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

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ABSTRACT

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

Keywords: adaptive radiation; coevolution; comparative analyses; herbivory; host-plant specialization; phylogeny; speciation

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 2012; Nosil *et al.* 2002; Rundle & Nosil 2005; Schluter 2009). **Phytophagous insects***[1] have always been at the forefront of these investigations (Drès & Mallet 2002; Elias *et al.* 2012; Forbes *et al.* 2017; Funk *et al.* 2002; Matsubayashi *et al.* 2010). 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; Walsh 1864). 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 (Berlocher 2000; Bush 1975; 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 *et al.* 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 *et al.* 2007) and some studies have uncovered genomic regions that determine host-plant preference and performance on alternative hosts (Egan *et al.* 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; Janz 2011; Winkler & Mitter 2008; Yokoyama 1995). However, these macroevolutionary scenarios are often presented in the literature as narratives for specific insect lineages commenting on a phylogenetic reconstruction of the history of host-plant associations. Many phylogenetic studies still fail to clearly formulate hypotheses and predictions about the speciation processes that underlie the observed patterns and the role played by host-plant adaptation in those. The reason might be that the macroevolutionary patterns that arise when **host-plant specialization*** is the driver of speciation events are not always clear. There is no review on what to expect and how to formally test these predictions.

The increasing availability of robust molecular phylogenies and recent developments in phylogenetic comparative methods are offering an unprecedented opportunity to test evolutionary

[1] See glossary

hypotheses in a robust phylogenetic framework. Our purpose here is to present the macroevolutionary scenarios for the diversification of phytophagous insects that have been put forward in the literature, decipher the role that ecological speciation driven by host-plant adaptation plays in them and synthetize predictions from these scenarios. We then identify tools from the "comparative phylogenetic toolbox" that provide ways to test some of these predictions. This toolbox can be divided into three compartments.

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

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

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

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

I Macroevolutionary scenarios of phytophagous insect diversification

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

More than 50 years ago, Ehrlich & Raven (1964) put forward a macroevolutionary scenario that inspired most of the current research on plant-feeding insect diversification: it is known as "***Escape and radiate***" (Thompson 1989). They hypothesized that when insects acquire the ability to circumvent the chemical defenses of a plant group, it promotes their rapid diversification by ecological release, *i.e.* the availability of novel resources and reduction in direct competition. Insects undergo an **adaptive radiation***. In this scenario, adaptation towards host-plants is therefore the driving force of insect species formation. The *Escape and Radiate* scenario also hypothesizes that, in response to phytophagous insect predation, plants acquire novel chemical defenses which allow them in turn to diversify very rapidly (Marquis *et al.* 2016). Ehrlich & Raven' s seminal study suffers from several shortcomings that have been pinpointed before (Janz 2011). First, although the authors frame their theory within the concept of adaptive radiation, they do not explicitly lay out any speciation mechanisms for the partners of the interaction. Following their scenario, a trade-off in resource use and specialization towards specific host-plants is necessary to explain the formation of numerous insect species (*i.e.,* species radiation) after the capture of a new host-plant lineage. Such a trade-off is not mentioned in the original paper (Janz 2011). In addition, as underlined by contemporary researchers of Ehrlich and Raven, it is difficult to conceive how the selection pressures exerted by insects on plant defences can drive plant speciation (Jermy 1976;

Jermy 1984). Plant traits that reduce phytophagous insect attacks are rarely linked with reproductive isolation between plant populations (but see Marquis *et al.* 2016 for a review of scenarios of herbivore-induced speciation in plants) and the evidence for bursts of speciation in plants following the evolution of chemical defence is scant (Futuyma & Agrawal 2009). However this study has been and remains a great source of inspiration for studies on the diversification of plant-insect associations. This is probably because it is one of the first studies that attempts to explain how microevolutionary processes (host-plant adaptation) translate into macroevolutionary patterns (radiation onto newly acquired plant lineages). Several predictions that can be tested on phylogenetic trees have been derived from the *Escape and Radiate* scenario (Table 1).

