Adaptive strategies of *Nepenthes*: A review

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Abstract: The evolution of *Nepenthes* pitcher plants illustrates a remarkable case of morphological innovation shaped by ecological pressures. Across the genus, diverse pitcher forms have emerged in response to nutrient-poor habitats, enabling both efficient carnivory as well as resource capture from other nitrogen sources. Variation in pitcher morphology aligns closely with environmental factors, reflecting intricate relationships between form, function, and survival strategy. These patterns reveal not only the adaptability of *Nepenthes* but also illuminate broader evolutionary processes such as convergence, niche specialization, and constraint-driven innovation.

Introduction

The greatest concentration of *Nepenthes* species is found in the Malay Archipelago, particularly Borneo, Sumatra, and the Philippines. *Nepenthes* are also found in Madagascar, Seychelles, Sri Lanka, India, Australia, and New Caledonia. *Nepenthes* pitcher plants have evolved a variety of tailored adaptations to survive in this highly diverse ecological region. As a review of the current literature, this paper explores some of these specialized adaptations shaped by ecological conditions.

The landscape of these regions varies greatly. In Borneo alone, the lowlands including Kota Kinabalu, Sandakan, and the coastal regions, experience average temperatures of 26–32°C, while the highlands maintain cooler conditions between 18–24°C. These temperature gradients, paired with the island's fragmented geography create a variety of distinct microenvironments, which in turn promote allopatric speciation among *Nepenthes*, the process by which geographic isolation ultimately results in genetically distinct species. As a result, plants in those types of environments have evolved in isolation, adapting to their niches (Thorogood *et al.* 2018). Thorogood notes that in addition to the different altitudes, the evolutionary path of *Nepenthes* is further shaped by varying rainfall, soil types, and sunlight in these regions, creating distinct species suited to the local ecological conditions. The combination of these environmental factors plays a crucial role in driving the evolutionary patterns seen in *Nepenthes*, highlighting how physical isolation and local climate differences foster diversity within the genus.

While *Nepenthes* vary heavily in shape and size, there are generally some characteristics shared between all species. *Nepenthes* utilize carnivory through highly modified leaves, which can trap and digest organisms for nutrients, a vital adaptation in environments where the soil lacks essential elements, namely nitrogen. They use a passive-trapping method—unlike the active thigmonastic traps employed by the famous Venus Flytrap. Their leaves attach to the pitcher cup through a tendril, which can wrap around other objects for stability. *Nepenthes* typically have a peristome, a slippery rim on the edge of the pitcher cup which may have specific coloring to help attract prey (Scott *et al*. 2000). The majority of *Nepenthes* have a lid which partially blocks the orifice of the pitcher, preventing rainwater from overflowing the cup, which, if absent, could lead to the loss of nutrients and dilution of digestive fluid. Like the peristome, the lid is often unique in color and patterning, and in certain species, it serves as a major site of nectar production (Merbach *et al*. 2001). It is hypothesized by some that the nectar is intoxicating to insects, causing them to become uncoordinated – and increasing the chances of being captured (Lathika *et al*. 2000). According to anecdotal reports from some observers, as well as my own experience, insects found on the peristome react somewhat lethargically when touched, although conclusive research identifying what specific compounds might contribute to this effect is lacking at this time. The production of nectar, coupled with the slippery peristome, increases the likelihood of prey capture. While their primary prey consists of insects, larger *Nepenthes* species may also trap small vertebrates like frogs and lizards, further highlighting the diversity of their carnivorous diet. The combination of these adaptations makes *Nepenthes* plants efficient in nutrient acquisition, enabling them to thrive in otherwise nutrient-poor environments.

