Differential Response of Herbivores to Plant Defence

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Martin Volf

Contents

Abstract

The differential response of insect herbivores to plant traits is one of the mechanisms promoting diversity and specificity of insect-plant interactions. The response differs mainly among generalist insects on the one hand and specialized or adapted insects on the other hand. While generalists are often strongly affected by toxic defences of their hosts, specialists have evolved various adaptations to overcome such defences. These adaptations include tolerance, detoxification, or sequestration of secondary metabolites of the host. In addition, behavioral adaptations help herbivores to avoid particularly potent defences. The response of herbivores is also tightly linked to their feeding mode (i.e., herbivore guild), physiology, metabolism, or size. The resulting specificity of interactions gives rise to diversification of host defences as no single trait can provide an efficient defence against diverse communities of insects. The diversification of host defences then seems to be one of the key factors promoting diversity of insects in a reciprocal way.

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1 Introduction

Herbivorous insects and vascular plants represent two of the most numerous groups of multicellular organisms, driving major ecological processes in many terrestrial habitats [1–3]. They owe their diversity largely to a long-shared history and to the specificity of their interactions [4–6]. Various insect herbivores often show specific responses to host plant defences, which reciprocally support diversification of plant defensive strategies and in turn the diversity of plants and insects themselves [4, 5, 7, 8]. In this chapter, I summarize how the specificity of insect responses arises and discuss the consequences for insect-plant coevolution. I focus on the role of insect specialization and mode of feeding (i.e., a feeding guild) as two major factors governing their response to host plant defences.

The first insects began utilizing plants as a food source in the Early Devonian period, only several million years after vascular plants colonized terrestrial habitats [9, 10]. This led to a progressive radiation in the diversity of herbivorous insects and their feeding guilds. The pioneer insect herbivores were sap-suckers, stem-borers, and consumers of spores [11]. Thalli, which evolved into leaves some time later, only started to be consumed by chewing herbivores shortly after that in the Middle Devonian [10]. All modern herbivore guilds, with the possible exception of leaf-miners, were present by the Late Carboniferous, more than 300 million years ago [10].

The proliferation of herbivore lineages and guilds has increased and diversified herbivory pressure on plants and led to an arms-race between plants and insects [4, 5] (Box 1). This generally required plants to employ a broad suite of defences in order to maintain efficient protection against diverse communities of herbivores [12, 13].

Box 1

In their seminal paper, Ehrlich and Raven [4] proposed the so-called *escape-and-radiate* scenario of insect-plant coevolution. According to the *escape-and-radiate* scenario, the genesis of novel defensive traits allows plants to escape herbivory, leading to speciation of the respective plant lineage. However, after some evolutionary time, herbivores adapt to the novel defence and overcome it. This allows herbivores to colonize that plant lineage, opening a novel niche to them. The adapted herbivores speciate, and the process starts over. This should, on the one hand, lead to diversification or escalation of host plant defences over evolutionary time and on the other hand to co-diversification of the plant and insect lineages involved.

Recent studies suggest that clear cases of co-diversification are relatively scarce [128, 129], with *sequential radiation* and *phylogenetic tracking* being

(continued)

Box 1 (continued)

more prevalent [22]. In such a situation, herbivores colonize an existing lineage of plants well after its divergence, often specializing on hosts with similar defences [5].

Reciprocally, the resulting diversification of host plant defences probably supported further proliferation of feeding strategies in insect herbivores, in many cases leading to their specialization. Although there are numerous exceptions, the specialization of insect herbivores remains one of the main factors governing their response to host plant defences in virtually all the systems where this was examined (e.g., [7, 13–15]).

2 Roles of Insect Specialization in Their Response to Host Plant Defences

Insect herbivores show a broad range of host specialization (Box 2). Specialization to a limited set of hosts should allow herbivores to become well adapted to host defences and *vice versa* feeding on multiple host species should come at a cost of being maladapted to host defensive traits (e.g., [16]). Unspecialized insects are often excluded from strongly defended plants [17–19]. For example, there are few generalist herbivores found on milkweeds, which are strongly defended by cardenolides [17]. Generalist herbivores also strongly respond to unique or rare secondary metabolites as predicted by *feeding specialization* and the *biochemical barrier* hypotheses [20]. Indeed, plant lineages with a specialized defence often have highly specialized herbivore fauna [18, 19].

Box 2

Herbivore specialization, defined as the number or diversity of host plant species used, is one of the most widely used concepts in insect-plant ecology [14, 130]. Insect herbivores are traditionally classified as specialists or generalists. But there is a broad continuum between the two – from herbivores feeding on a single host (monophagy), through herbivores feeding on a limited set of hosts (oligophagy), to herbivores feeding on multiple hosts (polyphagy). The definition of oligophagy and polyphagy is sometimes ambiguous. Most definitions of specialization derive from simple counts of host species. However, most herbivores show some level of specialization when examined in detail. For example, most insect herbivores feed on closely related hosts [131]. The majority of herbivores in lowland tropical forests in Papua New Guinea seem to prefer to feed on congeneric or confamilial tree hosts [132], for example. A similar trend is apparent on a global scale and among several herbivore guilds [24].

(continued)

Box 2 (continued)

Recent studies have suggested that indices measuring herbivore specialization should comprise affinities among resources as well as their co-occurrence with consumers (e.g., [130]). Such indices allow to define specialists as herbivores using significantly clustered sets of resources, feeding on related or otherwise similar hosts. For example, specialization can be measured as phylogenetic or chemical relatedness of the used resources. This allows distinctions to be made between lineage specialists, herbivores tracking a lineage of hosts, and trait specialists, herbivores tracking certain host defences [130]. On the other hand, generalists can be defined as herbivores using overdispersed resources. Intermediate species are classed as indiscriminate consumers.

