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Carnivorous plants and their biotic interactions

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ABSTRACT

Carnivorous plants reverse the order we expect in nature: here, animals do not feed on plants, but plants hunt and feed on animal prey, primarily insects, thereby enabling these plants to survive in nutrient-poor environments. In addition to this strategy, some carnivorous plants also form unique symbiotic relationships with animals other than insects to access nutrients. Other important interactions of carnivorous plants with insects, such as pollinators and herbivores, have received far less attention or have been largely neglected. This review describes and summarizes various ecologically relevant biotic interactions between carnivorous plants and other organisms reported in recent studies. In particular, our understanding on how carnivorous plants, for example, handle the pollinator–prey-conflict or interact with and respond to herbivores is still incomplete. Strategies and mechanisms on how carnivorous plants address these challenges are presented. Finally, future directions in carnivorous plant research are proposed.

1. Introduction

Plants have adapted to utilize all available habitats, from tropical to arctic climates, arid to semi-arid zones, damp to waterlogged areas, and maximum sunshine to full shade. Therefore, as an adaptation to nutrient-poor environments, insectivory – or in a broader sense carnivory – may have evolved in some plants to compensate for shortages in soil composition (Juniper et al. 1989; Ellison and Adamec 2018a). Catching and digesting prey, mainly insects, by using specialized traps (Figure 1) is considered as an alternate mechanism for acquiring supplemental nutrients such as nitrogen, phosphorus, and potassium (Ellison 2006; Mithöfer 2011). Since all carnivorous plants can still fix carbon dioxide and absorb inorganic and organic nutrients from captured prey, they are mixotrophic. The 'carnivorous syndrome' refers to development by changes in anatomical structure, glandular structure, gene expression, and evolutionary characteristics (Pavlovič et al. 2007). About 810 of the 250,000 flowering plants species are carnivorous, mostly belonging to Nepenthales and Lamiales (Adamec et al. 2021). The carnivorous syndrome in plants has developed independently in the plant kingdom at least 11 times and can be found in 13 different plant families including a recently described new species (*Triantha occidentalis*; Tofieldiaceae) (Fleischmann et al. 2018; Lin et al. 2021). Therefore, carnivorous plants are a polyphyletic group with distinct features and prey-capturing abilities.

Charles Darwin was the first one who experimentally proved the fact of plant carnivory and laid the foundation for all subsequent research related to this topic in his book 'Insectivorous Plants' (Darwin 1875). Darwin described the traps structures in eight different plant genera (*Drosophyllum, Drosera, Dionaea, Aldrovanda, Roridula, Pinguicula, Utricularia, and Byblis*), all being able to catch insects or other prey. He further described the structure of sticky, hinged, and suction traps in detail, but also mentioned gliding traps. Darwin noted that pepsin-like enzymes directly digest the animal proteins (Darwin 1875; also in Hepburn 1922; Hepburn et al. 1927). Francis Darwin (1878) further concluded that the plant absorbs these nutrients, which contribute to the plant growth and development. In the last 25 years, molecular and all '–omics' approaches provided deep insight into the biology, physiology, and evolution of carnivorous plants. In particular, intensive work on Darwin's 'most wonderful plant of the world,' the Venus flytrap (*Dionaea muscipula*), gained fascinating insights into the molecular physiology and origin of plant carnivory and contributed significantly to our understanding of carnivorous syndrome in this particular plant and also in general (for review, see Hedrich and Fukushima 2021). In addition, comprehensive publications recently covered the systematics, evolution, and (eco)physiology of carnivorous plants (Ellison and Adamec 2018a; Adamec et al. 2021). In this article, I provide an overview on the various biotic interactions of carnivorous plants (Figure 2). Besides summarizing their interactions with prey and addressing the related question whether carnivorous plants are predators, I focus, in particular, on the often neglected interactions with pollinators and herbivores, emphasizing the signals involved in attraction and defense responses.

2. What makes a carnivorous plant?

There are several definitions for the term 'carnivory' in the plant kingdom. The basic definition implies that a carnivorous plant has the ability to absorb products of prey decomposition. This is done either directly through the leaves or through the roots, and increases fitness and seed production at the same time (Chase et al. 2009). Accordingly, all plants can be carnivorous to some degree, but only those that can
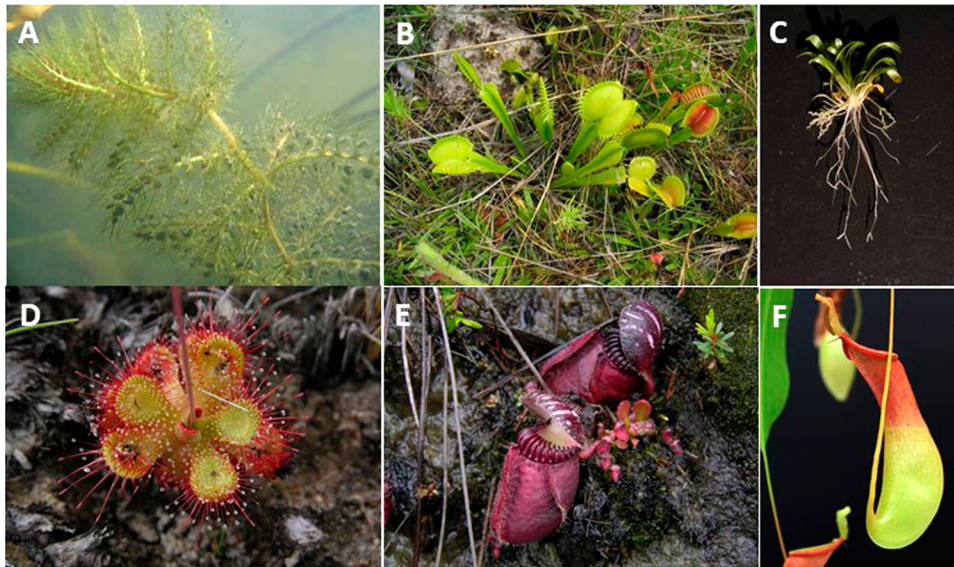
Figure 1. Carnivorous plant species with typical traps. (A) *Utricularia spec.* (bladder-trap); (B) *Dionaea muscipula* (snap-trap); (C) *Genlisea spec.* (eel-trap); (D) *Drosera sessifolia* (flypaper-trap); (E) *Cephalotus follicularis* (pitfall-trap); (F) *Nepenthes x ventrata* (pitfall-trap). (A–E, Copyright ©: A. Fleischmann; F, Copyright ©: A. Mithöfer).