Specialized adaptations for carnivory

While all *Nepenthes* species are carnivorous to some degree, many have evolved extraordinary adaptations that significantly enhance their trapping efficacy. From potent nectar to deadly teeth and sticky fluids, these modifications enhance the ability to capture prey. Whether by luring insects to a slippery edge or forcing them into dangerous positions, many species have developed unique approaches to survival. These specialized traits underscore the evolutionary innovation of *Nepenthes* to the nutrient-poor environments where they thrive. One such adaptation is seen in *Nepenthes lingulata*, a rare highland species (Lee *et al*. 2006). Its most distinctive feature is a thin, tongue-like filament that juts out from the underside of the pitcher lid. Unlike the lid glands of most *Nepenthes*, which secrete nectar broadly across the surface, *N. lingulata* produces nectar exclusively at the tip of this long, dangling "tongue" (*lingua*). Lee and colleagues observed that insects must crawl out onto the slender projection, hanging directly over the pitcher's deadly opening, to access the reward. A single misstep or gust of wind can easily send them tumbling into the trap below. While minor nectar-producing crests are common in species like *N. izumiae*, which has a short 1 cm ridge, *N. lingulata*'s extreme 2–4 cm extension represents an effective evolutionary tactic. In the nutrient-poor, high-altitude forests where it grows, and where prey is scarce, this strategy ensures that any insect drawn in is placed in maximum peril.

Most *Nepenthes* species have a ribbed peristome—small ridges that face inward toward the pitcher cup. These ridges make the surface difficult for insects to grip and help guide prey toward the trap opening. While in many species the ribbing is subtle (only fractions of a millimeter in size), others have evolved dramatic, tooth-like structures along the peristome. One striking example is *Nepenthes hamata*, whose fearsome, hook-shaped teeth can extend up to 7 mm from the pitcher rim (Cheek & Jebb 2001). These structures increase the effective surface area of the peristome, creating more opportunities for insects to lose their footing and fall in (Thorogood *et al*. 2018). The hooked shape of *N. hamata*'s teeth also serves to block escape, helping to ensure prey cannot climb back out once trapped (Fukushima 2023). Another species, *Nepenthes edwardsiana*, features similarly elaborate peristome ornamentation, though its teeth are flatter and more blade-like. These comb-like edges, when combined with nectar secretion and the slippery surface of the peristome, destabilize footing and further entice prey toward the trap. In extreme cases, like *Nepenthes macrophylla*, the teeth resemble interlocking spines, forming a jagged, almost cage-like barrier around the pitcher mouth (Cheek & Jebb 2001). These "toothy" *Nepenthes* species are all native to high-altitude environments, where insect life is less abundant, and nutrients are harder to come by. In such habitats, every successful catch matters, and the evolution of complex peristome structures likely reflects strong selective pressures favoring efficient prey capture and retention.

The peristome, one of the most striking features of *Nepenthes*, is absent in some species. While the peristome functions to lure prey to the pitcher, provide a slippery surface, and prevent prey from escaping, *Nepenthes inermis* diverged evolutionary from most other *Nepenthes* species. The pitcher cup is funnel-shaped and relatively small—only 5 to 9 cm in height—and is fully green. The ends of the pitcher cup of this species simply taper off, forming a thin edge. It appears extremely delicate and inefficient at prey capture. Despite its appearances, *N. inermis* is lethal. Well described in Matt Candeias' blog (Candeias 2019), *In Defense of Plants*, to compensate for a lack of peristome, the pitcher fluid inside *N. inermis* is thick and viscous, and comparable to honey. When poured out, the fluid can stretch multiple meters before it breaks. Instead of elaborate trapping methods like other *Nepenthes*, once an insect steps inside the fluid of *N. inermis*, it gets trapped and begins to sink further into the cup. Additionally, the pitchers lack a waxy zone, demonstrating their reliance on the pitcher fluid. This strategy allows *N. inermis* to thrive in its misty, highland environment where heavy rainfall could otherwise dilute thinner pitcher fluids, especially since the lid, which usually can help protect the pitcher from rain, is essentially vestigial (Candeias 2019). Despite its pared-down structure, the trapping efficacy of *N. inermis* highlights the genus's wide range of adaptive strategies.

