Type of article: Invited Review

Title: Construction costs and tradeoffs in carnivorous pitcher plant leaves: towards a pitcher leaf economic spectrum

Authors:
Kadeem J. Gilbert[a,1*], David Armitage[b,2], Ulrike Bauer[c,3], Kenji Fukushima[d,4], Laurence Gaume [e,5], Rachel Love[f,6], Qianshi Lin [g,7], Sukuan Liu[h,8], Sylvie Martin-Eberhardt[a,9], Jonathan Millett[i,10], Tanya Renner[g,11], Mathias Scharmann[j,12], Chris Thorogood[k,l,13]

[a] W.K. Kellogg Biological Station, Department of Plant Biology, and Program in Ecology, Evolution & Behavior, Michigan State University, Hickory Corners, MI, USA
[b] Integrative Community Ecology Unit, Okinawa Institute of Science and Technology Graduate University, 1919-1 Tancha, Onna-son, Kunigami-gun, Okinawa, Japan
[c] Department of Biosciences, University of Exeter, Geoffrey Pope Building, Stocker Road, Exeter, UK
[d] Center for Frontier Research, National Institute of Genetics, 1111 Yata, Mishima, Shizuoka 411-8540, Japan
[e] French National Center for Scientific Research (CIRAD), 42, rue Scheffer, 75116 Paris, France
[f] Science, Math, Business, and Economics Learning Centers, Kalamazoo College, 1200 Academy Street Kalamazoo, MI, USA
[g] Department of Entomology, The Pennsylvania State University, 501 Agricultural Sciences and Industries Building, University Park, PA, USA
[h] Department of Ecology and Evolutionary Biology, University of Colorado Boulder, Boulder, CO, USA
[i] Department of Geography & Environment, Loughborough University, Epinal Way, Loughborough, Leicestershire, UK
[j] Institute for Biochemistry and Biology, Genetics Research Group, University of Potsdam, Building 26, Room 1.50, Karl-Liebknecht-Str. 24-25 14476 Potsdam, Germany
[k] University of Oxford Botanic Garden, Rose Lane, Oxford, OX1 4AZ
[l] University of Oxford Department of Biology, Zoology Research and Administration Building, 11a Mansfield Rd, Oxford OX1 3SZ

[1] https://orcid.org/0000-0003-0105-8020
[2] https://orcid.org/0000-0002-5677-0501
[3] https://orcid.org/0000-0002-4701-793X
[4] https://orcid.org/0000-0002-2353-9274
[5]https://orcid.org/0000-0001-7647-7321
[6] https://orcid.org/0000-0001-6024-6406
[7] https://orcid.org/0000-0001-5477-8000
[8] https://orcid.org/0000-0003-3561-9623
[9] https://orcid.org/0009-0000-0977-5281
[10] https://orcid.org/0000-0003-4701-3071
[11] https://orcid.org/0000-0003-0442-0056

[12] https://orcid.org/0000-0001-8523-6888
[13] https://orcid.org/0000-0002-2822-0182

*corresponding author, gilbe334@msu.edu

Abstract

- *Background*
  Leaf economic theory holds that physiological constraints to photosynthesis have a role in the coordinated evolution of multiple leaf traits, an idea that can be extended to carnivorous plants occupying a particular trait space that is constrained by key costs and benefits. Pitcher traps are modified leaves that may face steep photosynthetic costs: a high-volume, three-dimensional tubular structure may be less efficient than a flat lamina. While past research has investigated the photosynthetic costs of pitchers, the exact suite of constraints shaping pitcher trait variation remain under-explored—including constraints to carnivorous function.
- *Scope*
  In this review, we describe various constraints arising from the dual photosynthetic and carnivorous functions of pitchers arising from developmental, functional, budgetary, and environmental factors. In addition, we identify the data required to establish the leaf economic spectrum (LES) for carnivorous pitcher plants (CPPs), and — owing to the multifunctional roles of pitcher leaves — discuss difficulties in placing pitchers onto existing frameworks.
- *Conclusion*
  Because pitcher traps serve multiple functions, both photosynthesis and nutrient acquisition (carnivory), they are difficult to place in the context of the LES, especially in light of a current lack of trait data. We describe a spectrum across the independent CPP lineages in approaches to balancing carnivory-photosynthesis tradeoffs. Future efforts to collect relevant data can clarify the forces that shape observed pitcher trait variation, and increase understanding of principles that may be ultimately generalized to other plants.