be referred to as 'true' carnivores (or holocarnivores) should have the ability to (1) specifically attract, (2) capture, and (3) digest prey and utilize the metabolic products for their own growth (Lloyd 1942; Chase et al. 2009). Recently, Ellison and Adamec (2018b) have rephrased the definition for holocarnivory. They postulated five essential characteristics for the carnivorous syndrome: (1) capture of prey in specialized (and attractive) traps, (2) killing, (3) digesting, (4) absorption of nutrients from the digested prey, and (5) utilizing nutrients for plant growth and development. In holocarnivorous plants such as *Nepenthes* and *Drosera*, endogenous, specific hydrolytic enzymes can facilitate digestion. Plants that do not meet all the requirements are to be recognized as holocarnivorous, or those that cannot supply the enzymes needed for digestion are called hemicarnivorous (Ellison and Adamec 2018b; Adamec et al. 2021). Most *Heliamphora* species are an example of this, which require the assistance of microbes living in passive traps, but can absorb the resulting nutrients itself (Chase et al. 2009). However, these classifications are not fixed but are very dynamic and depend on new findings.

Traps and trapping strategies can be divided into active and passive traps according to their potential of mobility of the evolved trapping mechanisms (Król et al. 2012). Morphological changes or metamorphoses of leaf structures have produced the different trap types involved in prey capture (Figure 3) (Fukushima et al. 2015; Dkhar and Pareek 2019; Dávila-Lara et al. 2020; Whitewoods et al. 2020). Interestingly, certain traps are often the result of convergent evolution, for example, pitcher traps in the families Nepenthaceae, Cephalotaceae, and Sarraceniaceae (Thorogood et al. 2017). Altogether, there are five different trapping mechanisms, three of which are active, two are passive traps (Figure 1). An active trap is the one in which accelerated trapping motion is an integral feature of the trapping process; for example, the snap-trap of *Dionaea muscipula* (Venus flytrap), the flypaper-traps of *Drosera* (sundew) and *Pinguicula* (butterwort), or the sucking bladder-traps of *Utricularia* (bladderwort). In passive traps, accelerated movement is absent in the trapping mechanism surface

(Pietropaolo and Pietropaolo 2001). The eel-trap of *Genlisea* (corkscrew plant) is one example; others are pitfall (pitcher) traps of *Cephalotus follicularis* (Albany pitcher plant), *Darlingtonia californica* (cobra lily), and species of the genera *Sarracenia* (trumpet pitchers), *Heliamphora* (sun pitchers), and *Nepenthes* (tropical pitcher plants or monkey cups). Strikingly, many of the genes triggered in traps after prey capture and involved in carnivore processes appear to have evolved or been reassigned from herbivore defense mechanisms. Among those are genes encoding various hydrolytic enzymes involved in prey digestion (for a detailed overview, Ravee et al. 2018), ion channels, and transporters, as well as defense-related proteins and biosynthetic enzymes for signaling and defensive compounds. It is now generally accepted that the plant carnivore syndrome evolved from plant defense mechanisms, and the tools available to combat attackers were now used to capture, digest, and exploit prey (Mithöfer 2011; Pavlovič and Saganová 2015; Bemm et al. 2016; Fleischmann et al. 2018; Hedrich and Fukushima 2021).

