speciation in phytophagous insects.
900   Entomologia Experimentalis et Applicata 134:1-27.

901   Matsuo, T. 2008. Rapid Evolution of Two Odorant-Binding Protein Genes, *Obp57* and *Obp57*, in the
902   *Drosophila melanogaster* Species Group. Genetics 178:1061-1072.

903   McBride, CS, MC Singer. 2010. Field Studies Reveal Strong Postmating Isolation between
904   Ecologically Divergent Butterfly Populations. Plos Biology 8:e1000529.

905   McKenna, DD, AS Sequeira, AE Marvaldi, BD Farrell. 2009. Temporal lags and overlap in the
906   diversification of weevils and flowering plants. Proceedings of the National Academy of
907   Sciences of the United States of America 106:7083-7088.

908   McKenna, DD, AL Wild, K Kanda, et al. 2015. The beetle tree of life reveals that Coleoptera survived
909   end-Permian mass extinction to diversify during the Cretaceous terrestrial revolution.
910   Systematic Entomology 40:835-880.

911   McLeish, MJ, JT Miller, LA Mound. 2013. Delayed colonisation of *Acacia* by thrips and the timing of
912   host-conservatism and behavioural specialisation. BMC Evolutionary Biology 13.

913   Meseguer, AS, A Coeur d'acier, G Genson, E Jousselin. 2015. Unravelling the historical biogeography
914   and diversification dynamics of a highly diverse conifer-feeding aphid genus. Journal of
915   Biogeography 42:1482-1492.

916   Mitter, C, BD Farrell, BM Wiegman. 1988. The phylogenetic study of adaptive zones: has phytophagy
917   promoted insect diversification? American Naturalist 132:107-128.

918   Moran, NA. 1992. The evolution of aphid life cycles. Annual Review of Entomology 37:321-348.

919   Mullen, SP, WK Savage, N Wahlberg, KR Willmott. 2011. Rapid diversification and not clade age
920   explains high diversity in neotropical *Adelpha* butterflies. Proceedings of the Royal Society B-
921   Biological Sciences 278:1777-1785.

922   Nakadai, R. 2017. Species diversity of herbivorous insects: a brief review to bridge the gap between
923   theories focusing on the generation and maintenance of diversity. Ecological Research.

924   Nakadai, R, A Kawakita. 2016. Phylogenetic test of speciation by host shift in leaf cone moths
925   (Caloptilia) feeding on maples (Acer). Ecology and Evolution 6: 4958–4970.

926   Nevado, B, GW Atchison, CE Hughes, DA Filatov. 2016. Widespread adaptive evolution during
927   repeated evolutionary radiations in New World lupins. Nature Communications 7:12384.

928   Nosil, P. 2012. Ecological speciation. Oxford: Oxford University Press.

929   Nosil, P, BJ Crespi, CP Sandoval. 2002. Host-plant adaptation drives the parallel evolution of
930   reproductive isolation. Nature 417:440-443.

931   Nosil, P, Z Gompert, TE Farkas, AA Comeault, JL Feder, CA Buerkle, TL Parchman. 2012. Genomic
932   consequences of multiple speciation processes in a stick insect. Proceedings of the Royal
933   Society B-Biological Sciences 279:5058-5065.

934   Nosil, P, AO Mooers. 2005. Testing hypotheses about ecological specialization using phylogenetic
935   trees. Evolution 59:2256-2263.

936   Nylin, S, N Janz. 2009. Butterfly host plant range: an example of plasticity as a promoter of
937   speciation? Evolutionary Ecology 23:137-146.

938   Nylin, S, J Slove, N Janz. 2014. Host plant utilization, host range oscillations and diversification in
939   nymphalid butterflies: a phylogenetic investigation. Evolution 68:105-124.

940   Nylin, S, N Wahlberg. 2008. Does plasticity drive speciation? Host-plant shifts and diversification in
941   nymphaline butterflies (Lepidoptera : Nymphalidae) during the tertiary. Biological Journal of
942   the Linnean Society 94:115-130.

943   Nyman T, RE Onstein, D Silvestro, S Wutke, A Taeger, N Wahlberg, SM Blank, T Malm. 2019**.** The
944   early wasp plucks the flower: disparate extant diversity of sawfly superfamilies
945   (Hymenoptera: 'Symphyta') may reflect asynchronous switching to angiosperm hosts.
946   Biological Journal of the Linnean Society 128**:** 1-19.

