WHY ARE THERE NOT MORE HERBIVOROUS INSECT SPECIES?

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Insect species richness is estimated to exceed three million species, of which roughly half is herbivorous. Despite the vast number of species and varied life histories, the proportion of herbivorous species among plant-consuming organisms is lower than it could be due to constraints that impose limits to their diversification. These include ecological factors, such as vague interspecific competition; anatomical and physiological limits, such as neural limits and inability of handling a wide range of plant allelochemicals; phylogenetic constraints, like niche conservatism; and most importantly, a low level of concerted genetic variation necessary to a phyletic conversion. It is suggested that diversification ultimately depends on what we call the *intrinsic trend of diversification* of the insect genome. In support of the above, we survey the major types of host-specificity, the mechanisms and constraints of host specialization, possible pathways of speciation, and hypotheses concerning insect diversification.

Keywords: evolution, genetic, host shift, host-plant, host range, intrinsic trend of diversification, phyletic relations, specialization, speciation, herbivorous insect.

INTRODUCTION

Ever since Darwin, laymen and scientists are equally fascinated by the bewildering wealth of life forms on earth. A large proportion of global biodiversity is represented by the described 265,000 plant and 990,000 insect species (Price 2002). Recent models (Hamilton *et al.* 2010, Stork *et al.* 2015, Stork 2018) assume 2–5.5 million insect species. It is generally accepted that roughly half (Schoonhoven *et al.* 1998, Price 2002), but at least one-third (Rainford & Mayhew 2015) of the known insect species relies on plant resources. The role of herbivory in the diversification of insects is generally assumed (e.g. Ehrlich & Raven 1964, Mitter *et al.* 1988, Farrell 1998), and herbivorous insect species richness frequently correlates with host diversity (Novotny *et al.* 2002, Lewinsohn & Roslin 2008, Condon *et al.* 2008*a*, Braga *et al.* 2018). However, the hypothesis that herbivorous insects show higher diversification rates than non-herbivorous ones (Wiens *et al.* 2015) is controversial, because no significant differences were found, e.g. in one of the largest order (Coleoptera), between the number of insect species with and without herbivorous lifestyle (Hunt *et al.* 2007). Moreover, herbivorous insect sister clades differing in die-

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tary patterns, did not differ in species richness (Rainford & Mayhew 2015). A conspicuous feature of this diversity is that ca. 70% of the herbivorous insect species have a narrow host range (Bernays & Chapman 1994, Schoonhoven *et al.* 1998).

Pondering over the number of described animal species Hutchinson (1959) concluded that the diversity of terrestrial plants ensured animal diversity. Small animals like insects were able to subdivide niches and thus avoid competitive exclusion. The resulted complexity provided stability for communities. However, Felsenstein (1981), using a model, pointed out that Hutchinson ignored genetic constraints that hinder reaching the upper limit to species richness set by competitive exclusion. He proposed that natural selection favoured speciation, whereas recombination was the force opposing it. Thus, Felsenstein drew attention to the importance of genetic, i.e. intrinsic, factors limiting the process of diversification.

The vast number and the extremely varied life histories of herbivorous insect species present an excellent model for studying the process of insect diversification. The question of whether ecological (e.g. availability of niches) or genetic constraints are the prime factors determining the rate of diversification in herbivorous insects are still under debate. In general, the conditions for ecological speciation involve genetic differences between populations. For instance, an eco-geographical survey coupled with molecular phylogenetic analysis revealed hidden genetic differentiations and cryptic speciation in the *Bemisia tabaci* Genn. complex adapted to local environmental factors in Ecuador, notwithstanding extreme phenotypic plasticity (Paredes-Montero *et al.* 2020). Phenotypic differences manifested in behavioural, habitat and host preferences may eventually result in reproductive isolation. The demonstration of the genetic background of such differences is a cumbersome task, but has been done for many species (e.g., Wu 2001, Via 2009, Dworkin & Jones 2009, Feder & Nosil 2010, Michel *et al.* 2010). There is a pronounced asymmetry for the favour of genetic constraints limiting diversification convincingly indicated by the phyletic pattern of extant herbivorous insect-host relations. In this paper, we argue that despite existing immense ecological opportunities for speciation, it is most of all the genetic constraints that are limiting diversification, and hence the number of herbivorous species [see papers in Magurran & May (1999) and in the "Speciation" special issue of Trends in Ecology & Evolution 16, 2001), but see Nosil (2012) for discussion of ecological speciation genes].

The reconstruction of species relationships within a clade by molecular phylogenetics can provide information on the rate and timing, and to some extents, on causes of speciation (e.g. Barraclough & Nee 2001, Winkler *et al.* 2018). By a similar approach, we propose that the thorough examination

of extant patterns of insect-plant associations (host-plant relations) enables one to evaluate available hypotheses on insect specialization and speciation explaining the evolution of those patterns. In order to achieve this,

(1) we create groups of herbivorous insects based on host specialization. We think that the specialization in congeneric insect species partly mirrors the phyletic pattern of insect-plant association. Then we discuss factors affecting specialization;

(2) we continue discussing the process and mechanisms of host specialization under neural, physiological and ecological constraints;

(3) we survey the main hypotheses of insect diversification and how far they explain the evolution of the phyletic pattern;

(4) finally, we present genetic (we call them "intrinsic") factors that are, by our conception, ultimately responsible for the process of diversification in herbivorous insects and determine the phyletic patterns of insect-plant associations.

THE PATTERNS OF HOST SPECIALIZATION

The extant pattern of food specialization in herbivorous insects is the result of past specialization and speciation (involving host shifts). Therefore, the patterns themselves can provide information on proposed hypotheses of evolutionary processes. The following main types of pattern may be distinguished in the order from strict specialists to generalists by the limited number of examples:

Type 1. Congeneric insect species utilize one plant species

(a) Utilizing the same organ of the host-plant: e.g. larvae and adults of four *Crioceris* spp. (Coleoptera: Chrysomelidae) may graze side by side on *Asparagus officinalis* L. (Liliaceae) plants (Szabolcs 1973); six *Chelobasis* species (Coleoptera: Chrysomelidae) inhabit the rolled leaves of a single *Heliconia imbricata* (Kuntze) Baker (Heliconiaceae) population (Strong 1982); four *Bruchus* species (Coleoptera: Chrysomelidae) may respectively occupy seeds in a pod of a single *Vicia tenuifolia* Roth (Fabaceae) plant (Jermy & Szentesi 2003); six cryptic species of *Blepharoneura* (Diptera: Tephritidae) are specialized to the flowers of *Gurania lobata* (L.) Pruski (Cucurbitaceae) (Condon *et al.* 2008b); the larvae of 16 species of three related genera in the family of Micropterigidae (Lepidoptera) feed on the liverwort species *Conocephalum conicum* (L.) Underw. (Imada *et al.* 2011), etc.

(b) Utilizing different organs of the same host-plant: e.g. 19 gall-forming *Andricus* species (Hymenoptera: Cynipidae) attack *Quercus robur* L. (Fagaceae)

(Crawley 1998); 14 species of *Asphondylia* (Diptera: Cecidomyiidae) flies cause galls on *Larrea tridentata* (Sessé & Moc. ex DC.) Coville (Zygophyllaceae) (Joy & Crespi 2007); 13 species of *Blepharoneura* live in flowers and seeds of a single *Gurania* sp. (Condon *et al.* 2008*a*), etc.