It is worth to mention that attributes that differentiate carnivorous plants are also present in plants not considered to be carnivorous (Porembski and Barthlott 2006), such as visual and odiferous lures, directional guides, secreting glands, trapping, absorbing glands, and rapid movement. For example, some non-carnivorous plants like *Arum* species arrest visiting flies within the inflorescence during the male phase of anthesis, in order to secure pollen export (Bröderbauer et al. 2013). Some leaves display fast motion in plants like *Mimosa pudica* and *Desmodium* spp (Paudel and Shrestha 2018). Secreted sticky material (mucilage) can provide various functions such as modifying soil structures, attracting microbes, or helping climbing (Galloway et al. 2020). While all the individual characteristics of carnivorous plants can also be found in other plants, only the organism that has integrated all these characteristics into one plant is special: a carnivorous plant whose adapted leaves can attract, capture, and digest prey as an additional nutrient source to eventually derive benefit resulting in growth, survival, or reproduction (Brownlee 2013).
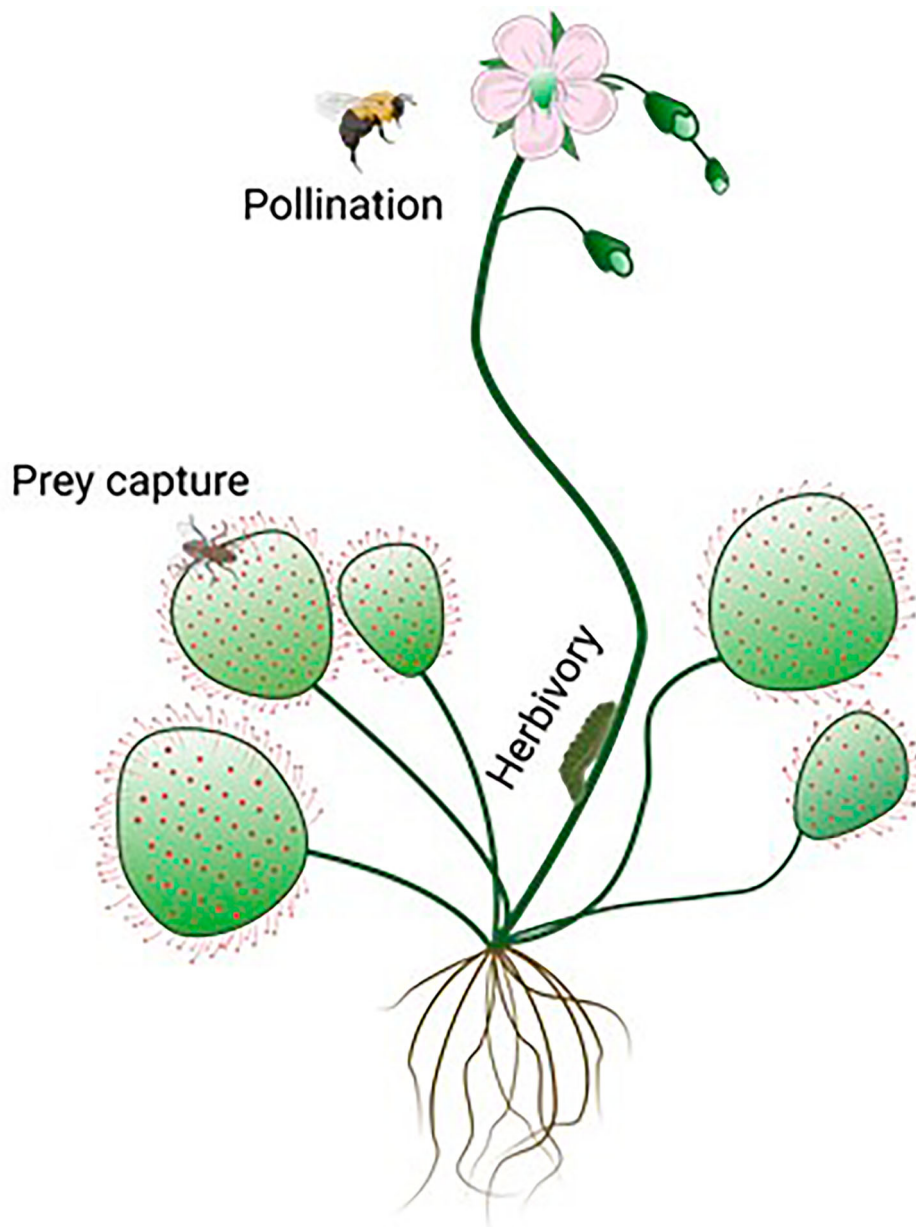
Figure 2. Scheme of carnivorous plant (sundew, flypaper-trap) and its typical interaction with invertebrates. Created with 'BioRender.com'.

3. Carnivorous plants – prey interaction

A comprehensive analysis by Ellison and Gotelli (2009), covering 30 studies on 8 carnivorous genera (46 species) between 1923 and 2007, suggested that carnivorous plants are not selective predators concerning prey composition. The main prey of carnivorous plants are invertebrates, i.e. arthropods, mainly insects. This holds true, in particular, for terrestrial carnivorous plants. Due to their aquatic (*Utricularia* spp) and wet-terrestrial (*Utricularia* and *Genlisea* spp) lifestyle, these plants also catch, for example, nematodes and protozoa. Submerge living *Utricularia* catch all kind of aquatic invertebrates, mainly copepods and water fleas (Cladocera) (Ellison and Gotelli 2009; Horstmann et al. 2019), but anecdotally also small young fish and even tadpoles (Lloyd 1942) (given that the trap is big enough). A zooplankton prey spectrum can be found for the aquatic *Aldrovanda vesiculosa* (Horstmann et al. 2019; Poppinga et al. 2019). Among terrestrial carnivorous plants, ants and flies dominate captured prey (Figure 4). Pitcher plants

(*Nepenthes* and *Sarracenia*) showed the highest proportions of ants in their diets, while flies (Diptera) dominated in plants with flypaper traps (*Drosera, Pinguicula*) (Ellison and Gotelli 2009). These findings reflect that besides the trap size, the different morphological trap specializations in these genera are also prey selection criteria (Darnowski et al. 2018).