947   Nyman, T, HP Linder, C Pena, T Malm, N Wahlberg. 2012. Climate-driven diversity dynamics in
948   plants and plant-feeding insects. Ecology Letters 15:889-898.

949   Nyman, T, V Vikberg, DR Smith, JL Boeve. 2010. How common is ecological speciation in plant-
950   feeding insects? A 'Higher' Nematinae perspective. BMC Evolutionary Biology 10.

951   O'Meara, BC, JM Beaulieu. 2016. Past, future, and present of state-dependent models of
952   diversification. American Journal of Botany 103:792-795.

953   Onstein, RE, WJ Baker, TLP Couvreur, S Faurby, J-C Svenning, WD Kissling. 2017. Frugivory-
954   related traits promote speciation of tropical palms. Nature Ecology & Evolution 1:1903-1911.

955   Owen, CL, DC Marshall, KBR Hill, C Simon. 2017. How the aridification of australia structured the
956   biogeography and influenced the diversification of a large lineage of australian cicadas.
957   Systematic Biology 66:569-589.

958   Page, RDM. 1994. Parallel phylogenies: reconstructing the history of host-parasite assemblages.
959   Cladistics 10:155-173.

960   Pagel, M. 1999. The maximum likelihood approach to reconstructing ancestral character states of
961   discrete characters on phylogenies. Systematic Biology 48:612-622.

962   Peccoud, J, A Ollivier, M Plantegenest, JC Simon. 2009. A continuum of genetic divergence from
963   sympatric host races to species in the pea aphid complex. Proceedings of the National
964   Academy of Sciences of the United States of America 106:7495-7500.

965   Pellmyr, O. 2003. Yuccas, yucca moths, and coevolution: a review. Annals of the Missouri Botanical
966   Garden 90:35-55.

967   Pena, C, M Espeland. 2015. Diversity dynamics in nymphalidae butterflies: effect of phylogenetic
968   uncertainty on diversification rate shift estimates. Plos One 10.

969   Pena, C, N Wahlberg. 2008. Prehistorical climate change increased diversification of a group of
970   butterflies. Biology letters 4:274-278.

971   Pena, C, H Witthauer, I Kleckova, Z Fric, N Wahlberg. 2015. Adaptive radiations in butterflies:
972   evolutionary history of the genus Erebia (Nymphalidae: Satyrinae). Biological Journal of the
973   Linnean Society 116:449-467.

974   Pennell, MW, LJ Harmon. 2013. An integrative view of phylogenetic comparative methods:
975   connections to population genetics, community ecology, and paleobiology. In: TA Mousseau,
976   CW Fox, editors. Year in Evolutionary Biology. p. 90-105.

977   Pitteloud, C, N Arrigo, T Suchan, et al. 2017. Climatic niche evolution is faster in sympatric than
978   allopatric lineages of the butterfly genus *Pyrgus*. Proceedings of the Royal Society B-
979   Biological Sciences 284.

980   Powell, THQ, AA Forbes, GR Hood, JL Feder. 2014. Ecological adaptation and reproductive isolation
981   in sympatry: genetic and phenotypic evidence for native host races of *Rhagoletis pomonella*.
982   Molecular Ecology 23:688-704.

983   Rabosky, DL. 2006. LASER: A maximum likelihood toolkit for detecting temporal shifts in
984   diversification rates from molecular phylogenies. Evolutionary Bioinformatics 2:247-250.

985   Rabosky, DL, SC Donnellan, M Grundler, IJ Lovette. 2014. Analysis and visualization of complex
986   macroevolutionary dynamics: an example from australian scincid lizards. Systematic Biology
987   63:610-627.

988   Rabosky, DL, EE Goldberg. 2015. Model inadequacy and mistaken inferences of trait-dependent
989   speciation. Systematic Biology 64:340-355.

990   Rabosky, DL, IJ Lovette. 2008. Explosive evolutionary radiations: decreasing speciation or increasing
991   extinction through time? Evolution 62:1866-1875.