Key Words: carnivorous plants, pitcher plants, leaf economic spectrum, *Cephalotus*, *Nepenthes*, *Sarracenia*, *Heliamphora*, *Darlingtonia*

Introduction

The Leaf Economics Spectrum (LES) is a conceptual framework that has advanced knowledge of the correlations among leaf traits, clarified environmental correlates of these traits, and revealed tradeoffs in leaf construction by way of constraints over nutrient and energy allocation (Wright et al. 2004). This framework focuses on a few key functional traits that can be measured in a standardized way across the global diversity of leaves. Doing so deemphasizes the idiosyncrasies of specific lineages to identify the general factors constraining the geographic, environmental, and phylogenetic distributions of traits. For instance, shorter-lived leaves tend to invest highly in photosynthesis and nutrient acquisition at the expense of leaf mass per unit area (LMA), in contrast to longer-lived leaves. This trade-off is predicted to be because the balance of the costs and benefits of increased LMA have a longer payback-time than a short leaf-lifespan allows. Because leaves are costly in terms of nutrient use, the key environmental controls over variability are found across light and nutrient gradients. In sunny conditions, thicker leaves with higher nitrogen concentrations are more effective at intercepting light; shade leaves tend to be thinner with lower nitrogen concentrations. In nutrient replete conditions, short-lived leaves with low LMA and high N concentrations are more effective at fast growth in a competitive environment; in nutrient poor conditions, long-lived leaves with have high LMA and low N concentrations use the limited nutrient resource more conservatively. The utility of this trait-based framework has been extended in consideration of other tissues and organs as well, including wood (Chave et al. 2009), roots (de la Riva et al. 2021), and flowers (Roddy et al. 2021). One major gap in knowledge concerns the tradeoffs involved in multi-function plant structures, such as those required for both carbon fixation and nutrient or water acquisition, for example the photosynthetic roots of epiphytic orchids and the prey-trapping structures of carnivorous plants — the latter of which are the focus of this review.

Plant carnivory is a habit defined by multiple components, including adaptations for the attraction, capture, retention, digestion, and assimilation of nutrients derived from animal prey. Carnivorous plants have evolved multiple times independently (at least 10 origins within Angiosperms, over 800 total species; Ellison and Adamec 2017). This has been linked to the selective pressures of nutrient-limited environments (Givnish et al. 1984). The leaves of this group of plants function as traps for catching and digesting arthropods, but the traits of carnivorous leaves are themselves very variable, comprising multiple distinct trapping strategies including snap traps, sticky traps, and pitcher traps, among others (Ellison and Adamec 2017). The need to function as a trap means that carnivorous plant leaves may fall outside the range of variation for more "typical" leaves, especially in pitcher plants. Additionally, it is interesting to contemplate why carnivory overall comprises such a wide variety of strategies, while other plant functions may be relatively more constrained. Considering specifically pitfall traps, this strategy is relatively rare amongst land plants (~200 pitcher plant species, ~837 carnivorous plants in total , Ellison and Adamec 2017, see Box 1), and species employing this trait tend to be patchily distributed and most abundant in remote regions that can be difficult to access. Furthermore, it is often unclear how some canonical plant leaf traits are measured on such complex, 3-dimensional structures. For these reasons, pitcher plants are not commonly included in large-scale trait-based studies (Box 2), yet the atypical traits of pitchers could serve as a key for a more comprehensive, global view of LES.

There are many reasons why pitcher plants represent an interesting extension of the LES. As the currency of the LES is carbon produced by photosynthesis, leaves tend to be relatively flat because a high surface-to-volume ratio is the most efficient form for photon capture. Thus, the high-volume, three-dimensional, tubular leaf structure of pitcher plants represents an extreme deviation from photosynthetic efficiency. Therefore, a first key question is whether the LES model is suitable for pitcher leaves to begin with. Beyond their three-dimensional architecture, pitchers are also multi-role organs that must capture light and also function as ‘above-ground roots’ to acquire growth-limiting nutrients such as nitrogen and phosphorus. This extreme alteration of the photosynthetic structure may also explain the widely reported gene loss in their plastid genomes, perhaps suggesting a downsizing of photosynthetic function at a molecular level (Wicke et al. 2014; Ross et al. 2016; Fu et al. 2023; Silva et al. 2023). From what has been measured thus far, pitcher plants tend to have low photosynthetic rates (AN), and may have atypically high rates of dark respiration (R) due to their unusually high levels of alternative oxidase (Pavlovič and Kocáb 2022). An in-depth exploration of pitcher traits with consideration to the particular set of functions the plants must achieve can reveal novel ways of applying LES, or even expand our view of the broader total trait space onto which leaves can fall. At one level, LES can be a tool to understand the vast variation in pitcher size and morphology observed in nature; at another level, incorporating pitcher into LES opens up the opportunity to test the general validity of LES for other highly modified leaves (e.g., succulent leaves, tendrils, spines, etc.).