Type 2. Congeneric insect species utilize congeneric plant species

For instance, nine species of *Phyllobrotica* (Coleoptera: Chrysomelidae) beetles live on nine species of *Scutellaria* (Farrell & Mitter 1990); and 14 species of *Tetraopes* (Coleoptera: Cerambycidae) beetles thrive on 14 species of *Asclepias* (Asclepiadeceae) (Farrell & Mitter 1998).

Type 3. Congeneric insect species are more or less narrowly specialized to species of one plant genus or family

Such plants may be characterized by specific secondary plant compounds. Examples: "crucifer-feeders" like species of *Pieris* (Lepidoptera: Pieridae) butterflies (Braby & Trueman 2006); the larvae of 26 species of the genus *Ectoedemia* (Lepidoptera: Nepticulidae) mine the leaves of *Quercus* species (van Nieukerken *et al.* 2010); 21 *Kladothrips* (Thysanoptera: Phlaeothripidae) species form galls more-or-less monophagously on phyllodes of 14 *Acacia* (Leguminosae) species in Australia (McLeish *et al.* 2007); 12 species of the cone fly genus *Strobylomyia* (Diptera: Anthomyiidae) live on larch (genus *Larix*, Sachet *et al.* 2006); eight gall-forming *Asteromyia* (Diptera: Cecidomyiidae) species live on Asteraceae, sometimes overlapping in host use (Stireman *et al.* 2010), etc.

Type 4. Congeneric insect species are specialized to plant species of different plant families or even of different plant orders

For example, 14 species of *Yponomeuta* (Lepidoptera: Yponomeutidae) moths are narrowly specialized to plant species belonging to four plant families of three plant orders (Menken *et al.* 1992); nine species of the plant hopper *Enchenopa binotata* (Say) (Homoptera: Membracidae) complex are narrowly specialized to tree species from six families in six orders (Lin & Wood 2002); more than a 100 *Longitarsus* (Coleoptera: Chrysomelidae) species feed on at least seven plant families (Fürth 1980, Döberl 1994); of the three species of the closely related leaf-miner *Acrocercops leucophaea* Meyrick (Lepidoptera: Gracillariidae) complex one feeds on Juglandaceae and two on Ericaceae (Ohshima & Yoshizawa 2006); 70 *Athalia* (Hymenoptera: Tenthredinidae) species live specialized on one to four plant families belonging to four plant orders (Opitz *et al.* 2012), etc.

Type 5. Congeneric insect species are polyphagous
with more or less overlapping host ranges

For instance, the larvae of *Agrotis segetum* Denis et Schiffermüller (Lepidoptera: Noctuidae) feed on more than 160 plant species from many plant families (Chumakov & Kuznetsova 2009), whereas the larvae of *A. exclamationis* L. feed on species of at least 16 plant families (http://www.brc.ac.uk/dbif/invertebratesresults.aspx?insectid=386, accessed in September 2020); from the scale insect species (Hemiptera: Diaspididae) *Diaspidiotus perniciosus* Comstock uses species of 81, *D. ostreaeformis* Curtis of 18, and *D. pyri* Lichtenstein of 9 plant families (Kosztarab & Kozár 1988); the sister species of *Papilio* (Lepidoptera: Papilionidae) butterflies strive on Magnoliaceae and Salicaceae (Mercader & Scriber 2007); several *Bactrocera* (Diptera: Tephritidae) species live on 18–19 plant families (Clarke 2017), etc.

Type 6. Two or more of the above patterns
occur among congeneric insect species

For example, *Callosamia securifera* Maassen (Lepidoptera: Saturniidae) survives exclusively on *Magnolia virginiana* L. (Magnoliaceae), whereas *C. promethea* Drury thrives on species of five plant families (Johnson *et al.* 1996); of two *Trypeta* species (Diptera: Trypetidae) that live on *Artemisia vulgaris* L. (Asteraceae), *T. artemisiae* Fabricius is monophagous, whereas *T. zoe* Meigen (*artemisicola*) is polyphagous (Denys & Schmidt 1998); from the 12 *Bruchus* species (Coleoptera: Bruchinae) found in Hungary, *B. rufimanus* Boheman is monophagous on *Vicia pannonica* Crantz, while *B. atomarius* L. is oligophagous being specialized at least to nine host-plant species which belong to two plant genera (Jermy & Szentesi 2003). Even sister species may strongly differ in host relations, e.g. *Heliothis virescens* Fabricius (Lepidoptera: Noctuidae) is polyphagous, whereas *H. subflexa* Guenée is restricted to the species of a single plant genus (Bernays & Chapman 2000); ca. 60% of known *Bactrocera* species are specialists (some are monophagous), whereas ca. 40% polyphagous, some being extreme generalists (Clarke 2017), etc.

The relative abundance of the Types and the diversity of species falling into each are difficult to assess properly, however, given that species with restricted host ranges are dominating most orders where herbivory occurs, Types 3 and 4 seem to be common, followed by Type 6 and 5, whereas Types 2 and 1 can be the rarest of all.

CONSEQUENCES OF THE HOST SPECIALIZATION PATTERNS

The evaluation of the above types of host specialization helps draw conclusions on the evolutionary background of the host-utilization patterns:

(1) Specialization and speciation (host shifts) may not fully depend on the availability of niches, because (i) several congeneric insect species and cryptic species can be specialized to the same organ of a common host-plant (Type 1a); (ii) there exist congeneric polyphagous insect species with more or less overlapping host ranges (Type 5); (iii) there are sister species that have strongly different host ranges (Type 6). Besides, (iv) there occur obligatory host-plant alternations between subsequent generations of insect species with the sequence of narrowly specialized and very polyphagous generations. Such is the case with several aphid species, where host alternations mirror adaptations to ephemeral and more permanent hosts. For instance, in Central Europe, the fundatrix of *Myzus persicae* Sulzer (Homoptera: Aphididae) prefers exclusively peach and, less often, black cherry, *Prunus serotina* Ehrh. (Rosaceae), while the summer generations may occur on more than 400 plant species from various plant orders (Börner & Heinze 1957, cit. Moran 1992). Similarly, four alien, host-alternating cynipid gall wasp species of the *Andricus* genus are established in the British Isles. The life cycles of all involve a sexual generation in spring on *Quercus cerris* L., and an agamic generation in autumn on *Q. robur* L. (Schönrogge *et al.* 1998). The obligatory host-plant change in subsequent generations presents a special case of changing phyletic relations during ontogenesis.

(2) Congeneric (or closely related) specialists on congeneric hosts (Type 2) use ca. 10% of the number of closely related available plant species. For instance, there are at least 62 *Scutellaria* species known in North America (Leonard 1927), however, only nine species are used as host plants by nine *Phyllobrotica* leaf beetle species (Mitter & Farrell 1990). There is a similar situation among seed predator bruchids on legumes of Hungary (Podlussány *et al.* 2001, Jermy & Szentesi 2003). Although congeneric plant species certainly differ in quality and quantity of secondary plant substances, still much niche space remain unoccupied in spite of the probable major chemotaxonomic similarities.