Many *Nepenthes* species attract insects with their enticing nectar. However, *N. albomarginata* has evolved a more deceptive strategy. At first glance, *N. albomarginata* does not appear particularly noteworthy, featuring a fully red pitcher cup and a somewhat plain shape. However, upon closer inspection, a distinct white "band" just below the peristome becomes visible. Described by Marlis Merbach and colleagues in the journal *Nature*, this band is made up of trichomes, small, hair-like structures, that specifically attract *Hospitalitermes bicolor*, a species of foraging termite (Merbach *et al*. 2002). The termites are drawn to the edible trichomes and begin to feast but in the chaos of competition, many fall into the pitcher's digestive fluid. In their scramble to reach the trichomes, termites push and shove each other, inevitably sending some to their deaths. Merbach noted *N. albomarginata* can capture up to 22 termites per minute, with each pitcher capable of trapping thousands of termites – most of which may be caught in a single night. Merbach reported that by morning, previously intact trichomes had been consumed, and the pitchers had filled with prey. This innovative method of prey capture makes *N. albomarginata* one of the only plants known to offer its own tissue as bait. The strategy proves highly beneficial: termites are not only among the most abundant insects in tropical rainforests but also provide a rich source of nitrogen compared to other insect prey.

Unique adaptations of lowland species

While many *Nepenthes* species have developed intricate ways to trap insects, others have evolved strategies to maintain viability in resource-limited surroundings. In the unpredictable and often harsh conditions of the rainforest, finding a consistent food source can be difficult. Research reveals how *Nepenthes* have adapted by shifting focus away from carnivory alone, developing traits that allow them to exploit new resources or thrive in a wider range of environments. These adaptations highlight the resilience and versatility of the genus in the face of constant environmental challenges. As insects can be a scarce resource for *Nepenthes*, instead other methods must be devised to acquire essential nitrogen for growth. For *Nepenthes ampullaria*, this means focusing its attention on falling leaves (Candeias 2016). *N. ampullaria* grows throughout the Malesian floristic region in southeastern Asia and can be found in lowland tropical forests including peat swamps and shaded nutrient-poor areas (Kiew 2012). Kiew notes that while *N. ampullaria* may be observed climbing, growing "to about 15 m tall with a stem 1–1.5 cm thick," its pitchers are most typically found covering the low-lying areas, forming dense regions of confluent growth. Falling leaves are abundant here with leaf litter coating the lowland rainforest floors of *N. ampullaria's* home. The plant sits with its mouth wide open, letting the leaf litter pile in its cups. To maximize their adaptations, *N. ampullaria* has urn-like pitchers – its peristome forms a circle, and slopes downward toward the digestive fluid. Normally, the lid of *Nepenthes* would prevent leaves and water from falling into the pitcher, but for *N. ampullaria*, this is no issue. As reported by Candeias (2016), the lid of *N. ampullaria* is vestigial and lacks nectar production. The waxy layer that normally coats the inside of the pitcher to prevent bugs from leaving is not present, hinting at the plant's unique method of survival. In fact, the pitchers of *N. ampullaria* make excellent and enduring homes for an inquiline community of insects and even frog larvae, lasting up to 6 months (Candeias 2016). With these novel adaptations, it is estimated that *N. ampullaria* receives 35.7% of its foliar nitrogen through leaf litter (Moran *et al.* 2003).

Nepenthes mirabilis is the most widespread species of pitcher plant – its species covers from China to Australia (Lavarack 1977). Unlike *N. ampullaria,* which supplements nutrients by capturing leaf litter, *N. mirabilis* relies more heavily on insect prey for nitrogen acquisition. Like many carnivorous species, its pitchers are adapted to efficiently trap insects using slippery surfaces and digestive fluids. However, its tolerance for varied habitats and soil conditions also hints at a flexible strategy for survival in nutrient-poor environments. Like *N. ampullaria*, *N. mirabilis* is a lowland species found typically from near sea level to 300 m (Druce 1917). While *N. mirabilis* grows pervasively in swampy locations of East Asia and Southeast Asia, it can also be occasionally found in drier areas and can tolerate a wide range of temperatures, demonstrating extraordinary survival capabilities (Lavarack 1977). Lavarack noted that the plants can withstand a great variety of soil types, ranging from peaty to gritty, remarking "I have quite often seen plants growing in dry sandy soil in full sun." *N. mirabilis* prefers partial shade, growing up to 10 m in these conditions, but can grow healthily fully exposed, even in areas where the soil may completely desiccate during a long dry season (Lavarack 1997). Lavarack also notes a "peculiar relationship between insect larvae and the pitchers," with certain species of mosquito breeding within the pitchers and other insects thriving in the "same fluid that means death to most." *N. mirabilis* demonstrates considerable resilience in variable lowland climates, and alongside its sustained dependence on insect prey, highlights its dual strategy of environmental tolerance and efficient carnivory.