The LES is, by definition, a framework for understanding covariances between leaf traits and relating these covariances to developmental, functional, ecological or evolutionary factors. To provide insight on pitcher trait space, we have chosen to focus on four potential constraints to the evolution of trait variance within this group: 1) developmental constraints, i.e., the mechanisms responsible for the production of pitcher plant morphologies, 2) functional constraints, i.e., the adaptive ends to variation in these structures/traits, 3) budgetary constraints, i.e., constraints due to a major functional tradeoff observed in this group and differential allocation to either function, and 4) environmental constraints, i.e. how abiotic factors may further shape their trait distribution. These four angles represent major axes that can be applied to diverse plant groups. Further, we specifically investigate each constraint in relation to two major functional categories pitcher leaves must achieve: photosynthetic and carnivorous functions. Recognition of the specific importance of both of these functional categories (and the tradeoffs between them) to pitcher plants is a major motivator for exploring this proposed framework. In the following sections, we present evidence — where available — and interpretations on the existence of trait variation and potential covariances or tradeoffs at each of these biological constraints. In a sense, these constraints can be envisioned as a series of filters from what is theoretically possible to that which is evolutionarily feasible and phenotypically realized. In considering which traits to measure and the potential factors constraining them, we also outline important, unanswered questions that only coordinated, trait-based approaches can address, which we hope will motivate additional research on pitcher plant traits and enable an LES analogue for these multi-function plant structures.

Developmental Constraints on Photosynthesis

Carnivorous plants face the unique challenge of balancing two primary functions within a single organ: photosynthesis and carnivory. As a response, some lineages, such as *Nepenthes*, spatially partition these functions: the distal portion of the leaf in *Nepenthes* forms a pitcher to capture prey, while the proximal portion is flattened and oriented optimally for photosynthesis. This division leverages the inherent segmentation found in most flowering plant leaves, which typically consist of three parts: the leaf blade, the petiole, and the leaf base (Franck 1976). In pitcher plants, either the leaf blade itself develops into a trap, or traps emerge from apical tendrils extending from the blade. In some *Nepenthes* species, trapping pitchers have almost no photosynthetic activity, indicating a high degree of functional compartmentalization and specialization (Pavlovič et al. 2007; Capó-Bauçà et al. 2020). The tendril in this genus can also have an important climbing and support function. The leaf base, including stipules, can contribute to photosynthesis in some flowering plant lineages and forms the flat, photosynthetic portion of *Nepenthes* leaves.

While *Nepenthes* uses a compartmentalized leaf organization, *Cephalotus* is phenotypically plastic, showing a shift in leaf type depending on environmental conditions. For example, in a controlled environment, *Cephalotus* generates photosynthetic leaves at 15°C and carnivorous leaves at 25°C. This shift aligns with the seasonal temperature variations of natural habitats and possibly correlates with the likelihood of capturing prey. Occasionally, these plants may produce leaves that are neither fully photosynthetic nor fully carnivorous (Fukushima et al. 2021), adding another layer of complexity to the adaptive benefits and costs of leaf development. *Sarracenia* utilizes a hybrid approach, combining leaf segmentation with phenotypic plasticity to optimize both photosynthesis and carnivory (Ellison and Gotelli 2002).

Developmental Constraints on Carnivory

Once leaves have evolved to form pitcher traps, there are still a number of structural or developmental factors constraining their overall morphological breadth. In *Heliamphora*, the morphological evolution of adult pitchers was found to be structurally constrained, as indicated by the strong evolutionary correlations between pitcher shape variations (i.e., pitcher stoutness and curvature) and maximum pitcher size (length) (Liu and Smith 2023). *Heliamphora* species with slender or straight pitcher shapes are associated with larger pitcher sizes, while taxa with stout or curved pitcher morphologies correlate with smaller pitcher sizes. Liu and Smith (2023) postulated that stout or curvy pitchers are less structurally stable compared to slender or straight pitchers because the center of their pitcher mass is further away from the growing point on the rosette, which provides structural support.