(3) Several congeneric insect species may be specialized to one plant species (Type 1) and may use even the same plant organ or tissue (Type 1a), casting doubts about strong competitive relations (exclusion), and drawing attention to possible within-plant microscale qualitative differences (Crawley 1998, Melika *et al.* 2000, Jermy & Szentesi 2003, Marsteller *et al.* 2009, Clarke 2017).

(4) It is long established that despite the enormous number of herbivorous insect species, the overall consumption rate and biomass removal on plants are generally low in terrestrial ecosystems (McNaughton *et al.* 1991,

Cyr & Pace 1993). Often cited impacts by outbreaks are relatively rare events and they tend to be site-, time- and insect-specific on some plant species. Compositional changes in communities induced by herbivorous insects, e.g. Carson and Root (1999), are the results of complex processes with participation of additional parties like microorganisms, nematodes, etc., or by the contribution of plant competition, whose effects are usually not investigated. Sometimes the effects are subtle, such as in the case of sucking insects whose consumptions are difficult to quantify.

Although herbivorous insects represent a very substantial slice of biotic diversity, their frequency on the average is also very low in natural communities as compared to the frequency of their hosts. For example, in the tropics, it was found somewhat above one individual on 10 plants per plant species (Price *et al.* 1995). Novotny *et al.* (2006) measured a mean of 2.7 Coleoptera and 45.5 Lepidoptera larvae on 100 m^2 foliage of tropical forest in New Guinea. As a consequence, herbivorous insects usually remove an average of 10% or less of living plant tissues (Schowalter *et al.* 1981, Crawley 1983, Seastedt *et al.* 1983, Root 1996, Hartley & Jones 1998, Jermy & Szentesi 2003, Szentesi & Jermy 2003, Rinker & Lowman 2004, Burgess & Chapman 2005, Ruhnke *et al.* 2009, Schwenk & Strong 2011, Turcotte *et al.* 2014, Kozlov *et al.* 2015), and the fossil records also corroborate this (Labandeira & Allen 2007). In spite of the relatively few biomasses removed, herbivory can influence plants' life history in many ways (Myers & Sarfraz 2017).

Clearly, many plant species may remain unoccupied by congeneric insect species, although they are close relatives of the insects' actual host-plants, leaving many *unused resources* ("vacant/empty niches": we use the expression as it is abundant in the literature, but see discussion on this later) both in taxonomic and in plant material senses, a fact that is very little considered (but see Root 1996). The low consumption rate in itself suggests that species packing among herbivorous insect species is not as tight as generally assumed (Price 1983).

(5) Host specialization patterns provide little evidence for the idea that interspecific competition among herbivorous insect species plays a role in specialization and speciation (Rosenzweig 1978, Hood *et al.* 2012). Although the data on competition are numerous (Denno *et al.* 1995, Damman 1993), its importance and role in population diversification are controversial (Lawton 1984, Price 1984, Shorrocks *et al.* 1984, Strong *et al.* 1984, Jermy 1985, Strong 1986, Gurevitch *et al.* 1992, Novotny *et al.* 2002, Després & Cherif 2004, Szentesi *et al.* 2006, Matsubayashi *et al.* 2009). In a meta-analysis, Kaplan and Denno (2007) concluded that there is very little proof that plant-feeding insects conform to theoretical predictions for interspecific competition. They suggested that indirect interspecific effects (i.e. plant- and enemy-mediated interactions; Ohgushi *et al.* 2007) and facilitation were more important, and that induced defence in many plant species made it more difficult to judge

the outcome of competitive relations. Somewhat later, DAUGHERTY (2009) has shown that food specialization promotes the coexistence of competing insect herbivores, i.e. guilds with different feeding modes could coexist. However, interspecific competition does not always play a role in shaping guilds of herbivorous insects (SZENTESI *et al.* 2006). The phylogenetic analysis of Nematinae sawflies (Hymenoptera: Tenthredinidae) indicated that numerous species occupy near identical niches questioning the role of direct or indirect competition in forming the assemblies (NYMAN *et al.* 2010).

As for the role of interspecific competitive exclusion in macroevolutionary events during the history of life, there is no evidence for it by BENTON (1987) and MASTERS and RAYNER (1993). Furthermore, its ecological and evolutionary effects can be the opposite (ABRAMS 1990). The mere demonstration of competition is not equivalent with its role in speciation (FEDER *et al.* 1995). Models indicate that competition can facilitate fast evolutionary changes in multispecies communities (KOPP & MATUSZEWSZKI 2014), and it may even cause host shift speciation in herbivorous insects. However, even if specialization prevails among herbivorous insects, interactions are not restricted to pairwise effects in communities; rather diffuse competition of lower intensity is more probable.

(6) Concerning only herbivorous beetles, the driving force of bursting species richness is connected to the Cretaceous angiosperm diversification *a posteriori*, and not only a lower diversification rate is assumed for beetles than for angiosperms (ZHANG *et al.* 2018), but a connection of diversification rates of beetles and angiosperms is lacking. Therefore, the high species diversity of beetles reflects a long phylogeny and low extinction rates (HUNT *et al.* 2007, CONDAMINE *et al.* 2016). It is also debated how fast the impact of flowering plants manifested on phytophagous insect diversity (KERGOAT *et al.* 2017).

It is a frequent argument that the clades of plant-feeding insects are more species-rich (speciose) than those of non-herbivorous ones (MITTER *et al.* 1988, FARRELL *et al.* 1991, FARRELL 1998). However, the statement is controversial, and the herbivorous nature itself cannot explain the total diversity (BARRA-CLOUGH *et al.* 1998, HUNT *et al.* 2007). Furthermore, species-rich taxa not only do not necessarily have higher diversification rates (MAYHEW 2002), but clade age and species richness do not correlate (RABOSKY *et al.* 2012). Among families of herbivorous insects, there are speciose and non-speciose genera. For example, the scale insect family Diaspididae comprises 157 genera with 654 species in the Palaearctic Region: the six largest genera count 170 species, whereas there are 63 (40.1%) monotypic genera (KOZÁR & WALTER 1985). The moth family Noctuidae counts 349 genera with 1863 species, and the number of species in the six largest genera is 392, but there are 252 (72.2%) monotypic genera (FAUNA EUROPEAE 2004). The 10 cynipid gall wasp genera occurring on

Quercus species in East-Central Europe have 94 species: *Andricus* comprises 69% of all species while five genera are monotypic (Melika *et al.* 2000).

The relative number of species reflects differences between speciation and extinction rates. Since the extent of past extinctions cannot be revealed precisely, the number of species is often regarded as expressing approximate relative speciation rates. Barraclough *et al.* (1999) found that the number of species in a clade and rates of genetic change taking place in plants can be positively connected and mirrored by the branch length (actually the rate of nucleotide substitution). Furthermore, the rate of molecular evolution (mutation rate) and speciation are closely connected (Barraclough & Savolainen 2001, Allen *et al.* 2006, Venditti & Pagel 2010), stressing the significance of genetic changes in speciation (Butlin *et al.* 2009, Nosil & Feder 2012, The Marie Curie Speciation Network 2012).