Some pitchers of *Nepenthes* and *Sarracenia* are so big that larger prey, such as frogs, rats, or lizards are found to be partially digested inside the pitcher (Adlassnig et al. 2011; Wells et al. 2011). This phenomenon shows that prey of carnivorous plants is not restricted to invertebrates only. Whether these catches really contribute regularly to the life style of carnivorous plants or represent accidents remains to be solved. It is also worth mentioning that few carnivorous plants can be seen as herbivores or omnivores. In particular, *N. ampullaria* plants possess large pitchers sitting on the ground with wide openings waiting for leaves and other organic material falling down, which can be digested
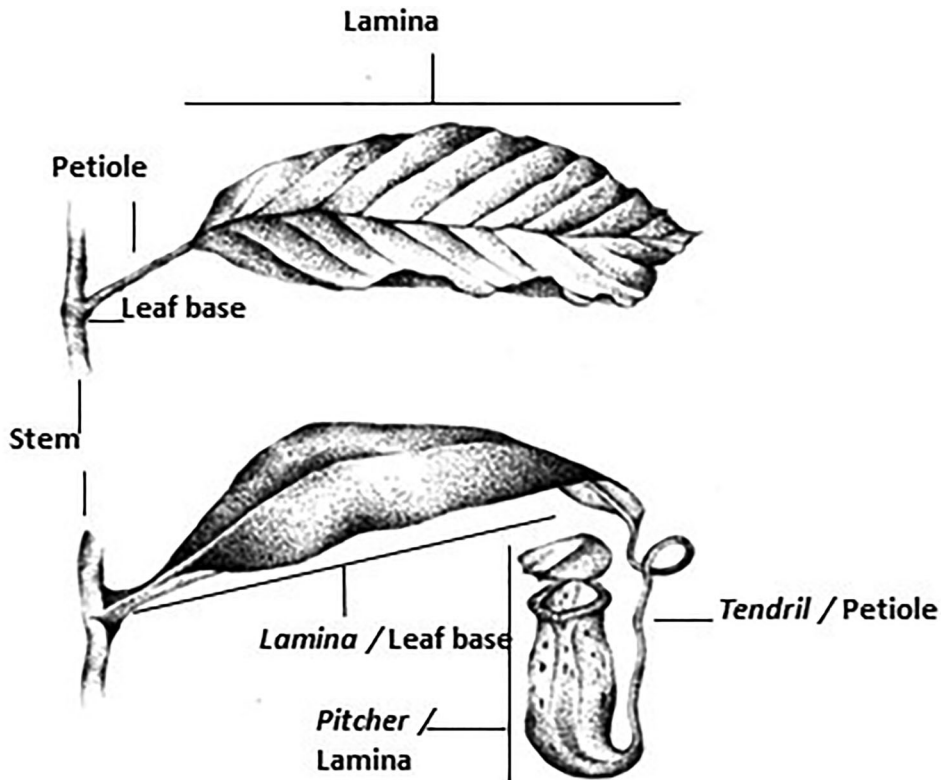
Figure 3. Metamorphosis of a *Nepenthes* leaf. Typical foliage leaves (upper), *Nepenthes* leaf (lower). In italics, the leaf parts developed in *Nepenthes* as result of metamorphosis of the typical leaf parts (CC-BY 4.0, S. Zunk).

(Moran et al. 2003; Pavlovič et al. 2011). In addition, adhesive traps, e.g. from *Pinguicula* and *Drosera*, in general, are suitable not only to capture small animals but also for the collection of plant-derived organic particles like pollen grains (Juniper et al. 1989; Adlassnig et al. 2010). However, most carnivorous plants consume a wide range of prey.

Figure 4. Prey distribution in selected terrestrial carnivorous plant genera. Slices of each 'star' plot are scaled to the average proportion of each prey taxon (order except for ants – family Formicidae). Only the 12 most common prey orders are shown. Color key is given in the lower right. Figure was modified after Ellison and Gotelli (2009), with permission of the authors.

Generally, in order to capture and digest prey, the plants face the challenge to attract prey. For aquatic carnivorous plants, the mode of attraction is unknown. However, for *Genlisea*, results of behavioral experiments showed that prey move to the traps by accident. The plant does not need special mediators for its attraction (Płachno et al. 2008). Very likely, the same counts for the free-floating *Utricularia* species, although chemical attractants are discussed as well (Albert et al. 2010). For carnivorous terrestrial plants, three main strategies for attracting prey are most likely important: (i) visual stimuli, (ii) olfactory stimuli, and (iii) extrafloral nectar (EFN) as a reward. Combinations of these strategies are also conceivable.
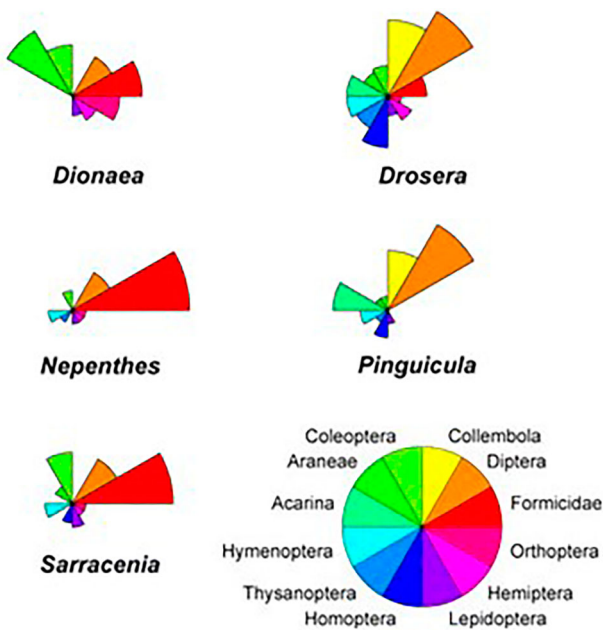
3.1. Visual cues – colors