There are some notable exceptions, and some herbivores feeding on multiple hosts, such as tiger moth *Grammia geneura*, are able to feed on plants with highly toxic defences. *G. geneura* is sometimes considered as a generalist as it feeds on several unrelated hosts high in pyrrolizidine alkaloids [21]. But even such herbivores are rarely indiscriminate consumers. In this particular case, *G. geneura* feeds on a pool of locally available alkaloidal hosts, making it a pyrrolizidine alkaloid specialist (Box 2). This may be rather common under *sequential radiation* and *phylogenetic tracking* scenarios [22], when herbivores colonize already existing plant lineages. In such a situation, host shifts can track similarities in host defences rather than strictly follow host phylogeny. For example, host shifts in *Melitaeini* nymphalid butterflies feeding on 16 plant families have been shown to follow the presence of iridoid glycosides [23].

Highly polyphagous insect species feeding on large number of hosts from various lineages disregarding their traits are relatively rare even among herbivores considered to be generalists [24]. In many terrestrial ecosystems, such highly polyphagous herbivores represent only a small portion of the herbivore community [25]. When forced to feed on toxic diet, consisting of a narrow set of toxic hosts, these herbivores generally perform poorly. This is because instead of employing elaborate detoxification mechanisms, some of these herbivores rather mix different diets to achieve optimal quality and dilute toxins [26, 27]. Their diet thus often includes a diverse set of plants belonging to different functional groups under natural conditions [28].

3 Tolerance and Adaptations of Specialized Insect Herbivores

Insect specialists have repeatedly evolved adaptations to overcome toxic or deterrent effects of host plant defences. For example, specialized sawflies on birch are able to detoxify flavonoid aglycones by glycosylation [29, 30]. One of the most iconic examples of secondary metabolite detoxification by insects involves specialized herbivores on Brassicaceae. Brassicaceae possess a strong chemical defence, known as the glucosinolate-myrosinase system, generally maintaining an efficient protection of *Brassicaceae* hosts to generalist herbivores [31, 32]. When the host tissue is damaged, formerly compartmentalized myrosinase enzyme gets into contact with glucosinolates. These are then hydrolyzed into isothiocyanates, which are toxic to herbivores [32]. Specialized herbivores, such as *Pieris* butterflies or *Plutella xylostella* diamondback moths, have evolved mechanisms to detoxify this defence [32, 33]. Larvae of *Pieris rapae* express a nitrile-specifier protein in their midgut, promoting the formation of nitrile breakdown products instead of toxic isothiocyanates [32]. *Plutella xylostella* diamondback moths employ glucosinolate sulfatase to desulfate glucosinolates, producing metabolites that no longer act as substrates for isothiocyanate production by myrosinases [33]. This illustrates that detoxification mechanisms have evolved several times independently in insect specialists even within a single insect-plant system. Although such detoxification mechanisms facilitate a similar response to host plant defences, their background is often different and crucial for understanding how tolerance to plant defences in particular cases is maintained.

Furthermore, some specialized herbivores were able to adapt to host defences to such an extent that they can use them for their own benefit. In these cases, specialized herbivores often respond positively to host plant chemical defences. This is also the case for several specialized herbivores adapted to salicylates in Salicaceae hosts. Salicylates are phenolic glycosides typical for willows and poplars. Although various derivatives of salicyl alcohol can be found in many plant lineages (e.g., [34]), in Salicaceae they reach the highest diversity with many compounds being unique and novel for this family [35]. Salicylates have been reported to serve an anti-herbivorous function primarily and their documented impact on generalist herbivores involves deterrent effects, retarded larval growth, and increased mortality [36, 37]. However, certain specialist herbivores show preference for willow hosts with high salicylate content, using salicylates as feeding cues [38]. This is probably because they are able to sequester salicylates and even use them to their own benefit. Such an ability was best documented in *Phratora* and *Chrysomela* leaf beetles. Larvae of these beetles use salicylates as a precursor for salicylaldehyde, a metabolite deterring invertebrate predators including ants and lady beetles [39, 40]. They secrete salicylaldehyde from specialized abdominal glands (Fig. 1). In addition, larval growth in several specialized leaf beetle and sawfly species has been shown to be promoted on hosts with high salicylate content, providing them with an additional advantage [41].

Another example of specialized herbivores showing a strong preference for highly toxic hosts are *Asota* tiger moths. *Asota* tiger moths are broadly distributed in Africa, south Asia, and tropical parts of the Australian region. Both adults and larvae are brightly colored and usually feed on alkaloidal hosts (Fig. 2). In lowland tropical forests in Papua New Guinea, *Asota* moths are largely specialized on *Ficus*. The abundance of the larvae shows a strong positive correlation with the content of phenantroidolizidine alkaloids in the host leaf tissue [7]. Other tiger moth species have been reported to be able to sequester host alkaloids, convert them into their