Particular traits, e.g. "key innovations" (Heard & Hauser 1995, Berenbaum & Feeny 2008, but see Hunter 1998) can speed up species-level diversification rate resulting in substantial differences in species richness among related clades (Rabosky & McCune 2010). It seems likely that such punctuation stages (Elena *et al.* 1996, Webster *et al.* 2003, Pagel *et al.* 2006) characterized by rapid evolutionary events, are in connection with changes in mutation rates and/or circumstances allowing higher manifestation levels of beneficial mutations (Stern & Orgogozo 2009), resulting in an intensive diversification rate of insect lineages. On the one hand, Janz *et al.* (2006) demonstrated that those sister clades of nymphalid butterflies that differed the most in species numbers actually did not typically differ in host-plant range (therefore, the difference in diversity must be for other reasons). On the other hand, Venditti *et al.* (2010) submitted evidence from investigation of a number of phylogenetic trees that the speciation rate of animal, plant and fungal taxa was not only constant in 78% of the cases, but it was the result of rare random events, behind which we can assume mutations.

What can we draw from the above points? First, the ratio of congeneric plant species occupied by congeneric insect species ("vacant niches" in a phyletic sense) is generally low. Second, congeneric insect species may be specialized to the same organ of their host species. Third, the overall exploitation rate of host material by the insects ("vacant niches" in resource availability sense) is low. All these suggest that competitive exclusion is unlikely to affect specialization and even less speciation of herbivorous insects. Rather, the occurrence of related speciose and non-speciose insect genera with identical or very similar demands for food (host) and other niche dimensions (abiotic factors) might suggest that insect speciation rate can depend on intrinsic (genetic) instead of extrinsic (ecological) factors.

THE PROCESS OF HOST SPECIALIZATION

Specialization of insect herbivores involves ecological and genetic (antagonistic pleiotropies or linkage disequilibrium) trade-offs (Agrawal *et al.* 2010, Vamosi *et al.* 2014), although these may not always be detected (Remold 2012). The trade-offs in host recognition (preference) and host use (performance) may involve negative fitness correlations on different hosts, but these are not always found (e.g. Agosta & Klemens 2009). Specialization by trade-offs, on the one hand, reduces niche-width and can increase the probability of stochastic extinctions if there is a negative correlation between preference and performance. On the other, a positive genetic correlation between the two might promote sympatric speciation. However, trade-offs can also originate from anatomical and physiological constraints and restrain further specialization. Here the first can refer, e.g. to the limited capability of the insect brain due to its size or to the frequently rudimentary dispersal ability to get to a new plant species as a consequence, for instance, of small body size. Physiological limits include lack of detoxifying enzymes when a plant species having unusual allelochemicals is encountered, shifts in diapause initiation, as well as changes in chemoreceptor sensitivity to sex- or host-specific chemicals.

Although it is generally assumed that specialization of herbivorous insects is – for several reasons, like decreased competition, enemy-free space, etc. – adaptive, it is not necessarily so: fragmented populations of scale-insects with limited dispersal are frequently isolated (Hardy *et al.* 2016), and host specificity is created by mutations and genetic drift, and without trade-offs (Gompert *et al.* 2015), as described in details by the "specialization-by-drift" hypothesis. However, specialization *per se* is not the cause but the consequence of diversity (see e.g. Armbruster & Muchhala 2009). We think that, although numerous factors evoke diversification, the ultimate processes generating diversity are genomic changes. Nevertheless, specialization influences speciation, e.g. through reproductive isolation.

Neural and physiological constraints

The sensory-physiological background of specialization has been studied first by Waldbauer (1962). In his classical experiment, maxillectomized caterpillars of *Manduca sexta* L. (Lepidoptera: Sphingidae) readily consumed the leaves of several non–host-plant species and grew on them normally, indicating that host specificity is determined primarily by the insects' host recognition traits. This has been proved repeatedly by behavioural and sensory-physiological studies (see Schoonhoven *et al.* 1998 for references). Thus, due to the limits of host recognition ability, the actual host range of a specialist

insect species is often narrower than the range of plant species that could serve as suitable food for the developmental stages (Wiklund 1975, Jermy & Szentesi 1978, Kibota & Courtney 1991, Gratton & Welter 1999, and others). In other words, host hierarchy in female oviposition preference and larval performance does not match. A meta-analysis on female oviposition preference and larval performance (Gripenberg *et al.* 2010) revealed that (a) although in several instances the female oviposition preference did not coincide with larval performance, there was generally an agreement between the two, (b) the progeny survived better on the plants preferred for oviposition, (c) females laid more eggs on plants where larval survival was higher and, (d) the more specialized (oligophagous) species were able to make sharper choices than generalists (polyphagous ones). The results might also refer to the limited neural capability of insects (Jermy *et al.* 1990, Bernays & Wcislo 1994): first, females cannot recognize and/or neurally process the substrate's suitability for larval development, which may be a serious constraint to host expansion. Obviously, natural selection favours females that do exercise distinctions among substrate suitability for larval development. Second, polyphagous species must select among a larger set of choices than specialists, in spite of the neural limitations (Bernays 2001). The lack of a strong correlation between preference and performance in the case of polyphagous herbivorous insects might refer more to neural processes than to plant quality (Carrasco *et al.* 2015). The high propensity of polyphagous species for learning can assist to optimize choice (Papaj & Prokopy 1989, Szentesi & Jermy 1990).

Ehrlich and Raven (1964) drew attention to the importance of genetic changes (recombination or mutation) in host specialization. The evolution of host recognition traits is driven by heritable changes that can alter an insect's host selection behaviour, even from monophagy to polyphagy and *vice versa*. Such a case has been found with a polyphagous mutant of the silkworm (*Bombyx mori* L., Lepidoptera: Bombycidae) that differed from the monophagous normal population supposedly just by one gene (Dethier 1987, Asaoka 2000). Furthermore, according to Berenbaum and Feeny (2008) the same P450 detox gene family may be involved both in host-plant selection by adults and host-plant utilization by larvae of *Papilio polyxenes* Fabricius, explaining the agreement in female oviposition preference and larval performance. Changes in the gene superfamily might have played an important role in host-usage evolution (Calla *et al.* 2017). Nevertheless, for most cases, it is not clear whether the inability to recognize a plant species as a host by an herbivorous insect species is due to the loss of chemoreceptor functions to a family of particular plant compounds or the lack of detoxifying enzymes or both. Such cases lead to even more restrictive preference/performance potentials, hence decreased propensity to diversification.