In the years following its publication, *Escape and Radiate* was often interpreted as generating **cospeciation*** patterns; however it is now recognized that it rather predicts the sequential speciation of insects onto an already diversified plant lineage (Janz 2011; Suchan & Alvarez 2015). According to this prediction: 1) the reconstruction of the history of host-plant associations on the phylogenetic trees of insects should reveal **host-plant conservatism***, *i.e.* the use of related plant species by related insects (Winkler & Mitter 2008); 2) the phylogenies of herbivorous insects and their host-plants should be more congruent than expected by chance and the diversification of the insects should lag behind that of their host-plants; this is called sequential evolution (Jermy 1984) or host tracking. Nevertheless, when the association between insects and their host plants is species-specific, a pattern of cospeciation can be expected through simple co-vicariance: geographic barriers affect the differentiation of populations of interacting lineages in a similar way and cause simultaneous speciation events (Althoff *et al.* 2012; Brookes *et al.* 2015; Martínez-Aquino 2016). In these cases, it is geographic isolation and not natural selection that initiates the reproductive isolation of insect populations and subsequent speciation. However, the specificity of the insects and host-adapted traits enhance the probability of shared vicariant events.

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

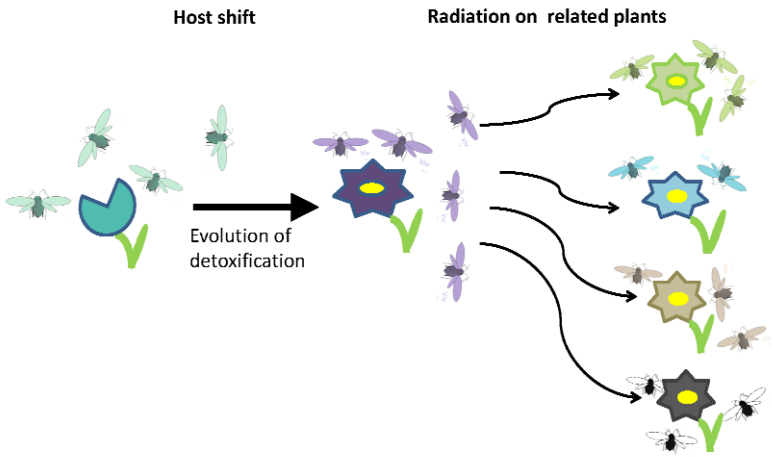
I.2) The *Oscillation Hypothesis* (Figure 1b)

The *Escape and Radiate* scenario was revisited more than a decade ago by Janz and collaborators (Janz & Nylin 2008; Janz *et al.* 2006; Nylin & Janz 2009).

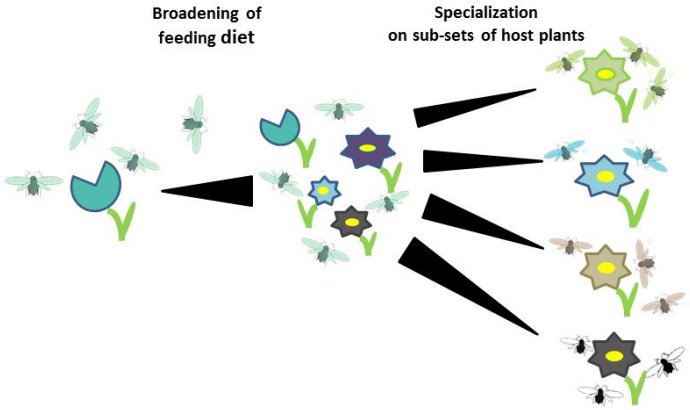
Using butterflies as study systems, they stated that expansions in diet breadth followed by specialisation onto new host-plant species constantly fuel the diversification of phytophagous insects. This has been termed the "***Oscillation Hypothesis*"** (Janz & Nylin 2008).

This hypothesis stipulates that transitions towards a generalist diet generally open up a new adaptive zone, which favours the capture of new host-plants. In this scenario, expansions in diet are enabled by the phenotypic plasticity of insects with respect to host-plants (Nylin & Janz 2009).

a) ***Escape and Radiate*** (Erlich & Raven 1964)



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



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

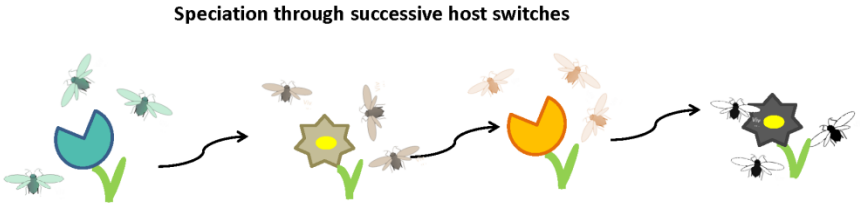


Figure 1: Schematic illustrations of the macroevolutionary scenarios of phytophagous insect diversification.