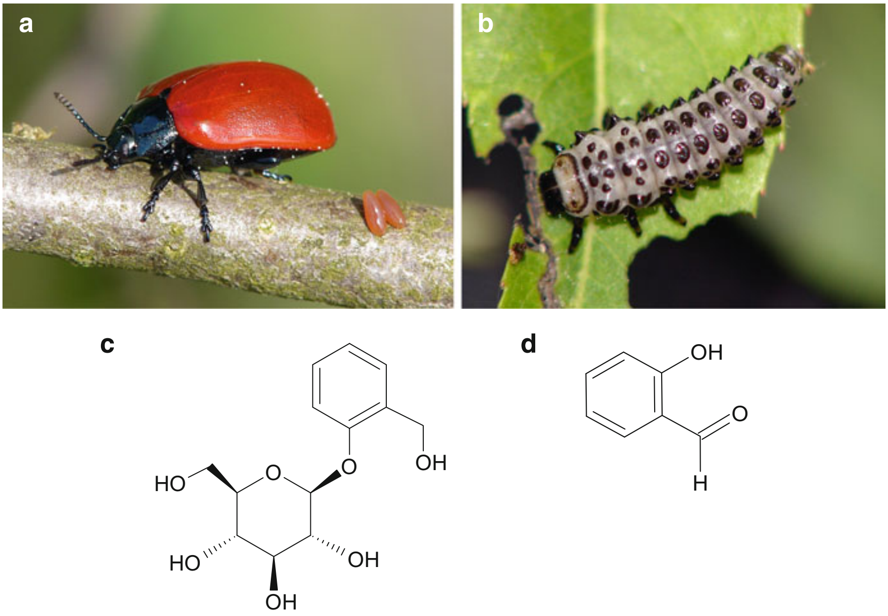

Fig. 1 A female of *Chrysomela populi* laying eggs on a poplar twig (**a**) and a larva of *Chrysomela vigintipunctata* feeding on a leaf of *Salix fragilis* (**b**). These leaf beetle species are specialized on feeding on Salicaceae hosts and often prefer species with a high content of salicylates, such as salicin (**c**). Their larvae use salicylates as precursors for production of salicyladehyde (**d**). They secrete salicyladehyde from abdominal glands as a protection against invertebrate predators

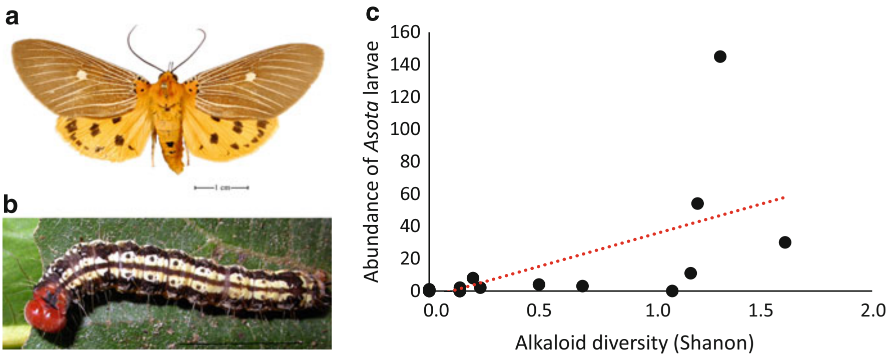

Fig. 2 An adult *Asota* moth (**a**) and its caterpillar (**b**). These brightly colored moths use highly alkaloidal host plant species. In lowland forests of Papua New Guinea, they specialize on *Ficus* species containing high concentration of phenantroindolizidine alkaloids, with abundance of larvae being strongly positively correlated to alkaloid content in host plant leaves (**c**). (Data taken from on Novotny et al. [42] and Volf et al. [7]. Insect photos were downloaded from “Caterpillars feeding on New Guinea plants” database [43] curated by the New Guinea Binatang Research Center)

nontoxic N-oxides, and store them in metabolically inactive tissues [21]. Although the specific mechanism of alkaloid sequestration remains unknown in the case of *Asota* moths, it has been suggested that they can use host alkaloids for their protection [44]. Indeed, both *Asota* adults and caterpillars are highly toxic to predators. They also show high toxicity to humans to such an extent that there were cases of mass lepidopterism fever outbreaks during an *Asota* population explosion in India [45].

In addition, herbivores have evolved behavioral adaptations and mechanisms to avoid defences of their hosts. *Passiflora lobata* has its leaves protected by dense hook-shaped trichomes, which have strong negative effects on non-adapted herbivores. However, larvae of specialized *Heliconius charithonia* butterfly are able to release themselves from the hooked trichomes if entrapped. Moreover, they produce silk mats and bite off the hooked tips of the trichomes in order to be able to move around the leaf. Such adaptations significantly improve their feeding efficiency. While trichomes deter generalist herbivores, specialists thus do not seem to be strongly affected by them in this particular case [46].

Another behavioral adaptation includes herbivores able to cope with hosts producing latex. Production of latex has independently evolved in multiple plant lineages, including around 10% of flowering plants species [47]. Latex serves as a mechanical protection directly interfering with insect feeding. In addition, latex serves as a vessel for various defensive compounds. In *Ficus*, latex contains high concentrations of cysteine proteases, interfering with processes in the insect mid-gut and being among the traits with the most pronounced effects on *Ficus* herbivores [7, 48]. In milkweeds, latex contains cardenolides, inhibiting the Na^+/K^+-ATPase enzyme and showing high toxicity to most animals [49]. As such, latex is usually an efficient form of defence, which probably supported diversification of plant lineages possessing latex [6]. To avoid latex, specialized herbivores have evolved behavioral adaptations including cutting leaf veins, impairing latex transportation and outflow. On hosts with non-articulated venation, herbivores cut the main vein only. Such a behavior can be observed in later instars of monarch butterfly caterpillars (*Danaus plexippus*), for example. On hosts with articulated venation, herbivores have to cut multiple veins by creating trenches over large parts of the leaf blade (Fig. 3) [47].

4 Nutrients, Natural Enemies, and Induced Defences

Host-plant defences can increase herbivore mortality directly (e.g., by intoxication) or indirectly through enhanced risk of predation or parasitism [50]. Negative effects of host defences may prolong the time herbivores need for feeding. Such a prolonged period of feeding exposes herbivores to higher risks of being predated or parasitized. A caterpillar has ca. 100× higher risk of being predated or parasitized when active and feeding [3, 51]. Therefore, the effects of host traits can be modulated by natural enemies of herbivores – by predators and parasitoids. There is some evidence that high predation can even facilitate host-shifts to novel hosts. For example,