Host shifts

Winkler and Mitter (2008) estimated that ca 50% of the speciation events are host shifts. According to Nyman (2010: 395) the "…present insect-plant associations mainly are a result of continuous host-shifting among pre-existing host taxa". The macroevolutionary changes in host range are primarily host (or niche) shifts (Janz 2011, Merrill *et al.* 2013), even though plant-mediated speciation is possible without host shift (Zhang *et al.* 2015). Host shifts are also present in systems, such as obligate brood pollination (Hembry & Althoff 2016) or in cryptic species complexes (e.g. in *Nemorimyza posticata*, Diptera: Agromyzidae) where host specialization might be associated with habitat specialization (Mlynarek & Heard 2018). Host shifts in insects among closely related plant taxa resulting from heritable changes most likely involve mutations, deletion of effector genes, whereas among more distant plant groups include the horizontal transfer of complex sets of effectors (Barrett & Heil 2012). Proximal causes are receptor modifications (Menken & Roessingh 1998) through gene duplications (Suzuki *et al.* 2018) or loss-of-function mutations, as aptly demonstrated in Drosophilidae by Dworkin and Jones (2009) and Goldman-Huertas *et al.* (2015). It seems that loss-of-function mutations affecting host preference are important in host shifts (Vertacnik & Linnen 2017). While host plant use is controlled by autosomal genes in *Heliconius melpomene* and *H. cydno*, it appears in linkage with morphological patterns and habitat, promoting reproductive isolation (Merrill *et al.* 2013).

Host shifts can include "host range expansion", when both the ancient and the new host are kept in use, and "*sensu stricto* host shifts", when the ancestral host is not used any more. Below three main types of host shifts is distinguished based on hosts' phylogenetic distances, however, that may retain both major versions (Jermy 1991):

"Sliding host shift" occurs if the resulting new host recognition (preference) trait makes the new insect strain recognize a non–host-plant as host. For example, the new host's phytochemical profile (phytochemical Gestalt; Dethier 1967) perceived by the insect, differ only slightly from the parental host ("tracking plant chemical evolution": see Berenbaum & Passoa 1999, Bernays 2001, Murphy & Feeny 2006, Wilson *et al.* 2012, Endara *et al.* 2018) so the new host will be a close relative of the parental one (Type 2 pattern above).

"Jumping (saltationary) host shift" results if the new insect strain's host recognition trait happens to be tuned to a very different complex of plant characters; in that case, the new host will be unrelated to the parental host (Types 3 and 4). For instance, with the help of the newly appeared key innovation, a glucosinolate detoxification system, the clade of white butterflies (Pieridae) living on the ancient legume hosts, was able to shift to the Brassicales (Wheat *et al.* 2007). It had to be also accompanied by appropriate chemosensory and

perceptual changes for the recognition of the new hosts. Such changes must have taken place in psyllids (Psylloidea) too, showing host-use throughout the angiosperm orders (Ouvrard *et al.* 2015).

"Within-host shift" occurs if the preference trait of the new insect strain is tuned to a specific part or to a developmental age class (Zhang *et al.* 2015) of the parental host-plant species, which was avoided by the insect species before (Type 1b pattern). It has been shown that this type of host shift was significantly more frequent in gall-forming wasps of the *Andricus* genus, than sliding host shifts (Cook *et al.* 2002).

Types (1) and (2) represent two ends of a continuum (Jermy 1991). The extent of changes should be the widest in case of jumping host shift to provide the conditions for colonizing distantly related or very different plant taxa.

Ecological fitting (exaptation or preadaptation)

An insect species encountering a plant species for the first time in its evolutionary history may immediately recognize and use it if the insect's host recognition and host utilization traits that have evolved elsewhere happen to be tuned (preadapted) to the new plant (Janzen 1985, Agosta 2006). Besides the well-known case of the Colorado potato beetle (Hsiao 1978), there are several further examples (see Ohmart & Edwards 1991, Cipollini & Peterson 2018). Thus, such a host shift does not initially involve evolutionary or genetic changes (Gillespie & Wratten 2011), because it is an outcome of phenotypic plasticity (Mason 2016). The presence of preadaptation (and the lack of trade-offs) is especially likely in cases, where a positive response is received, such as in cross-host correlation performances (García-Robledo & Horvitz 2012, Ueno *et al.* 2017). Although no speciation takes place, still it is possible that such a host shift is encouraged by cryptic genetic variations that might speed up preadaptation, because they can contain new genotypes preadapted to an altered environment (Hayden *et al.* 2011). Host shift by exaptation is far more frequent even in tight host-parasite associations (parasite paradox), being a major source of diversification in comparison with cospeciation (Agosta *et al.* 2010, Araujo *et al.* 2015).

Phenotypic plasticity

The significance of phenotypic plasticity in generating novel phenotypes, diversification, and ultimately, speciation is not yet properly understood, although its importance is becoming recognized (Agrawal 2001, West-Eberhard 2005*a,b*). Diet can change gene expression producing new phenotypes, as demonstrated in *Oedalus asiaticus* grasshoppers (Huang *et al.* 2017). Host

shifts may be initiated by phenotypic plasticity (Mason 2016). Such environ-
mentally selected phenotypes indirectly affect a whole suit of traits, possibly
promoting divergence among populations. Nylin and Janz (2009) suggested
that host shifts of butterflies might result from the plasticity of the females'
egg laying behaviour. Females of some species may lay eggs mistakenly onto
non–host-plant species. If the emerging larvae can grow on that non-host,
they enter the phase of *phenotypic accommodation* (West-Eberhard 2005*b*).
If this process is repeated for several generations, first phenotypic fixation
happens without selection, finally divergent natural selection may result in
genetic accommodation (West-Eberhard 2005*a*), i.e. in an insect line adapted
to the former non–host-plant as host, or by the loss of plasticity leading to
genetic assimilation (Ehrenreich & Pfennig 2016). Actually, the whole process
is determined primarily by the insects' genomes as phenotypic accommoda-
tion means phenotype-frequency change due to gene frequency change that
results from natural selection (West-Eberhard 2005*b*). However, Nylin and
Janz (2009) emphasize that host shifts start without any genetic change and
natural selection acts on genes only at a later stage. The same process explains
events taking place during female preference and larval performance. Based
on their studies on nymphaline butterflies, Janz and Nylin (2008) proposed
the *plasticity* or *oscillation hypothesis* of host-plant range evolution according
to which specialists may enter a state of host range expansion (generalist)
which enables the radiation into more specialists and *vice versa.* Such alter-
nating stages would then be considered the driving force of diversity (Wein-
gartner *et al.* 2006, Nylin & Wahlberg 2008), but see Hardy and Otto (2014),
and Hamm and Fordyce (2015) for different opinions. A substantial element
of the theory is preadaptation in the lineage-history to plants not yet used.
The diversification of the Papilionidae generally supports the 'oscillation hy-
pothesis' (Scriber 2010) and Wang *et al.* (2017) conclude that even a high level
of plasticity, e.g. in the polyphagous subfamily of Lymantriinae, promote di-
versification. Although Janz *et al.* (2006) and Vamosi *et al.* (2014) also con-
cluded that the oscillation hypothesis would make the idea improbable that
specialization can be a "dead end", there are cases when it seems true (Day
et al. 2016). However, Hardy and Otto (2014) found that the host range and
diversification rate were negatively connected and seldom coupled with spe-
ciation. Instead, host shifts dominated, and we assume that such transitions
need substantial genetic changes.