992   Ramirez, W. 1974. Coevolution of *Ficus* and Agaonidae. Annals of the Missouri Botanical Garden
993   61:770-780.

994   Ree, RH, SA Smith. 2008. Maximum likelihood inference of geographic range evolution by dispersal,
995   local extinction, and cladogenesis. Systematic Biology 57:4-14.

996   Roskam, JC. 1985. Evolutionary patterns in gall midge - host plant associations (Diptera,
997   Cecidomyiidae). Tijdschrift voor Entomologie 128:193-213.

998   Rundle, HD, L Nagek, J Wenrick Boughman, D Schluter. 2000. Natural selection and parallel
999   speciation in sympatric Sticklebacks. Science 287:306-308.

1000   Rundle, HD, P Nosil. 2005. Ecological speciation. Ecology Letters 8:336-352.

1001   Sahoo, RK, AD Warren, SC Collins, U Kodandaramaiah. 2017. Hostplant change and paleoclimatic
1002   events explain diversification shifts in skipper butterflies (Family: Hesperiidae). BMC
1003   Evolutionary Biology 17:174.

1004   Sánchez-Gracia, A, FG Vieira, J Rozas. 2009. Molecular evolution of the major chemosensory gene
1005   families in insects. Heredity 103:208.

1006   Sanchez-Guillen, RA, A Cordoba-Aguilar, B Hansson, J Ott, M Wellenreuther. 2016. Evolutionary
1007   consequences of climate-induced range shifts in insects. Biological reviews 91:1050-1064.

1008   Schluter, D. 2000. The Ecology of Adaptive Radiation. Oxford University Press, New York.

1009   Schluter, D. 2009. Evidence for Ecological Speciation and Its Alternative. Science 323:737-741.

1010   Schwander, T, D Arbuthnott, R Gries, G Gries, P Nosil, BJ Crespi. 2013. Hydrocarbon divergence and
1011   reproductive isolation in *Timema* stick insects. BMC Evolutionary Biology 13.

1012   Segar, ST, C Lopez-Vaamonde, JY Rasplus, JM Cook. 2012. The global phylogeny of the subfamily
1013   Sycoryctinae (Pteromalidae): Parasites of an obligate mutualism. Molecular Phylogenetics and
1014   Evolution 65:116-125.

1015   Simonsen, TJ, N Wahlberg, AD Warren, FAH Sperling. 2010. The evolutionary history of *Boloria*
1016   (Lepidoptera: Nymphalidae): phylogeny, zoogeography and larval-foodplant relationships.
1017   Systematics and Biodiversity 8:513-529.

1018   Singer, MS, JO Stireman. 2005. The tri-trophic niche concept and adaptive radiation of phytophagous
1019   insects. Ecology Letters 8:1247-1255.

1020   Slove, J, N Janz. 2011. The relationship between diet breadth and geographic range size in the
1021   butterfly subfamily Nymphalinae - A Study of Global Scale. Plos One 6.

1022   Smadja, C, RK Butlin. 2009. On the scent of speciation: the chemosensory system and its role in
1023   premating isolation. Heredity 102:77-97.

1024   Smadja, CM, B Canback, R Vitalis, M Gautier, J Ferrari, JJ Zhou, RK Butlin. 2012. Large-scale
1025   candidate gene scan reveals the role of chemoreceptor genes in host plant specialization and
1026   speciation in the pea aphid. Evolution 66:2723-2738.

Stadler, T. 2013. Recovering speciation and extinction dynamics based on phylogenies. Journal of Evolutionary Biology 26:1203-1219.

Stadler, T, F Bokma. 2013. Estimating Speciation and Extinction Rates for Phylogenies of Higher Taxa. Systematic Biology 62:220-230.

Stone, GN, A Hernández-Vera -Lopez, JA Nicholls, E di Pierro, J Pujade-Villar, G Melika, JM Cook. 2009. Extreme Host Plant Conservatism During at Least 20 Million Years of Host Plant Pursuit by Oak Gallwasps. Evolution 63:854-869.

Suchan, T, N Alvarez. 2015. Fifty years after Ehrlich and Raven, is there support for plant-insect coevolution as a major driver of species diversification? Entomologia Experimentalis et Applicata 157:98-112.