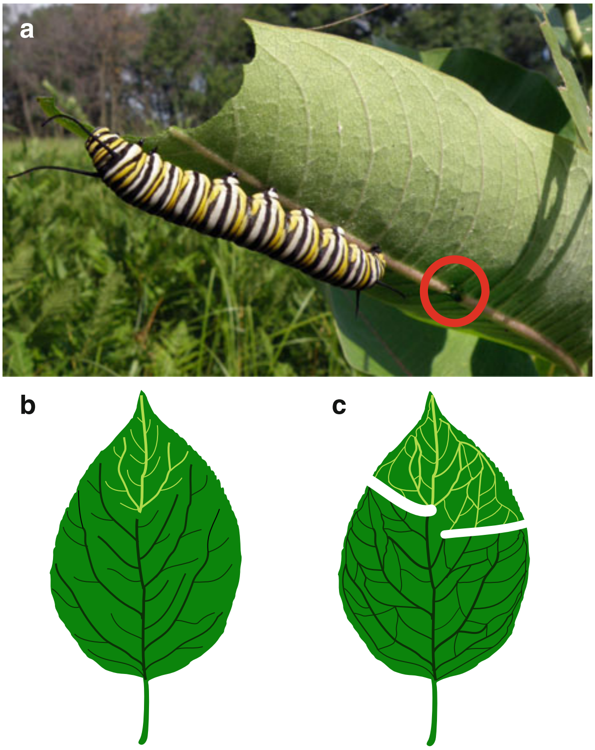

Fig. 3 A caterpillar of monarch butterfly (*Danaus plexippus*) feeding on a milkweed (**a**). Note the vein cut by the caterpillar (marked by a *red circle*). Specialized herbivores feeding on plants high in latex often cut the veins in order to limit the latex outflow during their feeding. On leaves with a non-articulated venation, herbivores can cut only the main vein to disrupt a latex outflow in a given part of leaf (**b**). On leaves with an articulated venation, herbivores cut the leaf by wide trenches (**c**) (Adapted from Agrawal and Konno 47). Leaf areas with disrupted latex outflow are in *yellow*

swallowtail butterflies in Alaska started to use novel hosts, despite being well adapted to their ancestral Apiaceae hosts, probably as the new hosts represent an enemy free space [52].

All insect herbivores are trying to achieve optimal feeding efficiency and growth rates. They pursue maximal nutrient value of their diet, while balancing other risks [3, 53]. However, generalist insects often cannot fully benefit from high nitrogen and nutrient content as they are not able to fully overcome toxic metabolites of their hosts, as mentioned above. Therefore, they often show lower growth rates and nitrogen content is a weaker predictor of their community composition than secondary chemistry of the host [54]. On the other hand, specialists are usually able to cope with toxins of the host and can pursue high nutrients more efficiently, making nitrogen an important factor structuring their communities [15]. As such, the abovementioned adaptations help specialized insects to avoid predation and parasitism not only by using secondary metabolites of their hosts [55] but also by fast growth, avoiding predators and parasitoids in time (if generalists are directly defended, they seem to rely on physical defences, such as spines or shelters [54]).

Many herbivores use behavioral adaptations, such as staying cryptic, to avoid their natural enemies in space [56]. Locating insect herbivores is thus not an easy task for predators and parasitoids that often have to rely on cues provided by host plants. Plants have evolved mechanisms to attract predators and parasitoids in order to facilitate their own protection against herbivores. These defences rely largely on volatile infochemicals [57, 58]. While many volatiles are produced by plants even when not attacked by herbivores [3], the true complexity of these interactions is revealed after a herbivore attack and an induction of the host defences. The previous examples in this chapter largely focused on constitutive defences, which are more or less steadily present in the plant tissue and their level is not directly governed by external stimuli, such as herbivory. Induced defences are deployed after a herbivore attack and represent an alternative form of plant defence with possibly differential effects on various insects.

Induced defences are based on several complementary mechanisms and often show a high degree of specificity, which makes them an efficient protection against a variety of herbivores. When induced, plants can upregulate defences (secondary metabolites, trichomes, leaf thickness, etc.) that target the herbivore [59, 60]. These defences directly affect herbivore preference and performance. Herbivores should be able to cope with the induction of direct defences in a largely similar way to constitutive defences, although it may require them to habituate to increased defence levels (e.g., they need to increase the efficiency of their detoxification mechanisms [61]).

However, plants can also employ elaborate indirect defences which help them to attract natural enemies of herbivores through the production of herbivore induced plant volatiles (HIPVs) [57, 58, 62]. HIPVs, such as shikimic acid derivatives, terpenoids, or alcohols, are generally well detectable even in complex environments, unlike the scents emitted directly by herbivores themselves, and help predators and parasitoids to navigate efficiently toward their prey [63]. Importantly, the induced responses in HIPV production seem to differ between herbivores, showing a large degree of specificity [64]. In a greenhouse experiment, Danner et al. [65] demonstrated that the responses in indirect induced defences differed among herbivores from different feeding guilds (see also below). Leaf-chewing herbivores induced a strong response in HIPVs, while sap-sucking herbivores were able to suppress their production. Induced responses may also differ between specialist and generalist herbivores, but these differences seem to be much more subtle and vary among systems [65, 66].

So far, the relative importance of different forms of induced defences in plant defence and their effects on specialist and generalist herbivores remain largely unknown [62]. For example, the attraction of predators is likely to benefit plants through the immediate removal of herbivores [59]. On the other hand, parasitism does not lead to an immediate termination of herbivory and in some cases it can even prolong the feeding period of parasitized larvae [59]. Several common direct defences, such as some phenolic secondary metabolites, have only limited effects on immediate insect mortality on their own, though they retard larval growth [60]. Their main defensive value can possibly result from an interplay with indirect defences as they can prolong larval growth and increase the exposure of herbivores to predators or parasitoids attracted by HIPVs. The effect of defensive traits is thus highly dependent on the third trophic level context.