Epigenetically mediated effects, such as imprinting on chemical cues of a
host (Szentesi & Jermy 1990) and resource polyphenism facilitating diverged
resource-use (Pfennig *et al.* 2010) may initiate processes eventually resulting
in assortative mating and reproductive isolation. For example, the evolution of
preference for apple in *Rhagoletis pomonella* Walsh (Diptera: Tephritidae) was

due primarily to an allele for the positive response of the fly to apple odour and an allele for negative response to non–host fruit odours (Feder & Forbes 2008). Another example of phenotypic divergence leading to speciation is the walking stick, *Timema cristinae* Vickery (Phasmatodea: Timematidae) (Nosil *et al.* 2002). Although phenotypic plasticity provides immense possibilities to take advantage of different environments (Wund 2012, Draghi & Whitlock 2012), these depend on the genetic variation underlying phenotypic plasticity.

MODES OF HERBIVOROUS INSECT DIVERSIFICATION

The several ways of how species achieve reproductive isolation are discussed in excellent reviews (e.g. Coyne & Orr 1998). Below we briefly survey the main types of herbivorous insect speciation with special reference to the role that plants may or may not play in the process. It is worth noting, however, that the importance of chance events in speciation is largely underrated or usually not even considered, but see Master and Rayner (1993), West-Eberhard (2005a), Jablonka and Lamb (2005), Venditti *et al.* 2010, Losos (2011), Forister and Jenkins (2017).

Plant-mediated speciation

Ehrlich and Raven (1964: 602) proposed that "If a recombinant or mutation appeared in a population of insects that enabled individuals to feed on some previously protected plant group, selection could carry the line into a new adaptive zone" where they "would be free to diversify largely in the absence of competition from other phytophagous animals." This *escape-and-radiate* model is echoed by the hypothesis of *ecological speciation,* which proposes that divergence is driven by divergent natural selection between environments and that ecological speciation is a common means by which new species arise (Rundle & Nosil 2005, Schluter 2009). Several authors stress the primary importance of selection exerted by the plants in the maintenance of genetic variation and speciation of herbivorous insects (Schluter 2001, 2009, Via 2001, Berlocher & Feder 2002, Drès & Mallet 2002, Funk & Nosil 2008, Fry 2003, Mayhew 2007, Nosil *et al.* 2009, Nyman 2010, Scriber 2010, Nosil 2012, Gloss *et al.* 2016).

Reproductive isolation emerges as a pleiotropic side-effect of divergent natural selection acting on host shifts, as it has been found with cases of sympatric host race formation (Carroll & Boyd 1992, Becerra & Venable 1999, Abrahamson *et al.* 2001, Nason *et al.* 2002, Diegisser *et al.* 2008, Winkler *et al.* 2009, Linnen & Farrell 2010, Peccoud & Simon 2010, Henniges-Janssen *et al.* 2011). It has been suggested that major host shifts that bridge plant families or

plant orders are followed by increased insect speciation (Farrell *et al.* 1991, Nylin & Wahlberg 2008, Fordyce 2010). However, this is not at all a general rule (Futuyma & Agrawal 2009) as, for example, the species of the European *Yponomeuta* genus shifted between four plant families of three plant orders, yet the genus comprises only 14 species (Menken *et al.* 1992); the North American *Enchenopa* species complex shifted between six plant families of six orders, yet it counts only nine species (Lin & Wood 2002). Furthermore, speciation in Micropterigidae was due to geographical isolation rather than to niche shifts (Imada *et al.* 2011). The striking differences in the extent of speciation after host shifts may mirror the genetically based propensity (speciose character) of insect clades to diversify.

The same can apply to the assumption that the high rate of herbivorous insect diversification found in the tropics results from floral diversity (Fordyce 2010, Mullen *et al.* 2011). It is possible, however, that insect diversification is not driven by the availability of more niches, rather it is the consequence of the likelihood of a new insect line with new host recognition traits "to hit" a new host species and the probability of ecological fitting. In addition, the likelihood of selecting recessive alleles of specific host recognition traits in phenotypically plastic insect lines can be higher in the tropics. Anyway, floral species richness may facilitate diversification of insect clades only, which are prone to diversify.

An important tenet of Ehrlich and Raven's (1964) escape-and-radiate model is the freedom of an insect population to diversify in the absence of other phytophagous competitors. The adaptive zone concept is essentially equivalent with the *enemy-free space* (Jeffries & Lawton 1984, Mlynarek *et al.* 2017), because plants or herbivorous insects would be not only temporarily free of their natural enemies (*enemy release*) but can radiate in both, although the escape-and-radiate model does not explicitly consider top-down effects. Yet for now, both remained largely conceptual issues with much debates and little evidence (Bernays & Graham 1988, Berdegue *et al.* 1996, Gratton & Welter 1999, Heard *et al.* 2006, Bunnefeld *et al.* 2018). *Ecological opportunity* (Yoder *et al.* 2010, Stroud & Losos 2016, Sahoo *et al.* 2017) comprises both, and it should be discerned from *ecological fitting*, which implies exaptation only. Host shifts might provide enemy-free space, however, host shift is not the result of enemy-free space, as it needs complex, concerted gene expression (Jermy 1988, Barrett & Heil 2012, Vertacnik & Linnen 2017). Nevertheless, enemy-free space can promote maintenance of already specialized races, such as *Acythosiphon pisum* (Homoptera: Aphididae), an oligophagous aphid (Vosteen *et al.* 2016), albeit its effectiveness to impair predation or parasitisation is doubtful, as most natural enemies hunt by vegetation structure and/or plant volatiles of injured plant tissue.

As for the genetic background of speciation in herbivorous insects, there are two restricting factors. First, the absence of phenotypic variation in host recognition traits (Jermy 1993, Caillaud & Via 2000), which is the prerequisite for host shifts, may result in speciation. Second, the new insect line can be established only if the larvae perform successfully on the new host-plant species. Thus, a prominent aspect of the process is the female's preference and larval performance relationship. The limited expression or loss of some genes may constrain the evolution of specialists, such as in the case of *Drosophila sechellia* Tsacas et Baechli (Dworkin & Jones 2009), decreasing chances for speciation and restricting host-use only on similar hosts. As a proximal genetic mechanism, Egan *et al.* (2008) found so-called "outlier loci" subjected to strong divergent selection in maple- and willow-associated *Neochlamisus bebbianae* (Coleoptera: Chrysomelidae) leaf beetle populations.

Populations follow different evolutionary trajectories even in a homogeneous environment (Buckling *et al.* 2009). However, the upgrading of microevolutionary changes to macroevolution (Reznick & Ricklefs 2009, Chouard 2010) in such cases remains one of the great puzzles. It is possible that the genetic mechanisms connecting divergence and reproductive isolation between populations are missing, blocking the critical step between the two stages (Rundle & Nosil 2005). For example, recombination powerfully counterbalances the effect of pleiotropy and linkage disequilibrium.