Mutualism with animal species

Nepenthes have adapted to their environment with the formation of complex symbiotic relationships with other organisms, including mammals and insects. These partnerships, which often involve the exchange of resources, underscore the plants' ability to survive in rainforest environments. Through these symbiotic interactions, *Nepenthes* have developed tactics that increase the likelihood of survival and growth in challenging ecosystems. One of the most remarkable examples of mutualism described in the literature is found in *Nepenthes lowii*, which has co-evolved with tree shrews (*Tupaia montana*); the plant provides sugary nectar, attracting tree shrews that in return, deposit nutrient-rich feces into the pitcher. Over time, *N. lowii* has developed a distinctive toilet-shaped pitcher, complete with a large, flared peristome and a concave lid which invites and encourages "*T. montana* to sit astride the pitcher whilst feeding, facilitating fecal deposition" (Clarke *et al*. 2010). This same shape can also be appreciated in *N. lowii*-hybrid cultivars, such as the author's *Nepenthes* 'Peter D'Amato' specimen (Fig. 1). Clarke notes that with this distinct shape, *N. lowii* is largely ineffective in capturing prey and relies heavily on this mutualistic relationship, with between 57% and 100% of its nitrogen intake derived from tree shrew feces. *Nepenthes lowii* is not the only "toilet pitcher." *Nepenthes macrophylla* and *Nepenthes rajah* have both evolved similar adaptations and have fine-tuned their relationship with *T. montana*. Notably, the distance from the end of the peristome to their lid is the exact average body length of the tree shrew. While the morphology of these three *Nepenthes* species correlates closely with that of the shrew, only *N. macrophylla* and *N. rajah* are closely related genetically to each other, an example of convergent evolution between those species and that of *N. lowii* (Thorogood *et al*. 2018). However, the reliance on *T. montana* comes with a major caveat: the "poop eaters" are essentially restricted to habitats above 1800 m in elevation. The tree shrew's diet mainly consists of figs and other fleshy fruits commonly found at lower elevations, but not abundant in the mountain environments. Since *T. montana* prefers these foods, the mutualistic relationship with pitcher plants does not occur at lower altitudes. As a result, *N. lowii*, *N. macrophylla*, and *N. rajah* are limited to alpine habitats, where *T. montana* must depend on them for food (Clarke *et al*. 2010).

Figure 1. *Nepenthes* 'Peter D'Amato' specimen, a hybrid of *N. lowii* and *N. ventricosa*. The toilet-shaped peristome configuration of the "poop eater" *N. lowii* persists in this hybrid cultivar.

In a similar fashion, *Nepenthes hemsleyana* relies on feces as its primary source of nitrogen but has adapted to attract a different partner – the Hardwicke's woolly bat (*Kerivoula hardwickii*). As reported in *National Geographic* by Ed Yong (2015), instead of offering nectar, *N. hemsleyana* provides shelter for the woolly bat, functioning almost like a "bat landlord" renting out a property. Its pitchers have abnormally low digestive fluid level, yet are extremely tall and cylindrical, making it ideal to accommodate its tenants. Yong's research reveals that woolly bats contribute nutrient-rich droppings, whose nitrogen is absorbed by the plant and used to grow. To ensure its guests find the right home, *N. hemsleyana* has evolved a unique auditory adaptation: the back wall of its pitcher is widened and curved, acting "like a parabolic dish…[which] strongly reflects incoming ultrasound" of the bat's echolocation calls, an adaptation that guides the bat to safe shelter in the vast rainforests of Borneo (Yong 2015).