HIPVs have been long known to attract insect parasitoids or predators [67, 68]. Recent results suggest that these volatiles can also be perceived by birds [58]. For example, Amo et al. [58] showed that birds were attracted to trees infested by lepidopteran larvae, even if the larvae and their damage was removed just before the experiment. This largely rules out the possibility that the birds used visual cues for locating the attacked tree in this case.

5 Feeding Guilds and Their Response to Host Plant Defences

The previous sections of this chapter mainly focused on leaf-chewing herbivores (Fig. 4). Indeed, leaf-chewing herbivores represent one of the main herbivore groups in terms of diversity, abundance, and the amount of damage they do to their host plants [3]. However, there are many other herbivore guilds, some of them displaying quite different responses to host plant traits compared with leaf chewers. The levels of specialization differ among herbivore guilds, ranging from polyphagous root-chewing larvae typically feeding on hosts from multiple plant families, through leaf-chewing larvae feeding on several congeneric or confamilial hosts, to gallers and miners with very limited host spectra [24, 42]. The variation in feeding modes provides herbivores from different feeding guilds various options to avoid host plant defences, largely shaping their response to host plant traits. For example, highly specialized endophytic herbivores evolved mechanisms to manipulate hosts, while some sucking herbivores specialized on feeding on resources with relatively low defensive metabolite content.

Endophytic herbivores such as leaf miners and gallers (Fig. 4) belong among herbivores with the most intimate interactions with their host plants. Their diet usually includes only a couple of closely related congeneric hosts or even a single

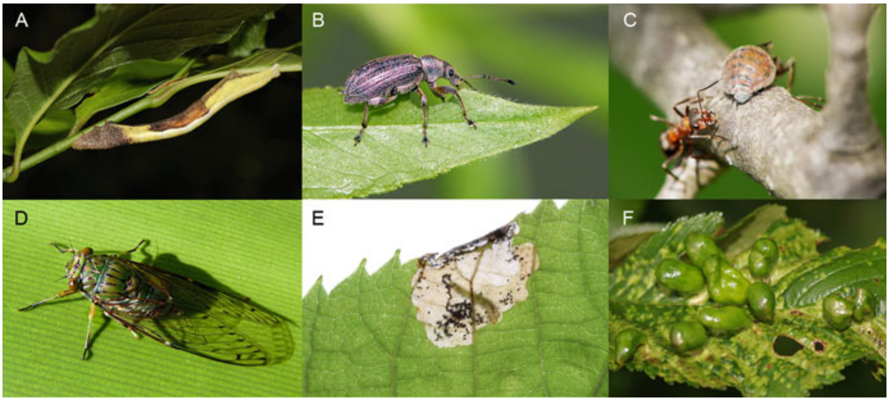

Fig. 4 Herbivores from various feeding guilds mentioned in this chapter: (**a**) a larval leaf chewer (a geometrid caterpillar feeding on *Magnolia kobus*, Japan), (**b**) an adult leaf chewer (*Phyllobius* sp. weevil feeding on *Salix alba*, Czech Republic), (**c**) a phloem sucker (Hemiptera feeding on *Salix aurita*, Czech Republic; note the ants guarding the phloem sucker), (**d**) a xylem sucker (Cicadidae, Papua New Guinea), (**e**) a miner (*Parna kamijoi* sawfly feeding on *Tilia maximowicziana*, Japan), (**f**) gallers (galls of *Tetraneura ulmi* on *Ulmus glabra*)

host species [42, 69]. These herbivores live inside the plant tissue, either inside the leaf lamina or in induced galls. Their endophytic lifestyle provides them with some protection against biotic and abiotic factors such as UV irradiation and drought, and in some cases probably also with protection against predaors or generalist parasitoids [3, 70, 71] (but there are many specialized parasitoids of mining or galling herbivores (e.g., [70, 72])). The highly specialized nature of miners and gallers also allows them to escape negative effects of certain defences of their hosts.

First, a miner larva living inside the leaf lamina does not have to deal with a tough leaf surface and can preferentially feed on cells with high nutrition value [73]. Indeed, leaf toughness is an important predictor of food choice in leaf-chewing insects, which cannot avoid chewing on the tough cuticle of the leaves [3, 74]. Some plant groups such as palms or grasses, which contain high levels of silica-based physical defences have especially tough leaves, which erode mandibular jaws of chewing herbivores, significantly lowering their feeding efficiency [75, 76].

Second, their highly adapted nature allows gallers to manipulate their hosts to form galls by using metabolites closely resembling or identical to phytohormones [77, 78]. The ability of host manipulation was probably a key innovation in several taxa of gall-forming herbivores because there have been repeated and often dramatic radiations of gall-forming Arthropods including various insect orders and mites [79]. The radiations of several galler taxa have been characterized by associations with key plant genera – e.g., radiation of Cynipidae wasps on *Quercus*, Pemphigidae aphids on *Pistacia*, and Tenthredinidae sawflies on *Salix* [79]. A gall itself can have a significantly different chemical profile than the rest of the plant tissue, and gallers can control host plant defences, such as secondary metabolites [80]. Galls thus can have lower content of defensive secondary metabolites, while they have higher nutrient values than normal plant tissue (but note that increase of certain defensive metabolites in galls is also possible). Downregulation of host defences has been recorded in many plant-galler systems as reviewed by Giron et al. [78] and include downregulation of various phenolics, proteases, or volatile compounds (e.g., [80–83]). As suggested by Stone et al. [84] gallers "represent examples of an alternative coevolutionary arms race paradigm, not between toxins and detoxification systems as in the Ehrlich and Raven model, but between host plant susceptibility and gall inducer virulence." This may lead to a situation when abundance or diversity of gallers does not respond to host chemical defences [15]. This is quite different from leaf chewers, which often show negative or positive correlation to the secondary metabolite content of the host [13, 19]. Indeed, in some cases host selection in gallers seems to focus on plant species with high nitrogen content disregarding their defences, possibly as such hosts may be more easily manipulated to contain even higher nutrient concentration [15]. Relatively recently, host manipulation toward higher nutrients and lower defences was also recorded in the case of miners [78, 85], suggesting that some members of this guild can, to some extent, ignore host defences as well.