Mutations vary considerably in their effects on speciation events. Those causing pleiotropy can still decrease fitness because of simultaneous positive and negative effects but can produce extreme phenotypes of quantitative traits (Stern & Orgogozo 2009). Those responsible for epistasis may decrease the rate of evolution, although they enhance phenotypic variance. Mutations can reduce the plasticity of the phenotype. Still, mutations are rarely the direct source of variation, and the rate of evolutionary change is restricted more by natural selection and less by the availability of genetic variation (Futuyma 2010). The direct effect of a mutation causing speciation through loss of enzyme function is known in *Drosophila pachea* Patterson et Wheeler (Diptera: Drosophilidae, Lang *et al.* 2012), and "speciation genes" responsible for postzygotic reproductive isolation (hybrid sterility, incompatibility) are also reported (Presgraves 2010). However, how frequent is this way of speciation among herbivorous insects is not known. Most probably, it is extremely rare, considering that a change in olfaction, taste and oviposition behaviour would need orchestrated modifications of gene complexes regulating such traits (Futuyma 2010).

It is likely that the random nature of genetic change greatly reduces the probability of the emergence of an insect line with a new complex of female oviposition preference and larval performance traits, which are tuned to a non–host-plant species whose occurrence in the surrounding flora also is a chance event representing a serious ecological constraint.

Non–plant-mediated speciation

This type of speciation is created by mechanisms such as random events, including polyploidisation, gene duplication, hybridization, drift, founder effect, QTL-regions, mutations, etc. (Feder *et al.* 2012, Doellman & Feder 2019). For instance, in cases when congeneric insect species are specialized to the same organ of one plant species (Type 1a), plants may not mediate insect speciation. The occurrence of cryptic species with identical host preferences (e.g. Marsteller *et al.* 2009, Forbes *et al.* 2013, Winkler *et al.* 2018) indicates that, in such cases, modes of speciation could have operated other than ecological speciation. Key-innovations (either developmental, such as the complete metamorphosis [Rainford *et al.* 2014], or biochemical, such as the nitrile specifier proteins in Pieridae [Wheat *et al.* 2007]), suddenly appearing during evolution also indicate non-ecological speciation.

Allopatric speciation occurs in geographically isolated populations the evolution of which is unconstrained by gene flow and recombination (Mayr 1963), however, genetic differentiation can start before geographic isolation materializes (Abrahamczyk *et al.* 2014). Phylogenetic analysis of Micropterigidae (Imada *et al.* 2011), "higher Nematinae" (Nyman *et al.* 2010), or some dipterous *Blepharoneura* (Ottens *et al.* 2017, Winkler *et al.* 2018) demonstrate such cases. The latter species today utilize near identical niches in multiple sympatric non-interbreeding populations.

Sexual selection has been shown to be one important means of non-ecological speciation. Condon *et al.* (2008*b*) even regard it as an accelerator of diversification, and mutations can be important in the process (Phillimore & Price 2009). It is based on differences, e.g. in courtship behaviour using wing shape (Marsteller *et al.* 2009), wing pattern (Giraldo *et al.* 2008), sound signals (Lin & Wood 2002), sex-pheromones (Yasukochi *et al.* 2011), etc.

Polyphagous insects (Type 5) present a special case in speciation as some species were found to be comprised of populations narrowly specialized to different plant species (e.g. Drès & Mallet 2002, Carletto *et al.* 2009, Peccoud *et al.* 2009). In such cases, speciation may occur via host race formation, while in "genuine generalist" species, such as in the green peach aphid (*Myzus persicae*) feeding on more than 100 plant species in 40 families, the role of plants in speciation is questionable. The acceptance of a new plant species is possible by rapid transcriptional plasticity of aphid-specific multi-gene copies (Mathers *et al.* 2017). Speciation is hardly mediated by plants *per se* with these, since among narrowly specialized congeneric species polyphagous ones also occur. For example, in Type 6 *Callosamia securifera* and *C. promethea* (Johnson *et al.* 1996), *Trypeta artemisiae* and *T. zoe artemisicola* (Denys & Schmidt 1998), *Heliothis virescens* and *H. subflexa* (Bernays & Chapman 2000), and the Central European *Bruchus* species (Jermy & Szentesi 2003) represent such species

groups. These cases may indicate that the rate of specialization and speciation is primarily influenced by the speciose character (i.e. propensity to radiate) of the insects' genomes rather than by the surrounding flora.

Recently, the role of habitat modification due to climatic changes, even ambient temperature and (bio)geographic events has also received greater emphasis in speciation (Rundle & Nosil 2005, McKenna & Farrell 2006, McLeish *et al.* 2007, Winkler *et al.* 2009, Ezard *et al.* 2011, Joy & Crespi 2012, Hua & Wiens 2013, Ben Slimen *et al.* 2017, and others). Species with wider host ranges have larger geographic ranges (and *vice versa*), and such changes could provide opportunities for population fragmentation and specialization (Slove & Janz 2011).

WHY ARE THERE NOT MORE HERBIVOROUS INSECT SPECIES?

Constraints are internal and external mechanisms that jointly and simultaneously influence responses to selection (Hansen & Houle 2004, Schwenk & Wagner 2004). We use the same notion here by emphasizing the effects of those factors that restrict the diversification of herbivorous insects.

External (ecological) constraints

In a previous section, we argued against the role of competition in shaping specialization and speciation among herbivorous insect species. If competition is less important, the radiation through ecological release (Yoder *et al.* 2010) is less likely too. It is also a conceivable question whether an adaptive zone accumulates more species and whether these are freer of enemies than other species elsewhere. Nyman *et al.* (2007) investigated the questions in the case of *Salix* species, and their gall-forming tenthredinidid insect species, including parasitoids of the latter. They found that the escape-and-radiate hypothesis was too simple an assumption. There was no increase in species number after getting to an adaptive zone. The species richness was lower in the parasitoid-poor *Euura* (Hymenoptera: Tenthredinidae) clade compared to the one having a rich parasitoid community. On the contrary, Feder (1998) contributes the lower parasitisation of *R. pomonella* on apple to enemy-free space, and Nosil and Crespi (2006) attribute the divergent selection on *Timema* to predation. While Weingartner *et al.* (2006) and Janz and Nylin (2008) consider the plasticity hypothesis a more plausible scenario over escape-and-radiate, Fordyce's (2010) findings are in agreement with the latter.

As mentioned earlier, escape-and-radiate and enemy-free space, described as adaptive zones, characterized by the absence of competition, yet radiations are taking place. As they are connected with the niche concept, we

consent with Masters and Rayner's (1993) opinion that escape-and-radiate and "vacant niche" (Lawton 1984, Price 1984, and others) are myths as palaeoecological data prove that speciation mostly occurred when emigration was hindered. As a proximate mechanism, dispersal is a key activity in influencing the type and direction of evolution and, therefore, speciation rate (Futuyma 1998). Thus, in the case of adaptive zones, "… we find that it is not only the absence of competition that drives diversity, but the absence of any form of natural selection whatsoever" (Masters & Rayner 1993: 92). In other words, there is no need for "empty niches" or adaptive zones for speciation to happen. Palaeoecological evidence also does not prove the importance of competition in macroevolutionary events (Benton 1987), and several studies (e.g. Després & Cherif 2004, Nyman *et al.* 2010, Ricklefs 2010) do not consider competition to be primarily important in ecological speciation. Lastly, although other views exist, we also hold that the assumption of "vacant niches" is straightforward against its very essence: niche only exists in the presence of an organism (Lewontin 1983). It is the organism that creates the niche, and niches can only be observed when they are already filled. Therefore, it makes no sense to argue about the chance for speciation provided by "vacant niches". In principle, none of the above ecological factors contributes to the speciation of herbivorous insects to such an extent as is generally assumed. A timely remark is, as Yoder *et al.* (2010) highlight: entering the adaptive zone is possible by evolutionary key innovation, dispersal to a new habitat and by the extinction of an antagonistic organism. These, but the last one, which refers to competition, coincide with the arguments of Benton (1987) and Masters and Rayner (1993).