In contrast to the expectation that drastic genetic changes would be needed for transforming a flat leaf into a pitcher, studies on the development of pitcher leaves in *Sarracenia* (Fukushima et al. 2015) and the formation of follicle-shaped traps in the carnivorous bladderwort genus *Utricularia* (Whitewoods et al. 2020) indicate that a pitcher-shaped leaf may have evolved through relatively simple genetic alterations. These genetic alterations specifically modify the adaxial-abaxial patterning during early leaf development. In the case of *Sarracenia*, this modification in tissue patterning is achieved through a distinct pattern of cell division (Fukushima et al. 2015). While the formation of a pitcher shape is a crucial step, existence of a fluid-holding pitcher structure alone is insufficient for successful nutrient capture. Instead, the trap leaves must also invest in materials for prey attraction, retention, digestion, and nutrient absorption. This involves a suite of complex morphological traits including localized hypertrophy leading to the development of remarkably variable and often specialized peristomes and opercula (Arber 1941). Thus, physical limits to vascular packing and resource provisioning during pitcher development may constrain the size and complexity of the leaves. Nevertheless, the realization that modifying the basic leaf structure is less complicated than previously assumed offers new perspectives. It suggests that the primary challenges in the evolution of pitcher leaves likely lie in areas other than simply altering the overall leaf shape, hence there is a need for further study on the bioenergetics of pitcher leaf development, which arises from tradeoffs in nutrient and energy capture.

Functional Constraints on Photosynthesis

Most carnivorous plant leaves, and all pitcher traps, must solve the balancing act of photosynthetic functioning and nutrient acquisition. As shown by the cost/benefit model of carnivory, the photosynthetic costs of carnivorous may not pay off if the environment is also limited in water and light (Givnish et al. 1984). Pitcher traps have indeed been shown to have lower photosynthetic rates than flat leaves; trap photosynthetic efficiency increases when they are fed (Pavlovič et al. 2009; Pavlovič and Saganová 2015). Considering the role of specific leaf traits, photosynthesis is usually most effective when a leaf is oriented horizontally, i.e., perpendicular to the sun; however, for prey retention in a pitfall trap, vertical trap walls are most effective. In a sufficiently warm, bright and humid environment, the rate of photosynthesis is directly proportional to the chlorophyll content of a leaf. In other words, greener leaves may be more efficient at photosynthesizing. On the other hand, greenness may or may not be an advantage to pitcher traps as contrasting colors such as red and yellow are hypothesized to function as attractive signals, as in flowers (Juniper et al. 1989)—however, evidence for the functional role of red pigments in carnivorous trap leaves is equivocal (Millett et al.; Schaefer and Ruxton 2008; Bennett and Ellison 2009; Foot et al. 2014; Annis et al. 2018; Gilbert et al. 2018) , pigmentation may, for example, rather be necessary for photoprotection in open, sunny habitats. Nevertheless, pitcher traps are apparently not constrained by a need for photosynthetic pigments. This is most strikingly apparent in species with white or translucent patches on their pitchers. This reduced investment in chlorophyll relative to other pigments (or lack thereof) may explain why pitcher leaves tend to have especially low photosynthetic rates for their leaf mass areas (LMA), relative to other plants, perhaps implying that the additional demands on leaves (necessitating a particular LMA) constrains photosynthetic rates (A_{max}) (Farnsworth and Ellison 2008). Thus, the demands of photosynthetic and carnivorous functions may not necessarily be aligned, which in turn, might be the reason for pitcher plants residing on the margins of many leaf trait scaling relationships such as the negative association between A_{max} and LMA.