Visual signals seem to be important in the attraction of diurnal prey. It is obvious that the traps of many carnivorous plants (Droseraceae, Nepenthaceae, and Sarraceniaceae) have an intensive red color, due to the presence of anthocyanins (Dávila-Lara et al. 2021b). Red coloration increases capture efficiency of *Nepenthes* traps by providing attractive visual signals, i.e. the rates of caught insects positively correlate with levels of red pigmentation (Schaefer and Ruxton 2008). Thus, red color may directly enhance the trap efficiency or indirectly provide a useful background for better recognition. However, the relative importance of visual cues has been a pivotal point of debate. While Schaefer and Ruxton (2008) considered red coloration of pitcher plant traps serving as an attractant, Bennett and Ellison (2009) questioned the conclusion. Instead, they suggested that the pitcher color patterns do not provide important signals for

prey attraction but EFN. In addition, for *Drosera rotundifolia*, it was demonstrated that the red trap color was not involved in prey attraction (Foot et al. 2014). It should be mentioned here that most insect taxa found as prey are red-blind or at least cannot perceive all wavelengths that constitute the color 'red' to our human perception (Briscoe and Chittka 2001). Even if red traps reflect wavelengths in blue or green-yellow wavelengths (Moran et al. 1999), their visibility to a red-blind insect would depend on the contrast against the background of the surrounding green vegetation (Jürgens et al. 2009). Other studies suggested an impact of visual cues within the UV light range, which is visible for insects, rather than within the longer wavelength range (Joel et al. 1985; Kurup et al. 2013). Thus, to what extent any trap coloration is involved in prey attraction remains an open question. Another possible strategy to attract and guide prey into a trap is realized by the presence of (semi)-translucent areas in pitcher plants with hooded traps. *Nepenthes aristolochoides* has a translucent dome at the rear of the pitcher (Moran et al. 2012). Other pitcher plants have spots in the back of the hood tissues, so-called fenestrations, or areoles in case these fenestrations contain a white pigment (*Darlingtonia californica* and *Sarracenia* species) (Schaefer and Ruxton 2014; McGregor et al. 2016). For insects, these transparent windows mimic exits of the pitchers; however, they ultimately guide the prey deeper into the trap.

3.2. Olfactory cues – scent

Many carnivorous plants from various taxa are capable of releasing volatile compounds from trapping leaves. For example, various *Sarracenia* species, *N. rafflesiana* (here the pitchers from the upper, climbing part), and *D. muscipula* emit volatiles mimicking flower or fruit scents (Di Giusto et al. 2008; Jürgens et al. 2009; Kreuzwieser et al. 2014). Much lower scent and less compounds are released from *Drosera binata* and *S. purpurea;* here, the emitted compounds are more comparable with typical leaf volatiles (Jürgens et al. 2009). By using choice assays in the absence of any visual cue, in *N. rafflesiana*, the scents of the nectariferous peristome were particularly attractive to ants and flies, and those of upper pitchers were more attractive to flies than those of lower pitchers (Di Giusto et al. 2010). This study supported the finding of Moran (1996) who found more flying prey in the upper pitchers than in the lower ones. Unique in the carnivorous plant kingdom is the specialization of *N. albomarginata*, whose food source is restricted to only one prey taxon. With a wreath of white feeding hairs (trichomes) directly under the peristome, it attracts exclusively termites of the subfamily Nasutitermitinae (predominantly *Hospitalitermes spp.*), which are virtually blind. The termites congregate there in massive quantities, consequently fall into the pitcher and are digested (Merbach et al. 2002). Some species of carnivorous plants emit a different blend of volatiles from their flowers and traps to attract, on the one hand, the prey insect species and, on the other hand, repel pollinators from the traps (El-Sayed et al. 2016). All these studies support the role of olfactory cues in the attraction process.

3.3. Extrafloral nectar – a reward

Many insects are attracted by sweet extrafloral nectar, in particular ants. The presence of nectaries and the production of EFN has been shown for almost all carnivorous plant taxa but the focus of studies was on pitcher plants (Płachno 2007). In *N. bicalcarata*, EFN is involved in a very special myrmecophilic interaction (see subsequently). In *S. purpurea,* Bennett and Ellison (2009) demonstrated the attractiveness of EFN for insects, mainly ants. For some *Nepenthes* species, it has been shown that the EFN on the peristome is part of the trapping mechanism because water droplets spread rapidly and form homogeneous thin films, which make the peristome extremely slippery for insects that finally fall into the trap (Bohn and Federle 2004). The EFN production in carnivorous plants occurs close to or within the trapping zones; thus, the insects reaching for the nectar need to enter and remain in a highly dangerous area. This will definitely increase the probability of being captured – but not for sure. Therefore, escaped, but EFN-rewarded, social insects such as ants will tell others in their colony and many more will return (Bauer et al. 2015). However, it is unknown how prey finds the EFN, whether just accidently when passing by or if there is something attractive. Altogether, with few exceptions, under natural conditions, there is usually a high variability of prey composition making conclusions on its specificity for most carnivorous plants difficult.

4. Are carnivorous plants predators?

When talking about carnivory in plants, it is necessary to take the next step and ask: Are these plants hunting and are they predators? Ellison (2020) has recently discussed this deeply. Including different theories and foraging strategies, he concluded that carnivorous plants are predators that do hunt following the sit-and-wait strategy. While active foraging involves active searching for suitable patches and for prey, carnivorous plants remain rooted to a single location and depend on the abundance and movement of their prey. Since carnivorous plants use traps for capturing prey, probably the sit-and-wait strategy of spiders hunting with spiderwebs is a comparable strategy. However, because carnivorous plants sit and never move, they can be considered as the purest form of sit-and-wait predators. Thus, they might be comparable to sessile filter feeders (e.g. barnacles and mussels).

Interestingly, it was suggested that carnivorous plants may benefit from group foraging, like a wolf pack (Savage and Miller 2018). Based on a field experiment, the authors found that larger groups of *S. flava* caught a greater mass of prey. However, the rate of all prey per leaf and the number of individuals from different insect orders were statistically indistinguishable between groups of different sizes (Savage and Miller 2018). In contrast, another field observation suggested that high neighborhood density in *Drosera makinoi* increased both the number of larger prey (≥ 3 mm) and the captured prey biomass per plant (Tagawa and Watanabe 2021). Here, however, the explanation might be that more sticky tentacles from different plants are able to catch and hold stronger and larger insects, preventing prey from escaping, than a single plant ever could. Thus, the trapping mode may contribute to the success of group foraging. Nevertheless, up to now, there is no clear scientific evidence that carnivorous plants benefit from group foraging.