Population fragmentation and their specialisation onto newly captured host-plants then lead to the formation of new species. Hence this scenario explicitly predicts that species formation results from insect populations evolving towards the utilization of a restricted set of host-plants. Nevertheless, it suggests that this specialization process is often a consequence of the geographic isolation of generalist insect populations in areas inhabited by different host-plant species (Janz *et al.* 2006). Therefore the *Oscillation* hypothesis does not necessarily postulate that natural selection is the main driving force of species formation. However, subsequent papers quoting this scenario emphasize the central role of host-plant specialisation (Hardy & Otto 2014; Nakadai 2017; Wang *et al.* 2017).

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

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

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

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

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

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

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

As opposed to the *Oscillation* hypothesis, Hardy and Otto (2014) proposed an alternative scenario in which speciation in herbivorous insects is driven by host-switching rather than transitions in diet breadth. The authors named their scenario *"**the Musical Chairs**"* (Hardy & Otto 2014). In this scenario, phytophagous insects speciate by the sequential capture of new host-plants and therefore speciation in a plant-feeding insect lineage is merely driven by the number of plants it can colonize. Host-driven speciation remains at the centre of this hypothesis.

The *Musical chairs* hypothesis yields several predictions that differentiate it from the previous macroevolutionary scenarios (Table 1):

- contrary to the *Escape* and *Radiate* hypothesis, the capture of a new host plant lineage does not initiate a radiation;

- contrary to the *Oscillation* hypothesis, gains of new hosts are not associated with host breath expansion (Hardy 2017), host breadth contraction is not associated with cladogenetic events (Hardy & Otto 2014) and overall there should be a negative correlation between host-plant breadth and speciation rates (Hardy & Otto 2014);

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

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 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 *et al.* 2006) - speciation rates higher in lineages with labile host breadth (Hardy & Otto 2014)
Musical chairs	No prediction	Less conservatism of host plants 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)

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

The lack of connection between host breath contraction and speciation events and the negative association between host-breadth and speciation rates clearly differentiate the *Musical chairs* from the *Oscillation* hypothesis. However, several authors have pointed out that if generalist feeding diets are indeed ephemeral as expected when specialization towards host-plants is adaptive, it will be difficult to reconstruct its history accurately on phylogenetic trees (Hardy *et al.* 2016; Janz *et al.* 2016). Consequently, the relationships between host breath and speciation rates will be difficult to explore and the set of predictions that differentiate the *Musical chairs* from the *Oscillation* hypothesis will not always be testable.

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

II Phylogenetic approaches for testing ecological speciation scenarios

II.1) Comparing the phylogenies of plants and insects

Several phylogenetic studies have compared the phylogenies of herbivorous insect and their host-plants. Some have investigated cospeciation patterns using dedicated tools such as tree reconciliation analyses (Conow *et al.* 2010; Page 1994) and distance-based methods for tree comparisons (Legendre *et al.* 2002). These tools statistically test the null hypothesis that the phylogenies of insects and their associated plants are more congruent than expected by chance and that speciation events are simultaneous. As stated above, this is only expected in very specific plant /insect interactions. As predicted by early taxonomic studies (Ramirez 1974; Wiebes 1979), cospeciation has been evidenced in figs and their phytophagous pollinating wasps but the degree of phylogenetic congruency observed varies according to taxonomic groups (see review by de Vienne *et al.* 2013 on cospeciation studies and Cruaud *et al.* 2012). Reciprocal adaptations of plants and insects (*i.e,* **coevolution***) have been unravelled in this study system (Jousselin *et al.* 2003; Weiblen 2004). However, it is not known whether the cospeciation patterns observed are the sole result of this coevolution, i.e. whether reciprocal selection exerted by both partners has driven the reproductive isolation of interacting populations (Althoff *et al.* 2014; Hembry *et al.* 2014), or whether matching speciation events have arisen through co-vicariance. In the other iconic model system for the study of plant/insect **coevolutionary diversification***, the *Yucca*–Yucca moth interaction (Pellmyr 2003), moth phylogenies parallel parts of the evolutionary history of their hosts. Some studies suggest that this pattern is the result of coevolution (Godsoe *et al.* 2009) while others hint towards co-vicariance (Althoff *et al.* 2012). In both *Yucca*-moths and fig-wasps the fact that the

phytophagous insects are specific pollinators of their host-plants and breed inside them necessarily links the reproductive success of the two partners and increases the likelihood of concomitant speciation events. Therefore host-plant adapted traits are certainly pivotal in the speciation process of these insects.