Relatively few studies have measured a suite of traits of fundamental interest to photosynthetic capacity, such as stomatal traits and leaf thickness (Paluvi and Mukarlina 2015; Mansur 2017; Osunkoya and Muntassir 2017; Meriko 2018; Ghazalli et al. 2019; Huda et al. 2022). Paluvi and Mukarlina (2015) observed intraspecific changes in *Nepenthes* leaf anatomy with light environment consistent with general expectation, namely *N. gracilis* had thinner epidermal leaf thickness in shade compared to open habitat. Of note, the results this anatomical study was not just limited to the leafy lamina, but held true for the tendrils as well. In addition to leaf thickness, stomatal density also differed, with lower stomatal counts for shade plants. Meriko and Abizar (2017) looked more specifically at stomatal trait differences across three *Nepenthes* species, *N. gracilis*, *N. reinwardtiana*, and *N. ampullaria*. While *N. ampullaria* was classified as being of the anomocitic type, the other two species were classed as the less common actinocitic type with radially arranged subsidiary cells. *N. reinwardtiana* stood out among the other two species in having a lower stomatal density (~115 per mm^2 compared to 344 and 323 in *N. ampullaria* and *N. gracilis*, respectively) and larger stomatal size (11776 μm^2 vs. 7360 and 8555 in *N. ampullaria* and *N. gracilis*, respectively). It would be fruitful to combine anatomical studies with physiological data to better understand interspecific variation in photosynthetic efficiency. For instance, Mansur (2017) investigated CO_2 absorption rates in 15 *Nepenthes* species and hybrids. *N. reinwardtiana* and *N. gracilis* were among these as having amongst the highest CO_2 absorption rates (9.30 and 9.71 µmolm^{-2}s^{-1}, respectively); *N. ampullaria* was observed to have the lowest rate (3.74 µmolm^{-2}s^{-1}). As it stands, anatomical data are too sparse to draw conclusions on whether stomatal type, size, or density or other traits impact CO_2 absorption potential. Mesophyll conductance was found to be an important constraint to photosynthetic efficiency in *Nepenthes* (Capó-Bauçà et al. 2020), thus more research on leaf anatomy should prove fruitful to this end.

The three major lineages of pitcher plants (Cephalotaceae, Nepenthaceae, and Sarraceniaceae) mitigate photosynthetic functional tradeoffs differently (Figure 1). Species in the Sarraceniaceae rely on a high degree of phenotypic plasticity in pitcher morphology throughout growth and development to separate these two functions temporally. *Darlingtonia* and *Heliamphora* produce juvenile pitchers upon germination that are morphologically distinct (i.e., in pitcher size and shape) from those in adult form. These two leaf forms may show divergent trade-off strategies between photosynthetic cost and prey capture during development. In *Sarracenia*, certain environmental conditions favor the conversion of the entire leaf into a flat keel, a structure known as a “phyllodium”. Many species produce phyllodia in late summer when conditions become less favorable for carnivory (Schnell 1980; Beaulac et al. 2002; Ellison and Gotelli 2002) or generally in response to excess nitrogen deposition in the environment, which obviates the benefit of prey capture (Ellison and Gotelli 2002). Similarly, the pitchers of *Heliamphora* growing in light-limited conditions produce pitchers with reduced carnivorous traits (i.e., elongated pitcher bodies, minimized/reduced funnel volume, loss of pigmentation, and nectar production on the pitcher and nectar spoon) as a temporal trade-off for photosynthesis (McPherson et al. 2011). Likewise, the ratio of anthocyanin to chlorophyll in the forked ‘tongue’ appendage in *Darlingtonia* decreases with sun exposure, indicating that leaves of this species can plastically respond to light availability with no apparent consequences for prey capture success (Armitage 2016a). For all these examples, a case can be made for considering the photosynthetic and the trapping leaf or part of the pitcher leaf part separately when considering their place in the leaf economic spectrum. This is corroborated by the fact that both can have vastly different life spans. Because leaf senescence in pitcher leaves generally begins at the distal end of a leaf, in *Nepenthes*, this results in the photosynthetic lamina outliving its associated trap by months (or possibly years if the period of time prior to trap production is factored in). In Sarraceniaceae leaves, however, the first region to senesce is also the most active region for light capture, but the digestive zone at the shaded base of the leaf can remain alive and function well into a second growing season.