Another example of a herbivore guild with a response to host plant defences largely different from leaf-chewers are sucking herbivores. Sucking herbivores have evolved specialized, so-called haustellate mouthparts. Such mouthparts evolved independently in Thysanoptera, Lepidoptera, and mainly in Hemiptera, which include most sucking herbivores [3]. The haustellate mouthparts are formed from several components, including maxillary and mandibular stylets, which serve for piercing plant surface. There are three main guilds of sucking herbivores feeding on aboveground plant parts – phloem suckers, xylem suckers, and leaf suckers [42] (Fig. 4). The different food source influences their level of specialization and host preference.

Phloem suckers feed on phloem fluids. This guild includes mainly aphids, scale insects, and most leaf hoppers. Their diet is high in primary metabolites such a sugars, while it is relatively low in nitrogen. Excess sugars are often excreted to attract ants, which protect the phloem sucker from predators. Phloem is also low in secondary metabolites. Hence, when the relative ratio of nutrients and defensive secondary metabolites are compared, phloem may be a more favorable food source than leaf tissue in some cases [3]. Xylem suckers include mainly cicadas and cercopoid froghoppers. These herbivores have specialized on an even poorer diet, the xylem fluids. Xylem is ca. 200× lower in nitrogen than Angiosperm leaf tissue [3, 86]. However, it is almost devoid of defensive secondary metabolites. Due to the avoidance of chemical defences, both phloem and xylem suckers are often primarily affected by nutrient content and physical characteristics of the host, such as thickness of the surface cuticle [3, 87]. Although there are some notable exceptions, both guilds show relatively low levels of specialization on the whole [42]. This is in sharp contrast to leaf suckers. Leaf suckers include specialized Heteroptera [88] and some cicadellids, which evolved from their phloem-feeding ancestors [89]. These herbivores suck on the content of individual leaf cells. Although they can avoid some compartmentalized secondary metabolites, they are probably still exposed to much higher content of defensive compounds than phloem- and xylem-sucking herbivores. This may be one explanation as to why this guild includes mainly highly specialized herbivores [42, 89].

In addition, sucking herbivores, such as aphids or some leaf hoppers, can suppress plant defences [65]. Aphids inject saliva containing suppressor proteins in the host tissue while feeding [90]. This has been shown to affect mainly Ca^{2+} signaling in the attacked tissue [91]. Suppressing Ca^{2+} signaling has pronounced cascading effects on induced responses to damage. Indeed, sucking herbivores have been shown to induce a weaker response of their hosts than leaf-chewing insects [65], probably allowing them to partially avoid indirect induced defences.

6 Roles of Insect Morphology and Physiology in the Response to Host Plant Traits

The response to host plant defences is also driven by morphologic and metabolic characteristics of insect herbivores, some of them being unrelated to their specialization. For example, small herbivores tend to respond to host defences differently than large ones. As outlined above, xylem suckers, which can feed on a diet low in defensive chemicals, include mainly large froghoppers or cicadas. This is not a coincidence as small herbivores would not be able to efficiently suck on xylem due to its negative pressure. On average, xylem suckers are thus larger than phloem or leaf suckers [89]. Small herbivores also often respond more strongly to physical defences. This is well illustrated by small, freshly hatched caterpillars, which sometime have troubles with chewing on tough, mature leaves. Small chewing herbivores also have problems cutting through sclerophyllous veins of grasses [76]. Other physical traits which probably also affect small herbivores more than large ones are trichomes [17]. Trichomes possess various functions and show high morphological variability. Glandular trichomes may serve for secreting defensive secondary metabolites [3]. Simpler, nonglandular trichomes serve mainly as mechanical protection. They prevent small herbivores from reaching the surface of the plant, make their movement more difficult, and increase their chance of falling. This makes herbivore feeding less efficient and increases predation risk [37, 92]. Trichomes also prevent females of small herbivores from ovipositing their eggs on the leaf surface [93]. On the other hand, females of some specialized herbivores can use trichomes to get a better grip on the plant, enhancing oviposition efficiency [94].

Different herbivores can also have different conditions in their guts, which largely affects how they process their diet and what traits of the host affect them. One such example is the response of caterpillars to tannin content and activity. Tannins represent a diverse group of phenolic compounds that are broadly distributed among plants [95]. It was proposed that one of the main defensive values of tannins in terms of anti-herbivore protection results from their ability to precipitate proteins in guts of herbivores under low pH. Such a mechanism is known in the case of mammalian herbivores, in which some tannin groups reduce apparent N digestibility [96]. The protein precipitation activity is especially high in procyanidins (condensed tannins) [97], which have been shown to affect food selection in beavers, for example [98]. Many of the previous studies on insect-plant interactions focused primarily on this group of tannins when interpreting herbivory by insects. However, most caterpillars tend to have alkaline mid-guts [99]. Several studies have shown that ability of procyanidins to precipitate proteins is limited in such conditions [95, 100, 101]. Condensed tannins thus probably serve simply as indigestible matter, lowering overall feeding efficiency in caterpillars [59, 102]. From the perspective of anti-caterpillar protection, groups of tannins other than procyanidins may be more important. These include ellagitannins, which show high oxidative activity. Recent results suggest that tannin oxidative activity tends to have much more pronounced effects on caterpillar community composition and diversity than does tannin protein precipitation capacity [7, 103]. The oxidation of ellagitannins in caterpillars' mid-gut can facilitate nucleophilic reactions with proteins and the formation of highly reactive hydroxyl radicals. In other words, the products of tannin oxidation can damage nutrients in the gut lumens of insect herbivores or produce cytotoxic effects in their tissues [95, 104]. The nutritional stress may be especially important as a form of defence against some herbivores specialized on high tannin content, such as

Lymantria dispar, in which the oxidative stress itself cannot reduce growth rates on its own [59, 105].