Studies that have investigated **phylogenetic tracking*** between phytophagous insects and their host-plants have shown that insects rarely mimic their host-plant phylogenies (see reviews by de Vienne *et al.* 2013; Winkler & Mitter 2008 and Hsu et al. 2018 for a more recent study); a third of the 20 studies reported in these studies found partial patterns of congruence between insects and host plant phylogenies. In many plant/insect interactions, a simple observation of the patterns of distribution of host plants in the insect phylogeny can actually rule out cospeciation or phylogenetic tracking and studies on plant-insect interactions have moved away from cospeciation studies.

In order to test for successive burst of diversification in plants and insects, many authors have thus simply compared the timing of divergence of plants and associated insects (*e. g*., Brandle et al. 2005; Gómez-Zurita *et al.* 2007; Kergoat *et al.* 2011; Kergoat *et al.* 2015; Leppanen *et al.* 2012; Lopez-Vaamonde *et al.* 2006; McKenna *et al.* 2009; McLeish *et al.* 2013; Pena & Wahlberg 2008; Segar *et al.* 2012; Stone *et al.* 2009; Vea & Grimaldi 2016; Wahlberg *et al.* 2013; Winter *et al.* 2017). Most of these studies suggest delayed colonization of already diversified groups of plants by insects groups at different temporal scales. They are generally based on mere qualitative comparisons of dates of divergence obtained from fossil calibrated phylogenies of both plants and associated insects, but can also include thorough statistical comparisons of dates obtained through phylogenetic methods (Loss-Oliveira *et al.* 2012; McLeish *et al.* 2013). They are often framed as supporting the *Escape and Radiate* theory. However these studies do not give any information on the speciation process behind the diversification of the insect lineages studied, they merely indicate the timing of host plant colonization. The comparison of the **diversification dynamics*** of both herbivorous insects and their host-plants provide a more direct test of host-driven speciation hypotheses: under host-driven adaptive radiation, insect diversification dynamic is expected to roughly follow the diversification of its host-plant lineage. This can be investigated through diversification analyses (see II. 3.2) but can also include the comparison of the fossil records of both insects and plants (Labandeira & Currano 2013; Labandeira *et al.* 1994). In general, the studies of fossil assemblage are decoupled from phylogenetic studies of plant/insect associations. We advocate for combining fossil and phylogenetic evidence whenever possible.

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

II.2.1) Evolution of host associations

Phylogenetic inferences are widely used to reconstruct the evolutionary trajectories of phenotypic traits throughout the diversification of a lineage. Most phylogenetic studies of phytophagous insects map the history of host association onto the resulting trees –at different taxonomic levels (host plant order, family, genus depending on the level of host specialization of the insect clade studied and multistate characters are used when species are polyphagous).

These reconstructions generally suggest a pattern of **host conservatism***. This assertion stems from mere observations of the reconstructions but numerous studies conduct statistical tests. These include the permutation tail probability test (PTP, Faith & Cranston 1991) or some index of phylogenetic signal such as Λ's of Pagel (1999) (see Winkler & Mitter 2008 for a review on host plant conservatism patterns and Leppanen *et al.* 2012; Wilson *et al.* 2012, Hernández-Vera *et al.* 2019 for more recent examples).

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

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

To test this hypothesis, early studies have conducted sister species comparisons of host ranges and more recent studies have reconstructed the evolution of insect ecological niches (defined as the combination of feeding habits and host-plant species) and estimated the number of niche shifts associated with speciation events (Table 2.1). Comparisons of alternative models of evolution of host-use have also been conducted. All studies but one showed that the numbers of niche shifts observed generally represented less than 50% of the speciation events and were lower than expected if the niches were randomized onto the phylogeny. This suggests that ecological speciation is not the main process behind the diversification of these lineages. Authors have also observed that host-use differentiation occurred at the root of the trees and therefore concluded that it played a minor role in recent speciation events (Table 2.1).

We must keep in mind that these methods may overlook many host shifts (shifts that resulted in population extinction). Therefore, the studies that estimate niche differentiation at speciation events probably present an overestimation of the impact of host shifts in speciation. It is nevertheless surprising that such studies have not been conducted on more study systems. This is likely due to the fact that they require a precise knowledge of the range of host-plants used by each insect species.