Vincent Bazile and colleagues (2012) investigated *Nepenthes bicalcarata*, which has forged a remarkable partnership with ants, using its two fang-like protrusions to house some of the largest nectar glands of any plant and support symbiosis with *Camponotus schmitzi*, a species of carpenter ant native to Borneo. *Nepenthes bicalcarata* provides *C. schmitzi* with both food and shelter, offering a swollen tendril ideal for housing ant larvae and a constant supply of nectar. Unlike other pitcher plants, *N. bicalcarata* is relatively ineffective at capturing prey on its own. Bazile found that its pitcher fluid is less acidic and viscous than that of other *Nepenthes* species, and it contains fewer digestive enzymes. Additionally, its pitcher walls are not particularly slippery, allowing some insects to climb out of what could otherwise be a deadly trap. This favors a mutualistic interaction with ants, contributing significantly to nutrient uptake in the plant species. Colonies of *Camponotus schmitzi* live exclusively on *N. bicalcarata* in the wild, making them dependent on the plant for survival. Bazile also observed the ants roosting inside the plant's tendril, which provides an ideal shelter for their queen and larvae. The fangs of *N. bicalcarata* contain massive nectar glands that feed the entire colony. In return, worker ants clean the plant's peristome, removing fungi and pests, which increases the effectiveness of the trap (Thornham *et al*. 2011). Most importantly, *C. schmitzi* aids in digestion. The prey insects that hang precariously on the fangs, lured by the sweet nectar, often lose their footing and tumble into the trap. When prey falls into the pitcher, the ants attack—demonstrating "an unusual and specific swimming behaviour" (Bazile *et al.* 2012). They break down the captured insects into smaller pieces and consume what they need, leaving behind nutrient-rich undigested remnants, as well as the ant's feces that *N. bicalcarata* then digests. This highly productive partnership may contribute to *N. bicalcarata*'s exceptional tenacity, as its vine can climb up to 20 m high (Bazile *et al*. 2012; Clarke 1997).

Conclusion

The adaptations seen across *Nepenthes* species highlight that evolutionary success in nutrient-poor habitats is not driven by a single strategy, but by a wide range of distinctive innovations. Whether it is through slippery peristomes and viscous digestive fluids to mutualistic relationships with mammals and insects, each species reflects a tailored response to ecological challenges. Even species like *Nepenthes inermis*, which at first appear minimalistic and ill-equipped, reveal complex and highly specialized strategies beneath their simple appearance. These diverse strategies not only underscore the ecological versatility of the genus but also provide valuable insight into broader evolutionary processes. Future research into the genetic and biochemical mechanisms underlying the traits will deepen our understanding of plant adaptations. Ultimately, *Nepenthes* stands as a compelling model for how life evolves to meet adversity through innovation.

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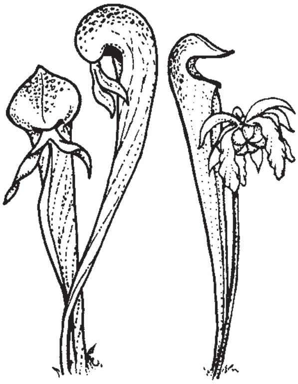

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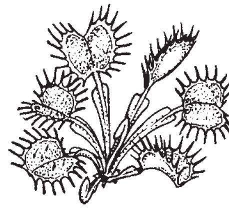

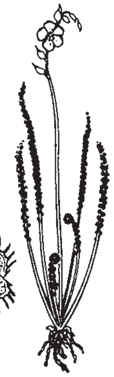

Front Cover: A fly in the exceptionally viscous fluid of a *Nepenthes inermis* upper pitcher on Gunung Kunyit, Sumatra. Photo by François Sockhom Mey. Related article on page 131.

Back Cover: A *Nepenthes lowii* upper pitcher after the visit of a tree mountain shrew (*Tupaia montana*) on Gunung Trusmadi, Borneo. Photo by François Sockhom Mey. Related article on page 131.

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