Thébault, E, C Fontaine. 2010. Stability of ecological communities and the architecture of mutualistic and trophic networks. Science 329:853-856.

Thompson, JN. 1989. Concepts of coevolution. Trends in Ecology and Evolution 4:179-183.

Vea, IM, DA Grimaldi. 2016. Putting scales into evolutionary time: the divergence of major scale insect lineages (Hemiptera) predates the radiation of modern angiosperm hosts. Scientific Reports 6:23487.

Via, S, AC Bouck, S Skillman. 2000. Reproductive isolation between divergent races of pea aphids on two hosts. II. Selection against migrants and hybrids in the parental environments. Evolution 54:1626-1637.

Vieira, FG, J Rozas. 2011. Comparative genomics of the odorant-binding and chemosensory protein gene families across the arthropoda: origin and evolutionary history of the chemosensory system. Genome Biology and Evolution 3:476-490.

Wahlberg, N. 2001. The phylogenetics and biochemistry of host-plant-specialization in Melitaeinae butterflies (Lepidoptera: Nymphalidae). Evolution 55:522-537.

Wahlberg, N, CW Wheat, C Pena. 2013. Timing and Patterns in the Taxonomic Diversification of Lepidoptera (Butterflies and Moths). Plos One 8.

Walsh, B. 1864. On phytophagic varieties and phytophagis species. Proceedings of the Entomological Society, Philadelphia:403-430.

Wang, HS, JD Holloway, N Janz, MP Braga, N Wahlberg, M Wang, S Nylin. 2017. Polyphagy and diversification in tussock moths: support for the oscillation hypothesis from extreme generalists. Ecology and Evolution 7:7975-7986.

Weiblen, GD. 2004. Correlated evolution in fig pollination. Systematic Biology 53:128-139.

Weingartner, E, N Wahlberg, S Nylin. 2006. Dynamics of host plant use and species diversity in Polygonia butterflies (Nymphalidae). Journal of Evolutionary Biology 19:483-491.

Wheat, CW, H Vogel, U Wittstock, MF Braby, D Underwood, T Mitchell-Olds. 2007. The genetic basis of a plant-insect coevolutionary key innovation. Proceedings of the National Academy of Sciences of the United States of America 104:20427-20431.

1064   Wiebes, JT. 1979. Co-evolution of figs and their insect pollinators. Annual Review of Ecology and
1065   Systematics 10:1-12.

1066   Wiens, JJ, RT Lapoint, NK Whiteman. 2015. Herbivory increases diversification across insect clades.
1067   Nature Communications 6.

1068   Wilson, JS, ML Forister, LA Dyer, et al. 2012. Host conservatism, host shifts and diversification
1069   across three trophic levels in two Neotropical forests. Journal of Evolutionary Biology 25:532-
1070   546.

1071   Winkler, I, SJ Scheffer, ML Lewis, KJ Ottens, AP Rasmussen, GA Gomes-Costa, LM Huerto
1072   Santillan, MA Condon, AA Forbes. 2018. Anatomy of a Neotropical insect radiation. BMC
1073   Evolutionary Biology 18:30.

1074   Winkler, IS, C Mitter. 2008. The phylogenetic dimension of insect-plant interactions: a review of
1075   recent evidence. In: K Tilmon, editor. Specialization, Speciation and Radiation: the
1076   Evolutionary Biology of Herbivorous insects: University of California Press p. 240-263.

1077   Winkler, IS, C Mitter, SJ Scheffer. 2009. Repeated climate-linked host shifts have promoted
1078   diversification in a temperate clade of leaf-mining flies. Proceedings of the National Academy
1079   of Sciences of the United States of America 106:18103-18108.

1080   Winter S, Friedman ALL, Astrin JJ, Gottsberger B, Letsch H. 2017. Timing and host plant
1081   associations in the evolution of the weevil tribe Apionini (Apioninae, Brentidae,
1082   Curculionoidea, Coleoptera) indicate an ancient co-diversification pattern of beetles and
1083   flowering plants. Molecular Phylogenetics and Evolution 107: 179-190.

1084   Yokoyama, J. 1995. Insect-plant coevolution and cospeciation. In: R Arai, M Kato, Y Doi, editors.
1085   Biodiversity and Evolution. Tokyo. p. 115-130.