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 less recent and 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	Geographic isolation is more important than host switching in speciation events
	 Nematinae (125 spp.)	Nyman *et al.* 2010	Investigate niche shifts at speciation nodes through ancestral state reconstruction	Ø	
	 *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 breadthand 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 breadthis 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
	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
	 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 plants	 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 patterns	 *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		√	
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**

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)

II.2.2) Host-breadth evolution

In order to investigate the role of specialization in insect species formation, phylogenetic studies have also investigated the distribution of host breadth throughout the evolutionary history of insects groups. According to the *Oscillation* hypothesis, host breadth should vary along the phylogeny of insects and the character state “generalist” should be transient; i.e. phylogenetic reconstructions should show many transitions between specialists and generalists. Many studies have indeed demonstrated the lability of host breadths (Table 2.2), which is compatible with the *Oscillation* hypothesis but does not prove it.

In order to test whether these changes are linked with speciation, some studies have investigated how gains and losses of new hosts along the phylogenetic history of lineage relate to the number of speciation events (Table 2.3), they obtained mixed support for alternative scenarios.

Maybe another way to investigate the link between ‘host-breadth changes’ and ‘gains of new hosts’ that underlies the *Oscillation* hypothesis, without using diversification analyses (see II.3.3) would be to test for the correlated evolution of these two characters; i.e. explore how often the gain of new hosts is associated with a transition from specialist to generalist.

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

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

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

In contrast to detoxification mechanisms, traits involved in host recognition and host-plant choice (chemosensory traits) have been less studied in a phylogenetic context. However their evolution probably plays as important a role as adaptations to plant defences in phytophagous insect speciation (Smadja & Butlin 2009). Matsuo (2008) showed that an odour binding protein can evolve relatively fast in closely related *Drosophila* species through gene duplications and losses, and proposed that this dynamic could explain the evolution of host preferences in this species complex. Comparative analyses of odour binding proteins and chemosensory proteins from the genomes of several Arthropoda species (Sánchez-Gracia *et al.* 2009; Vieira & Rozas 2011) revealed a high number of gains and losses of genes, pseudogenes, and independent origins of gene subfamilies. This dynamic, if analysed in relation to host

choices and host breadth in a phylogenetic context, could explain some host shifts and subsequent speciation events. Finally, deciphering the evolutionary dynamics of genes involved in mate recognition and their link with host association could also inform us on the role of host-plants in the speciation of insects that feed (and often mate) on them. For instance, Schwander *et al.* (2013) showed that cuticular hydrocarbon profiles involved in mate choices vary among *Timema* species (Phasmatodea), and that most evolutionary changes in hydrocarbon profiles occur in association with host-plant shifts and speciation events in this genus of phytophagous insects.

In summary, many studies have investigated the evolution of detoxification mechanisms in insects, framing their hypotheses within the *Escape and Radiate* theory. Studies investigating changes in traits involved in host recognition throughout the diversification of insects are rare and they are generally not framed within host-plant driven scenarios. Such studies are needed in order to determine which traits underlie host-plant associations and whether their evolution drives speciation events (see Perspectives).

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

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

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

Studies that posit that host-plant adaptation favours phytophagous insect diversification predict that those are much more diversified than non-phytophagous insects. However this assertion deserves to be statistically tested. The first study addressing this question suggested that herbivorous clades contain more species than their non-phytophagous sister clades (Table 2.5). However, comprehensive phylogenies associated with recent comparative methods suggest that several types of niche shifts beside phytophagy can explain insect species richness. Studies within insect orders have mostly been addressed within Coleoptera –as they are by far the most diverse order, but more in-depth analyses of other orders would also be insightful.

To our knowledge likelihood-based character state dependent diversification models (known as, the *SSE models, such as BiSSE, ClaSSE and QuaSSE for binary, multistate and quantitative traits, respectively FitzJohn 2010; Maddison & FitzJohn 2015; Maddison *et al.* 2007), which test whether transition in character states are associated with variations in speciation and extinction rates, have not been yet used to test the role of phytophagy in insect diversification. A robust estimate of diversification parameters by these methods requires dense and random species sampling throughout the phylogeny (more than 15% of the species must be included in the phylogeny in order to conduct unbiased tests, FitzJohn 2010). Therefore *SSE tests await the availability of comprehensive phylogenies in more insect

orders. Nevertheless, a caveat of these diversification models is that they may overlook more complex models involving many unmeasured and co-distributed traits. In particular, for phytophagy, other traits that can drive shifts in diversification may cause a spurious detection of increased diversification rates in phytophagous insects if these trait's states partly correlate with phytophagy, or may instead erase any signal due to phytophagy. The HiSSE model (Beaulieu & O'Meara 2016) which models hidden characters that influence diversification might help untangling these confounding factors.