5. Carnivorous plants and symbiotic interactions

Knowledge of the mechanisms underlying interactions between carnivorous plants and arthropod prey contributed

to the notion of evolutionary associations that reveal new symbiotic relationships. Some carnivorous plants have unique mutualistic relationships with other organisms that contribute to or replace prey capture and digestion, such as (i) digestive mutualism, (ii) coprophagy, and (iii) myrmecophily. In these cases, carnivorous plants show general concepts of coevolution. More examples of other, non-mutualistic relationships will be presented as follows as well.

5.1. Digestive mutualism

Digestive mutualism represents an alternative strategy of prey digestion. Here, the help of other organisms is necessary and involved to digest captured prey. Actually, with respect to the definition mentioned previously, these plants are hemicarnivorous. This phenotype can be often found in new-world pitcher plants of the genus *Heliamphora* and few *Sarracenia* species (*S. rosea* and *S. flava*) (Jaffe et al. 1992; Koller-Peroutka et al. 2019). In these cases, the plants provide a micro-environment in their pitchers which is colonized by micro-organisms such as protozoa, fungi, and micro-algae, rotifers, and various taxa of arthropods (Adlassnig et al. 2011). This is possible because the fluid in these pitchers is highly diluted and similar to water, in contrast to the old-world pitcher plants (*Nepenthes*), where the fluid is acidic and contains antimicrobial compounds and digestive enzymes (Buch et al. 2013). The inquilines contribute to the digestion with enzyme secretion, release of nutrients, mechanical break-up and remove of excessive prey, and even assimilation of nitrogen (Adlassnig et al. 2011). However, it is difficult to imagine that within the same genus, some species can secrete digestive enzymes into the pitcher fluid and others cannot. Maybe, this trait got lost during evolution. Strikingly, the presence of inquilines is not fully restricted to the new-world pitcher plants. Also for *Nepenthes*, there are examples where crab-spiders (Thomisidae) or dipteran larvae (Culicidae and Phoridae) somehow can inhabit pitchers (Lam et al. 2017; Lim et al. 2018). The dipteran larvae contribute to prey digestion, and the crab-spiders catch flies and defecate into the pitcher, thereby providing nutrients for the plant.

Another example of a mutualistic digestive mechanism is the interaction between *Roridula gorgonias*, an endemic species in South Africa, and the hemipteran bug *Pameridea roridulae* (Ellis and Midgley 1996; Anderson and Midgley 2003). These plants catch insects with their sticky tentacles (flypaper trap) but cannot digest the trapped insects. Instead, the bug *Pameridea roridulae* that lives on the plant sucks out insect juices and later the plant absorbs nutrients from the bug's droppings. Strikingly, *Pamerida* can only live on *Roridula* species. Due to their special hairy feet, they are able to walk on the leaves' surface without being caught. Although nutrient absorption in *Roridula* is an indirect process, it is extremely effective.

Digestive mutualism may be considered as a specialized adaptation to the carnivorous syndrome because they reduce the costs of produce digestive enzyme production. However, this applies more to *Roridula* than to the new-world pitcher plants, since in the latter, sometimes large number of inquilines also absorb the released nutrients.

5.2. Coprophagy

The former interaction between *Roridula–Pamerida* is an example where the plant gets nutrients from feces. This situation is also realized in three *Nepenthes* species, *N. lowii*, *N. rajah*, and *N. macrophylla*; but here the plants interact with vertebrates (Clarke et al. 2009; Chin et al. 2010; Greenwood et al. 2011). Actually, the plants benefit from the nitrogen in the feces of small mammals that defecate into the pitchers. Such an animal is the mountain shrew, *Tupaia montana*. The shrews are rewarded with nectar from the lid of the pitcher. To get there, they sit on the pitcher's opening and relax while feeding (Clarke et al. 2009). In addition, rats (*Rattus baluensis*) have been observed to visit *N. rajah* and behave similar (Greenwood et al. 2011). Similarly, while roosting inside, individuals of the bat species *Kerivoula hardwickii* defecate into pitchers of *N. hemsleyana* (Grafe et al. 2011; Schöner et al. 2017). In this case, the presence and employment of a tissue-localized urease enables the plant to efficiently metabolize the bat-derived nitrogen because it is mainly provided as urea (Yilamujiang et al. 2017). Hence, the visiting activity of mutualistic mammalians can significantly increase nitrogen content in the carnivorous host plants. However, these *Nepenthes* species retained the ability to catch and utilize prey.

5.3. Myrmecophily

The only known carnivorous plant that lives in a mutualistic interaction with an ant species is *N. bicalcarata* (Clarke and Kitching 1995). The ant species, *Camponotus schmitzi*, provides protection against an herbivorous weevil that feeds on pitcher buds and gets housing in hollow tendrils called domatia (Merbach et al. 2007). Ant colonies are small, comprising only about 30 individuals. *C. schmitzi* feed on the nectar excretions from the pitcher but in addition on carcasses of *N. bicalcarata* prey, which they remove from the fluid in the pitcher. Strikingly, these ants can dive and swim in the pitcher fluid and, furthermore, they can walk on the slippery wet peristome surface due to their specialized arolia (adhesive lobes) on their feet (Bohn 2007). This is almost impossible for all other known insects that encounter *Nepenthes* species. However, if some individuals try to escape, they are attacked by the *C. schmitzi* ants and forced back into the pitcher. This is further facilitated by a cleaning behavior of the ants. In this process, they remove everything such as particles and hyphae from the peristome to keep it as slippery as possible (Thornham et al. 2012). Finally, the ants remove the caught insects and feed on them before they dropped the remaining uneaten pieces back into the pitcher (Bonhomme et al. 2011). In addition, they feed the plant with feces and their dead bodies (Bazile et al. 2012). In this particular case, the ant–plant interaction could be a nutritional mutualism consisting of carnivory and myrmecotrophy.