7 Implications for Evolution of Host Plant Defences and Insect Diversity

The differential response of herbivores has important implications for evolution of host plant defences. Mainly, it restricts plants from developing a universal anti-herbivore defence [12, 13]. Specialists have been shown to prefer or tolerate hosts with high levels of specific defensive compounds in the case of multiple plant genera (e.g., [7, 13, 106, 107]). This might have been one reason for the decline in specific defences in *Asclepias* [107]. Similarly, specialized insects were able to adapt to salicylates and reach high densities on salicylate-rich willow hosts as outlined above [19]. Although salicylates play a significant role in structuring insect communities, their protective value against specialized herbivores appears to be low. Maintaining an efficient defence thus probably requires several defensive mechanisms, such as chemical defence and trichomes, which affect both generalists and specialists on willows [13]. As a result, defensive traits are often mutually independent or positively correlated, forming suites of complementary defences or so-called defensive syndromes [7, 108, 109]. Trade-offs between individual defensive traits may be expected only under specific conditions, such as low nutrients or in the case of negative dependence in metabolic pathways (e.g., a competition for a specific precursor) [110, 111]. Furthermore, some recent results suggest that defensive syndromes can consist of traits following different evolutionary trajectories, possibly making adaptation even harder for herbivores [7]. This seems to shape the evolution of plant defensive traits into a dynamic system, with traits undergoing periods of diversification, divergence, and sometimes decline [5].

Indeed, the differential response of insect herbivores can shape evolutionary trajectories in individual defensive traits. Ehrlich and Raven [4] proposed escalation of host plant defences over evolutionary time, allowing plants to escape herbivory by unadapted generalist herbivores. An escalation of host plant defences has been found in several plant genera, with *Asclepias* and *Bursera* being the most iconic examples [107, 112]. Divergent, rather than escalating, defences (Box 3) have been found in sympatric communities of closely related hosts. Such a divergence in defences between sympatric congeners appears to lower the risk of sharing specialized herbivores [113, 114]. As such, the ability to employ divergent defensive traits, which are harder to follow for specialized herbivores, may be beneficial and facilitate coexistence of closely related hosts [5, 115]. For example, divergence and a character displacement in leaf shapes help closely related *Passiflora* hosts to avoid herbivory by impairing host recognition by ovipositing butterfly females [116]. Similarly, a divergence in chemistry among closely related species growing in sympatry have been recently found in many plant genera such as *Bursera*, *Eugenia*, *Ficus*, *Inga*, *Ocotea*, and *Psychotria* [7, 113–115].

Box 3

Escalation of defences refers to the macroevolutionary increase in host plant defensive traits. Under this scenario, derived plant lineages should possess more diverse or escalated (potent) defences than their less derived counterparts [4, 133]. As such, their trait values are a function of their phylogenetic distance, and closely related species should possess similar defensive traits. On the other hand, divergent defences are those which show high disparity between closely related hosts. Divergent traits are more dissimilar between close relatives than expected under a conserved model of evolution.

On the global scale, Becerra [117] found a strong correlation between herbivory by specialized insects and chemical variability in the local communities. Plant communities exposed predominantly to herbivory by specialized insects were much more chemically diverse than those exposed predominantly to generalist mammalian herbivores. The composition of insect communities attacking the host largely forms its defences – assemblages of specialists should select mainly for divergent traits, whereas assemblages of generalists, sensitive to specialized defences, should impose selection for escalating and highly toxic defences [7, 113]. Therefore, plant lineages harboring diverse insect communities consisting of herbivores with various levels of specialization are expected to possess both escalating and divergent defences (Fig. 5).

Both escalation and divergence of defensive traits may contribute to diversity of host plant defences as suggested by recent evidence (e.g., [7, 106, 112, 115]). Escalation of host plant defences should promote α-diversity of defences within a given plant lineage [4]. Divergence in host plant defences promotes β-diversity of defences between closely related hosts [113, 117]. Divergence in defences seems to be especially prominent in speciose and dominant tree genera. These genera often represent a large proportion in the local forest communities and form so-called species swarms [115, 118]. For example, the five most speciose tree genera represent ca 25% of the local tree diversity in Barro Colorado Island, Panama [119]. Divergence in their defences can thus significantly increase defensive and chemical diversity on the community level [117]. This has important reciprocal effects on diversity of associated insects due to the specificity of their response. In turn, host plant chemical diversity has been shown to be an important driver of insect diversity almost invariably in all the systems where this was studied (e.g., [7, 115, 117, 120, 121]) (but see Salazar et al. [122]). For example, there is a strong positive correlation between the number of caterpillar species associated with *Ficus* species and host plant polyphenol and triterpene diversities (Fig. 6) [7]. High diversity of defences can probably lower the dominance of the abundant insect species, preventing any single herbivore from dominating the community and opening niches for the less dominant ones. Indeed, many insect herbivores appear at low densities in tropical forests [123], where both insect and chemical diversities reach their peak.