II.3.2) Testing for adaptive radiation

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

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

Among studies testing adaptive radiation patterns (Table 2.8), few have investigated whether the number of species reaches a plateau after an initial burst of speciation. This is better addressed using density-dependent models of diversification (DDD) that test whether rates of speciation decrease once the number of species supposedly reach the carrying capacity of the novel ecological niche (Etienne *et al.* 2012; Rabosky & Lovette 2008). But these tests can only be applied to lineages in which the number of species in each subclade is well known. In any case, studies generally provided weak support for adaptive radiation scenarios (Table 2.8). They all suggested that the diversification patterns of phytophagous insects cannot solely be explained by the availability of suitable host-plants and suggested that abiotic factors such as geography and temperature should be taken into account in diversification scenarios.

II.3.3) Correlating host breadth with diversification dynamic

Advocates of the *Oscillation* hypothesis suggest that clades showing a higher diversity of host-use (using more host-plant species altogether) should be more diverse than their sister clade (Janz *et al.* 2006), and this prediction has been verified in butterflies, Coccidae and some gall inducing flies (Table 2.9). Although these results support a model where the diversity of phytophagous insects is sustained by the diversity of the hosts they use; they could fit both a model of *Oscillation* and the *Musical chairs* hypothesis. To tell apart the *Oscillation* from the *Musical chairs*, it is more informative to test how host breadth variations affect insect diversification dynamics.

According to the *Oscillation* hypothesis, clades including generalist species should be more speciose than clades including only specialists. Early papers have used fairly basic

methods such as 'sister clade analyses" to test this prediction while more recent investigations have adopted trait-dependant diversification models (Table 2.10). These studies provided mixed support for *Oscillation* scenarios. Furthermore, even when a specific prediction was met, the authors could not always reach a firm conclusion: as previously mentioned, the transient nature of the generalist feeding diet under host-driven speciation scenarios complicates predictions. The negative or positive relationship observed between host breadth dynamics and diversification can always be obscured by the rapid evolution of host breadth (Janz *et al.* 2016; Nylin & Janz 2009). The way host breadth is measured (binary vs continuous) is also known to affect the results (Hamm & Fordyce 2015) and it has been long recognized that categorizing species into either specialist or generalist can be somewhat subjective (Janz *et al.* 2001). Furthermore, although the *Musical chairs* yield specific predictions, those are mainly rebuttals of the *Oscillation* predictions (but see Table 2.11). Yet, rejecting an *Oscillation* scenario does not instantly mean that a *Musical chairs* scenario is at play. Hence despite the existence of sophisticated methods and comprehensive phylogenies, the prevalence of these scenarios in insects is still debated.

Another caveat of these studies lies in the distinction between speciation and extinction rates. Indeed, if specialization towards host plants can accelerate speciation it can also increase extinction risks when host plants are not highly abundant. Consequently, predicting exactly how changes in host-plant breadth affect diversification rates is difficult. Finally diversification methods such as *SSE models are known to generate type I errors (Bouchenak-Khelladi *et al.* 2015; Davis *et al.* 2013; Rabosky & Goldberg 2015), and can thus inflate the role of host plants and host breadth in diversification when those are investigated. It is therefore, highly recommended to conduct the analyses on a set of randomized trees in order to test whether the constrained diversification model (*i.e.* the model in which evolutionary transitions in character states are associated with shifts in extinction and/or speciation rates) is also chosen in these analyses (as in Hardy *et al.* 2016).

Moving away from methodological issues, our survey also underlines that many studies that explore macroevolutionary scenarios have been conducted on Lepidoptera. In order to have a better understanding of the role of host-plant shifts in insect diversification, it seems necessary to test the predictions of macroevolutionary scenarios on more insect groups. Aphids (Hemiptera) could be good candidates for such investigations. Their range of host-plants is well documented (Blackman & Eastop 2006; Holman 2009). Although most aphids are host-specific, some species are polyphagous. Some species are even only polyphagous during part of their life-cycle. This temporary broadening of diet has already been suggested to facilitate the capture of new host-plants (Moran 1992) and subsequent speciation onto these new lineages. These life-cycle transitions could have thus favoured aphid diversification (Jousselin *et al.* 2010; Moran 1992). This scenario actually fits the *Oscillation* hypothesis and should be explored. Other Hemiptera which host plant repertoire is well known such as Coccidae (Garcia-Morales et al. 2016) and psyllids (Ouvrard et al. 2015) could also be used to test the predictions on the role of host breadth evolution in macroevolutionary scenarios. The limitation for these groups for now lies in the availability of robust and comprehensive phylogenies.