We think that it is hard to find ecologically-based answers to the following questions: Why are there speciose and non-speciose insect genera? Why is one sister species narrowly specialized, whereas another is polyphagous? Why are some conspecific insect species specialized to the same organ of a plant species while other conspecific species are narrowly specialized to plant species belonging to different plant families or even plant orders? Why are there so many plant resources in both phyletic and plant material senses not yet occupied by herbivorous insect species ("empty niches")? Finally, why are not there many more herbivorous insect species, although the available ecological space could harbour magnitudes more?

Genetic (intrinsic) constraints

Host-plant use frequently mirrors strong genetic constraints (Winkler & Mitter 2008). When herbivorous and non-herbivorous sister clades' species richness are compared, and if the herbivorous clade is found more di-

verse (Mitter *et al.* 1988, Farrell *et al.* 1991), it is considered as a proof of diversifying effect of adaptive zones. However, it is also possible that genetic factors could be responsible for the difference. Considering the constraints of herbivory (Crawley 1998 and see references in Introduction), it does not seem at all evident why phytophagy speeded up diversification as suggested by Southwood (1973). Furthermore, species-rich clades do not necessarily possess higher speciation rates, and it appears that phytophagy alone is not responsible for diversity but only in connection with synapomorphic traits (Mayhew 2002). As described above, the oscillation hypothesis (Janz & Nylin 2008) assumes diversification rates to increase during the phases of specialization. However, if speciation happens in bursts (punctuation stages) in adaptive zones, it suggests that the diversification rate is not constant, but decreasing in time due to lack of niches or resources (Gavrilets & Losos 2009, Morlon *et al.* 2010). Regrettably, we have only guesses about the factors that influence its rate, especially considering genetic and developmental systems (Futuyma 1998).

Niche conservatism, i.e. when species maintain the traits of their fundamental niches through time (Pyron *et al.* 2015), can be a further limiting factor in speciation (Wiens 2004, Hernández-Vera *et al.* 2019). Resource-related traits (e.g. acceptance of larger allelochemical groups and rejection of others in host identification) are phylogenetically conservative, thus species are, in a sense, often prisoners of their past (Futuyma 1983). Based on 76 papers and 299 species, Peterson (2011) found considerable niche conservatism in cases of short time spans (tens to hundreds of thousands of years) and no niche differentiation was detectable in speciation. Niche conservatism can restrict gene flow, and even if speciation occurs, it is not necessarily accompanied with innovations.

The sources of adaptive changes are the *standing genetic variation* and *mutations* (Barrett & Schluter 2008). On the one hand, there is a greater chance for fixation of traits (microevolution) based on the standing genetic variation (e.g. Bradshaw 1989), however, the mutations are also needed for macroevolutionary changes in the long run. On the other, the larger the population, the more mutations are probably affecting the speciation rate. Gene and genome duplication (Li *et al.* 2018) might be another possible genetic constraint, whose rate can be comparable with mutation rate (Feyereisen 2011), causing speciation (Fryxell 1996, Edger *et al.* 2015, Mathers *et al.* 2017). New diversity, herbivorous insects included, is only generated by speciation (Butlin *et al.* 2009, The Marie Curie Speciation Network 2012).

As has been discussed above, quantitative and qualitative features of the phyletic pattern of insect-plant associations, the process of host specialization, the modes of insect speciation, and analyses of insect–host-plant phylogenies

indicate that the extent of diversification may be determined primarily by the *genetically coded propensity* of any insect lineage to diversify rather than by the availability of niches. That means the flora of any region could harbour many more herbivorous insect species than those actually occurring. This scenario strongly supports Felsenstein's (1981) hypothesis on the limited number of animal species due to genetic limitation; and it unequivocally corroborates Futuyma's (2010) suggestion that "sluggish evolution and failures to adapt" characterize the process of evolution. The latter view is further underpinned by evidences of niche conservatism that host specialization of insect clades may remain unchanged over geological times despite multiple and basic changes of the environment. It is also important that the age of plant lineages does not determine the total species richness in herbivorous insects (Mullen *et al.* 2011, Joy & Crespi 2012). It is similarly indicated by several herbivorous insect clades with the same or younger age than their hosts' ages (e.g. Percy *et al.* 2004, Lopez-Vaamonde *et al.* 2006, Gómez-Zurita *et al.* 2007, McKenna *et al.* 2009, Endara *et al.* 2018, and others). This suggests that the propensity to speciate in these clades might be independent of the age of a plant lineage.

Although genome-wide genetic changes of actual herbivorous insect–host-plant interactions are known by now (e.g. Simon *et al.* 2015, Nallu *et al.* 2018), their ultimate cause is much less emphasized. We put forward a view stressing the prime importance of events connected with the insect genomes in determining the propensity for diversification. We designate it as the hypothesis of the *intrinsic trend of diversification*, which was first suggested in Schoonhoven *et al.* (1998), meaning that intrinsic autonomous genetic factors control the rate of herbivorous insect speciation. The randomness of that intrinsic trend is reflected in the extreme variety of the phyletic patterns of insect-plant associations, and it explains why there are not many more herbivorous insect species, although the Plant Kingdom provides an immense amount of specific resources.

CONCLUSIONS

(1) The extant phyletic pattern of insect-plant associations resulted from specialization and speciation of herbivorous insects. Specialization is the insects' ability to distinguish between host-plant(s) and non–host-plants due to the sensory (primarily chemosensory) system involved. Genetic variation determining the function of the sensory system (recognition) is the prerequisite of the insect's switching to a new plant species as a host. The switch, however, can be established only if the new insect line can use the new host successfully, which depends primarily on genetically determined new nutrition-physiological traits. Thus, a successful switch needs a concerted genetic

change of preference and performance traits. Furthermore, switches to new plant species may result in the insect's speciation if any kind of reproductive isolation between parental and new lines takes place. However, insect speciation may also occur without any change in the host-plant range.

(2) None of the non–host-plant species occurring in the surroundings of an insect population will become a host-plant unless random genetic variation in the insects' preference/performance traits "hits" one of the non–host-plant species, and unless the new insect line undergoes speciation. That means that ecological speciation may not play an outstanding role in the evolution of herbivorous insects as usually assumed.

(3) The extremely low likelihood of a concerted genetic variation necessary for the evolution of a new phyletic insect-plant relation explains why new relations occur so rarely; why specific relations may remain unchanged for geological times; why there are so many plant resources unused by insects, and finally, why there are not many more herbivorous insect species although resources are abundant.

(4) The evolution of the phyletic pattern of insect-plant associations strongly supports Felsenstein's (1981) hypothesis on the limited number of animal species due to genetic limitation and corroborates Futuyma's (2010) suggestion that "sluggish evolution and failures to adapt" characterize the process of evolution.

<center>*</center>

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