5.4. Non-mutualistic interactions

Other striking interactions are known as kleptoparasitism. Larvae of the predatory dipteran hoverfly *Toxomerus basalis* (Syrphidae) have been found crawling and living the complete larval stage on the sticky leaves of various *Drosera* species in Southeast Brazil. This syrphid obviously feeds on carcasses trapped by *Drosera* leaves, showing also a

kleptoparasitic behavior (Fleischmann et al. 2016). In contrast to the situation in *Roridula–Pamerida* relationship, here the syrphine larvae do not defecate during their feeding period until they pupate. Thus, no nutrient return to the plant from larval excretions occurs (Fleischmann et al. 2016). Similarly, the relationship between *Pinguicula vallis-neriifolia* and the slug *Deroceras hilbrandi* also shows kleptoparasitic characteristics (Zamora and Gómez 1996). The slug feeds on old, dry, and fresh carcasses that were captured by the plant; in the latter case, the plant is derived of nutrients. This behavior is possible because the slugs are able to crawl on the leaves without being trapped. In particular during summer, the slug spends long time periods on the plant.

Recently, a putative commensalistic interaction between *Nepenthes* and birds was described. Bauer et al. (2016) observed a diverse guild of vertebrates consisting of four sunbird species and a tree shrew species visiting pitchers of *Nepenthes* for nectar robbing. The vertebrates harvested nectar from the peristome of *N. rafflesiana* and from the lid of *N. gracilis*. Being too big to serve as a prey, these visits were without any obvious benefit for the plants. This interaction is more likely to be considered as a form of commensalism, because the loss of nectar from occasional visits does not seem to affect the plant. However, more research is necessary in order to get deeper insights into this interaction.

6. Carnivorous plants and pollination

Insects pollinate most carnivorous plant species. That generates a dilemma between pollination on the one side and prey capture on the other side, the so-called pollinator–prey-conflict (PPC) (Zamora 1999; Jürgens et al. 2012). Interestingly, this obvious conflict is not as relevant as expected. The reasons are as follows. Actually, the PPC can only become a dangerous situation for the pollinator insects in carnivorous taxa with sticky flypaper traps (*Drosera, Pinguicula* and *Drosophyllum*), pitfall traps (*Nepenthes, Heliamphora, Sarracenia, Cephalotus*, and *Darlingtonia*) and snap-traps (*Dionaea*). The eel traps of *Genlisea* and the suction traps of *Utricularia* are subterranean or submerged, which avoids the PPC. *Aldovanda vesiculosa* is obligate autogamous (Cross et al. 2018). For *Dionaea muscipula*, Youngsteadt et al. (2018) recently showed that the spatial separation of flowers and traps, probably by the long flower stalk, can help separate pollinators from prey. This principle of spatial separation can also be found e.g. in *Drosera, Pinguicula*, or *Sarracenia* (Figure 5). In addition, temporal separation might be another way to reduce PPC. This can be realized by different seasonal periods for flowering and trap activities, which occurs for example in some *Sarracenia* and *Pinguicula* species (Cross et al. 2018). In *Nepenthes* and *Heliamphora* species, trap activity correlates with periods of high humidity, which makes the peristome slippery (Bohn and Federle 2004). This in turn is a time without many flying insects involved in pollination. In addition, in particular, *Nepenthes* captures mainly ants as prey while winged insects act as pollinators (Cross et al. 2018). These aforementioned examples explain the observation that in pitfall traps no obvious pollinator–prey species overlap could be found, neither in *Nepenthes* nor in *Sarracenia* or *Heliamphora*. In addition to the flight ability, the size of the pollinating insects may often be important. Bees, humblebees, and moths are involved in pollination, while flies and ants serve as prey. Of course, bee capture has also been described for the invasive Africanized honeybees (killer bees) in pitchers of some *Heliamphora* species in Venezuela, but it remains the exception. (Fleischmann and McPherson 2010). In carnivorous plants with flypaper traps, small dipterans are the main prey. As reported for *Drosophyllum lusitanicum* (Bertol et al. 2015) and various *Drosera* species, again an overlap of pollinator and prey taxa is small or even absent (Murza et al. 2006; Anderson 2010; El-Sayed et al. 2016). At least for *Pinguicula*, size matters. The leaves could capture small pollinators, e.g. thrips, but not humblebees. The risk depends on the size of the pollinators (Zamora 1999). Beyond these findings, very likely there are additional players involved in pollinator and prey attraction. Chemical cues such as volatiles (scent) or floral nectar, as well as visible cues (color), can contribute and increase the attractiveness of the flower to pollinating insects and to traps for insect prey (Jürgens et al. 2012).

Figure 5. Flowering carnivorous plants. A: *Pinguicula leptoceras* (Copyright ©: A. Fleischmann); B: *Sarracenia purpurea* (Copyright ©: A. Mithöfer).

However, such cues and their specific role still wait for their identification. As inferred from the low similarity between insect pollinators and prey in the different taxa of carnivorous plants, the attraction of prey does not seem to be related to the attraction of pollinators (Jürgens et al. 2012).