III Perspectives

As seen throughout this review, phylogenetic comparative methods provide the template to test hypotheses on the role of host plant association in the speciation of phytophagous insects. While those methods have undoubtedly advanced the field since the *Escape and Radiate* paper, one must keep in mind that phylogenetic comparative methods often constitute mere correlation analyses. Significant associations between character changes and cladogenetic events might arise as a consequence of speciation itself when post-speciational character changes occur. Furthermore, comparisons of models of evolution such as those used in trait-dependent diversification analyses often rely on trees that encompass few transitions in character states and are therefore not always robust (see Beaulieu & Donoghue 2013). In such analyses, the "best model" is not necessarily the true model and significant *P* values should not be interpreted as strong evidence for an evolutionary scenario.

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

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

Geography and ecology are always closely intertwined in speciation scenarios. There have been several studies that have investigated geographic range expansion in herbivorous insects (Becerra & Venable 1999; Slove & Janz 2011); climate induced host shifts (see Nyman *et al.* 2012 for a review and more recently Lisa De-Silva, 2017; Owen *et al.* 2017; Pitteloud *et al.* 2017; Sahoo *et al.* 2017; Sanchez-Guillen *et al.* 2016; Winkler *et al.* 2009) and climate driven diversification dynamics (Kergoat *et al.* 2018). All these studies suggest that abiotic factors are entangled with host-plant changes in species diversification scenarios. However there are few studies that explicitly test the predictions of speciation through geographic isolation (Barraclough & Vogler 2000) and whether these events systematically accompany host shifts or sustain speciation events (but see Jordal & Hewitt 2004; Jousselin *et al.* 2013; Doorenweerd *et al.* 2015; Hardy *et al.* 2016). Such analyses are important if we want to tell whether adaptations to new host plants represent post-speciational changes following geographic isolation rather than the main driver of speciation events. Cospeciation methods that take into account the biogeographic history of interacting lineages (Berry et al. 2018) could also be used to investigate whether host shifts are associated with dispersal events in systems where host-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

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

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

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

Herbivores and the plants they feed on form interaction networks, and as such the structures of the networks can be characterized by several parameters, such as modularity (the propensity of a group of species to interact with a similar set of partners) and nestedness (the propensity of specialist species to interact with generalist species and vice-versa). Antagonistic interaction networks, such as plant-herbivore networks, tend to be highly modular (Thébault & Fontaine 2010). A recent study combining interaction network with phylogenetic approaches on simulated and real datasets predicted that the *Escape and*

Radiate scenario should produce a modular network structure, whereas the *Oscillation* scenario should produce a more nested structure (Braga *et al.* 2018). When applied to real data (two butterfly families, Nymphalidae and Pieridae), this approach revealed that host-plant butterfly networks tend to be both modular and nested, which the authors interpret as being the result of a complex pattern of diversification, involving both episodes of radiation on new hosts (producing modules containing closely related species) and occasional shifts to other host lineages, producing both nestedness within modules and connections between modules.

Additionally, phylogenetic and network approaches could be expanded to encompass other interacting partners (*e. g.,* Ives & Godfray 2006). Indeed, insect-host-plant communities can be seen as ecosystems where biotic interactions, such as parasitism and mutualism also take place (Forister et al. 2012). These partners can indirectly influence the interaction between plants and their herbivores: *e.g*., direct competition (Jermy 1988) apparent competition between herbivores, stemming from shared natural enemies (Holt 1977), and vice-versa (*e. g.,* when herbivory elicits anti-herbivore defences mediated by herbivore enemies, Fatouros et al. 2008). Multitrophic interactions probably explain many diversification patterns in herbivorous insects (Singer, Stireman 2005).

Finally, such approaches could be applied both at a large scale (*e. g*., Braga et al. 2018), to embrace global patterns of diversification and interaction, or at the community level (Ives, Godfray 2006; Elias *et al.* 2013), where interactions actually occur, and where fine-scale processes (*e. g.*, host-plant shift at the species or the population level) can be unveiled.

Conclusions

Many phylogenetic studies of plant-insect associations now include formal tests of macroevolutionary scenarios involving host-driven speciation. In an attempt to summarize the literature on this topic, we show that the predictions of host-plant driven speciation are not 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 used to explain the diversification of phytophagous insects. In order to move towards a standardization of phylogenetic approaches, we propose here a list of relatively simple tests that could be applied to an insect phylogeny to test some of the non-controversial predictions of host-driven speciation scenarios (Fig. 2). The limitations of these approaches 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 often 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.