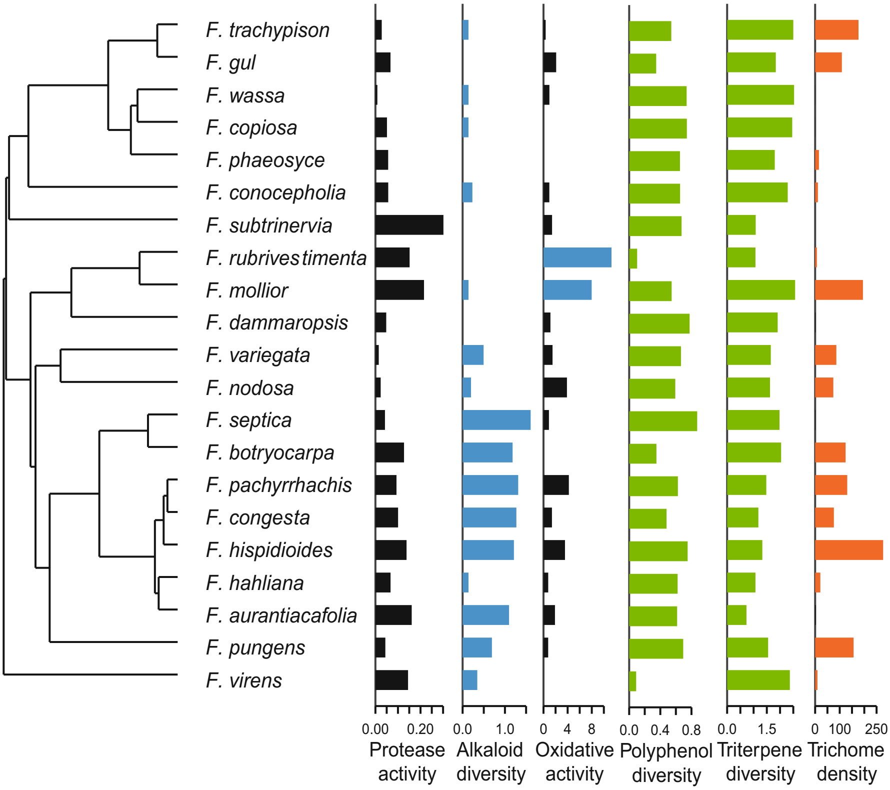

Fig. 5 Distribution of selected defences across *Ficus* phylogeny showing various trends in their evolution. *Ficus* harbors diverse communities of herbivores. Traits with various evolutionary histories probably help *Ficus* to maintain an efficient protection against herbivores with various levels of specialization and life histories [10]. Conserved traits are in *black*, escalating traits are in *blue* (traits showing only a local escalation within one *Ficus* lineage are only partly colored), traits showing divergence at deeper levels of *Ficus* phylogeny are in *green*, and traits showing high divergence at terminal levels of *Ficus* phylogeny are in *orange*. The shown *Ficus* traits include protease activity in latex (ΔA280), alkaloid diversity (Shannon), polyphenol diversity (Shannon), polyphenol oxidative activity (mg/g), triterpene diversity (Shannon), and trichome density (number of trichomes per 10 mm^2). (Adapted from Volf et al. [7])

8 Conclusions

Here I have tried to illustrate that the differential response of insect herbivores to plant defences is one of the mechanisms promoting high specificity of insect-plant interactions. The resulting specificity of interactions gives rise to diversification of host defences as no single trait can provide an efficient defence against diverse communities of insects. The diversification of host defences then seems to be one of the key factors promoting the diversity of insects in a reciprocal way. This chapter

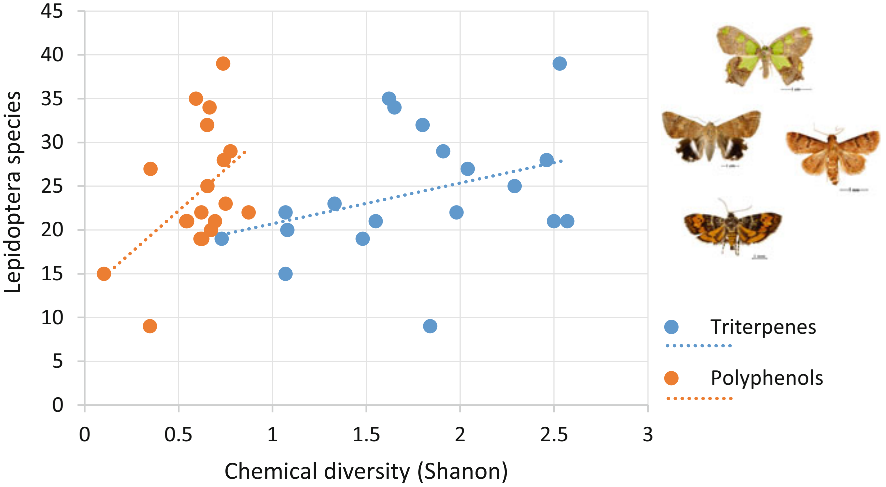

Fig. 6 Positive correlations between diversity of caterpillar communities and polyphenol and triterpene diversity of their *Ficus* hosts. The positive correlation remained significant in case of polyphenols when analyzed in the phylogenetical context using *Phylogenetic Least Squares* ($F_{(1, 17)} = 6.39$, $P = 0.022$) while the effect of triterpenes turned nonsignificant ($F_{(1, 17)} = 1.87$, $P = 0.189$). (The insect and chemical data were taken from Novotny et al. [42] and Volf et al. [7]. Insect photos were downloaded from “Caterpillars feeding on New Guinea plants” database [43] curated by the New Guinea Binatang Research Center)

primarily focused on the response of insect herbivores to host plant defences and nutrient content. There are also other plant traits such as growth-form, architecture, distribution, or abundance, which significantly affect insect herbivores [124, 125]. In some cases, these traits may modulate or drive responses of insect herbivores to host plant defences, often being tightly linked to them. In addition, insect herbivores strongly respond to host phylogeny, usually because of its covariation with host traits. The relative importance of host plant phylogeny and defensive traits is highly dependent on the phylogenetic scale and identity of the traits one considers [126]. For example, secondary metabolites often exhibit a weak phylogenetic signal among congeneric plant species, as outlined above, but the major differences in secondary metabolite presence or absence may be generally conserved when comparing hosts at the family level [7, 113, 114, 127]. The composition of herbivore communities, therefore, usually arises from the interplay between host phylogeny and functional traits, both with differential effects on insects with various levels of specialization and life histories [7, 13, 126].

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