7. Carnivorous plants under insect herbivore attack

Almost all studies on carnivorous plants focus on the carnivorous syndrome. However, plants also face the interaction with herbivorous insects but herbivory on carnivorous plants seems rare. In *Pinguicula moranensis*, more herbivory was detected in sunny- than in shade-field sites (Suarez-Piña et al. 2016). Surprisingly, with respect to the overall performance, simulated herbivory unraveled a high tolerance to tissue damage in *P. moranensis* (Ortuño-Mendieta et al. 2021). For the same species, both field and lab experiments showed that the presence of sticky glandular trichomes, which are involved in prey capture, also efficiently protect the plant from herbivory (Alcalá et al. 2010). Thus, here the trichomes have a dual role for the plant and it seems obvious that an originally defense-related feature was co-opted during evolution for carnivory. However, it is unlikely that all putative herbivores are captured and digested. The genus *Pinguicula* could be an exception due to its rosette-like growth habit and the general presence of sticky trichomes. In different *Drosera* species, sundew plume moth larvae (*Buckleria paludum*) were described to live and develop on the carnivorous plants, feeding on the sticky tentacles, leaf blade, flowers, and fruits or only licking the secreted mucilage (Eisner and Shepherd 1965; Osaki and Tagawa 2020). In particular, last instar larvae showed the licking behavior, very likely to remove sticky mucilage in order to escape the possibility of being captured (Osaki and Tagawa 2020). No defensive plant reaction in any of these interactions have been described so far.

Few studies that investigated the attack of insects on carnivorous pitcher plants where lepidopteran herbivory was described for *Sarracenia* species are published (Carmickle and Horner 2019; Lamb and Kalies 2020). One study showed infestation of *N. bicalcarata* by a weevil (*Alcidodes spec.*) but also protection by *Camponotus schmitzi* ants that attack this herbivore (Merbach et al. 2007); in *N. gracilis*, a higher herbivory level for green than for red, anthocyanin-containing pitchers, was detected (Gilbert et al. 2018). In contrast, for *P. moranensis*, such a correlation was not found (Ayestarán and Alcalá 2016). Recently, herbivore treatment with the generalist lepidopteran moth, *Spodoptera littoralis,* was investigated in *N. x ventrata* and the defense responses were analyzed (Dávila-Lara et al. 2021a). In that study, at least for *N. x ventrata* leaves, efficient chemical defenses against herbivores were identified – on the one hand, the induced trypsin protease inhibitor activities, which are well known in plant defense (Mithöfer and Boland 2012) and, on the other hand, the constitutive presence of naphthoquinones such as plumbagin (Figure 6), acting as a phytoanticipin. For plumbagin, its anti-feeding and growth-inhibiting activities were demonstrated (Rahman-Soad et al. 2021; Dávila-Lara et al. 2021a); moreover, naphthoquinones seem to be widespread among the taxa of carnivorous plants belonging to the Caryophyllales (Droseraceae, Nepenthaceae, and *Drosophyllum*) (Schlauer et al. 2005; Devi et al.
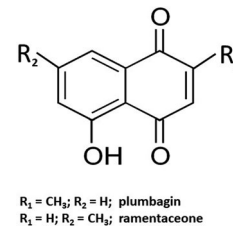

R₁ = CH₃; R₂ = H; plumbagin
R₁ = H; R₂ = CH₃; ramentaceone

Figure 6. Structure of the naphthoquinone plumbagin, acting as phytoanticipin in many carnivorous plants of the order Caryophyllales, and related derivatives.

2016). Strikingly, in *N. x ventrata*, only the induction of the trypsin inhibitor activity was jasmonate-mediated. In general, these phytohormones are well-known key-players in the defense regulation against herbivores in plants (Mithöfer and Boland 2012; Pavlovič and Mithöfer 2019). Both inducibility of jasmonates and their downstream signaling pathways in various carnivorous plants, e.g. *Drosera capensis* (Nakamura et al. 2013; Mithöfer et al. 2014), *D. muscipula* (Libiaková et al. 2014; Bemm et al. 2016), and *Nepenthes spp.* (Yilamujiang et al. 2016; Dávila-Lara et al. 2021a), indicate the presence and a function of typical defense responses in carnivorous plants. This has been reviewed recently in depth (Pavlovič and Mithöfer 2019).

8. Concluding remarks

After more than 150 years of research on carnivorous plants, they have not lost their fascination, and ongoing research on carnivorous plants is yielding many fascinating results. In addition to the new species discovered each year, novel interactions with other organisms, including vertebrates, are often examples of unexpected and exciting symbiotic relationships. For instance, based on similar traits, the genus *Nepenthes* exhibits many intriguing ecological specializations related to nutrient acquisition and seems to be a playground for coevolution – but why *Nepenthes* in particular? What makes this genus so special and adaptable to new symbiotic interactions? Studies of the genetic and physiological factors that determine the carnivorous syndrome will provide deeper insights into its ecology and evolution, and to address the question of how did plant carnivory evolve several times convergently in the plant kingdom, thereby independently evolving very similar traits.

However, as shown in this review, these plants should not be reduced to their carnivorous syndrome. Studies of their pollination have revealed interesting aspects of the pollinator–prey conflict that is not yet fully understood. Recently, carnivorous plants and their abilities to defend and repel insect herbivores, a long-ignored interaction, have been studied. It is tempting to speculate that many secondary metabolites involved in plant defense await identification; not least, because tropical carnivorous plants in particular are commonly used in traditional medicine. Interactions with pathogens are also still waiting to be discovered and studied. Why are only so few known? How could these plants co-opt molecular tools for defense against pathogens and herbivores for carnivory? Are carnivorous plants *per se* better protected against biotic attackers?

All of these interactions are in a different ecological context, but they interact and influence each other in a common

network that is far from known. Therefore, these plants and their biotic partners represent very special organisms that are of particular interest to the entire field of plant biology and ecology. In the future, interdisciplinary and '-omics' approaches will be able to address such questions and understand all the features of plant carnivory.

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