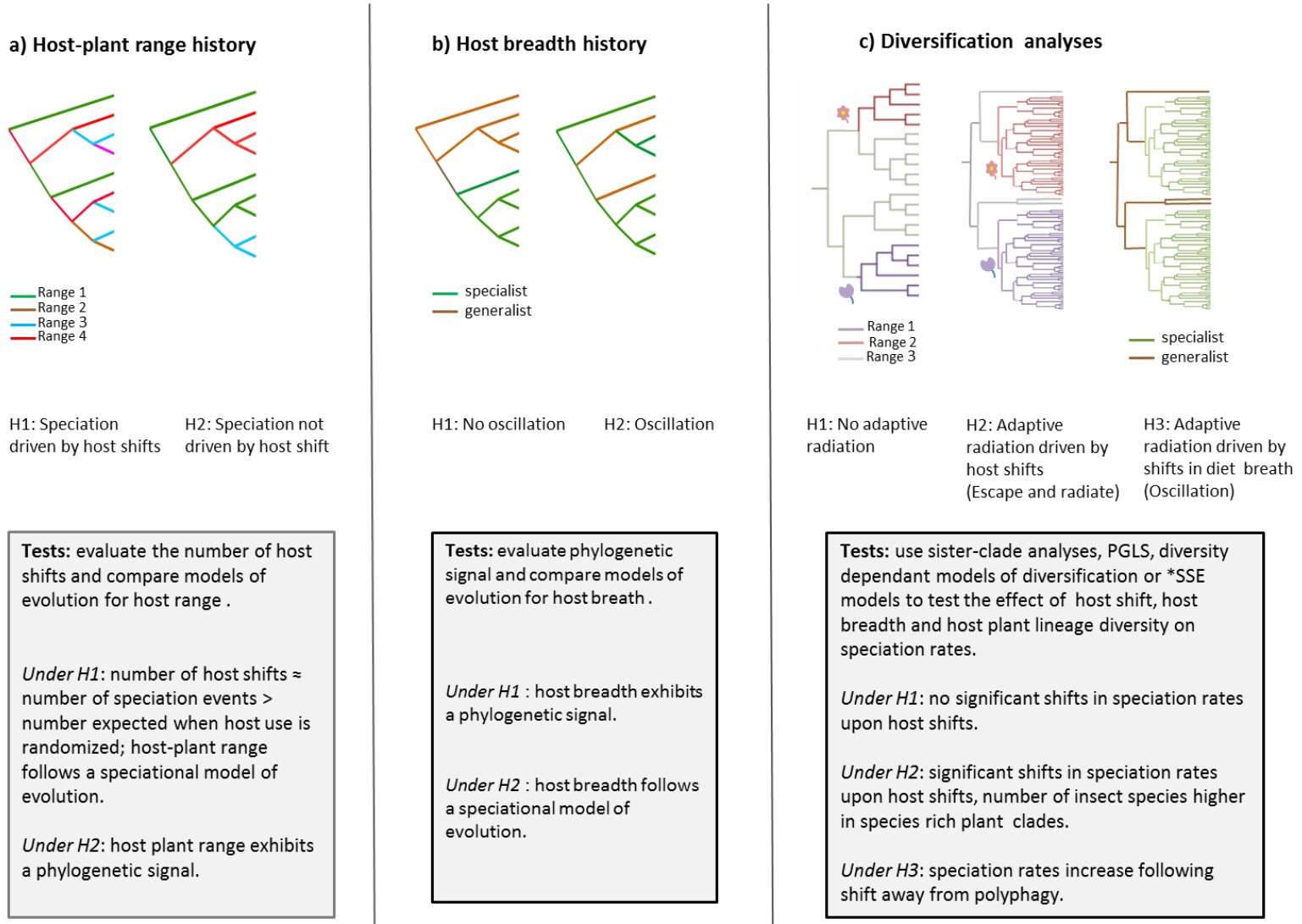


Figure 2: Suggestions of phylogenetic comparative methods that can be deployed to test some of the prediction of host-driven speciation scenarios: a) tests that rely on the reconstruction of host-plant range evolution; b) tests that rely on the reconstruction of host-breadth; c) diversification analyses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

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. Emmanuelle Jousselin and Marianne Elias are recommenders for PCI Evol Biol. Marianne Elias is a member of the managing board of PCI Evol Biol.

Author's contributions

EJ conceived the study, and extensively discussed the topic with ME. EJ wrote the first draft and both authors contributed to this and the previous versions of the manuscript.

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