Functional Constraints on Carnivory

While the traditional leaf economic spectrum is largely centered on the photosynthetic function of leaves, nutrient acquisition is also a key function of pitcher traps (i.e., carnivory). In this way, the functional analog for carnivorous pitchers may contain properties of both roots and photosynthetic leaves. Carnivory requires a specific suite of traits, which may have unique sets of costs and tradeoffs distinct from those associated with photosynthesis. Pitchers generally have extrafloral nectaries that attract prey with a sugar reward (i.e., a direct cost in carbon paid to carnivory). Some pitcher plants attract prey through the production of volatile organic compounds (VOCs) (Jaffe et al. 1992; Di Giusto et al. 2008; Jürgens et al. 2009; Ho et al. 2016; Hatcher et al. 2020; Dupont et al. 2023), nectar (Merbach et al. 2001; Bennett and Ellison 2009) and/or possibly through reflectance patterns (Joel et al. 1985; Moran et al. 1999; Moran, Clarke, Greenwood, et al. 2012), which may all have costs in terms of secondary metabolism. Constraints may be considered in concert or separately across any of the individual functional components of carnivory (attraction, capture, retention, digestion, and assimilation of prey nutrients).

While some data support the hypothesized attractive functions of the traits listed above, more experimental work is generally needed to confirm the role of specific traits as signals to specific prey. In contrast to the other four functional components, elucidating animal behavior is just as critical to empirically probing attractive function as is knowledge from the perspective of the plant. Capture and retention may also involve some elements of animal behavior, but digestion and assimilation can be broadly understood from plant physiology alone. One complex trapping strategy with strong empirical support from a behavioral experiment is the "light-trapping" strategy found in *Nepenthes aristolochioides*. This species produces pitchers with a dome-shaped roof and a near-vertically oriented (lateral) opening; the roof has extensive white/translucent patterns ("windows" or "fenestrations"). Moran, Clarke, and Gowen (2012) demonstrated that flies (*Drosophila melanogaster*) are attracted to the bright entrance, become disoriented by the false exit of light shining through the back, and therefore trapped. Various pitcher plant species across multiple genera possess such fenestrations, including *Nepenthes klossii*, *Sarracenia minor*, *S. psittacina,* and *Darlingtonia californica*. More work is needed to confirm the light-trapping strategy in these other species (but see (Schaefer and Ruxton 2014) for *S. minor*), further, the effectiveness of this strategy on a broader range of insect species remains to be tested.

In contrast to attraction, traits involved in capture and retention are generally better understood on a fundamental, mechanistic level. Most *Nepenthes* possess a collar-shaped pitcher rim (peristome) that turns slippery when wet to capture insects via aquaplaning (Bohn and Federle 2004; Bauer et al. 2008; Bonhomme, Pelloux-Prayer, et al. 2011; Lessware et al. 2024). Approximately two-thirds of *Nepenthes* species additionally produce a wax crystal coating on the inner pitcher wall that prevents insect attachment and aids the retention of captured prey (Di Giusto et al. 2009; Bauer, Clemente, et al. 2012). One laboratory experiment showed that most insects fell from the waxy surface and very few from the peristome (Gaume et al. 2002), thus wax may have a greater contribution to total prey capture than the peristome in species that possess both features. Two *Nepenthes* species (*N. gracilis* and *N. pervillei*) are known to produce two distinct forms of wax plates on the pitcher wall and underside of the lid, which function differently, as part of a complex trapping strategy (Bauer, Di Giusto, et al. 2012; Chomicki et al. 2024). In this case, ants are able to crawl on the lid underside and only become dislodged when the lid is struck by raindrops in this "spring-board" trapping strategy; this involves a particular wax platelet morphology and biomechanical modifications to the lid. Interestingly, the springing action of some lids is not a consequence of the springing lids being made of a different material than non-springing lids, but rather relies on *how* that tissue material is arranged (Chomicki et al. 2024). Sarraceniaceae generally lack a waxy layer, but instead may have downwards-pointing slippery trichomes (Bauer et al. 2013), though a few species like *S. leucophylla*, *S. alata*, *S. flava*, and *S. rubra* may have wax crystals as well (Poppinga et al. 2010). Pitcher fluid may also be involved in prey capture and retention, as prey drown in the fluid and can be harmed directly by the acidic conditions (Bazile et al. 2015). Pitcher fluid is largely plant-produced (especially in *Nepenthes*), thus fluid production could hypothetically incur a cost when water is limiting. Pitcher plants, like other carnivorous plants, are presumed to be constrained to conditions that are not water-limited (Givnish et al. 1984), but some *Nepenthes* species indeed occur in seasonally dry areas (McPherson et al. 2009), so it may be interesting to investigate whether fluid production traits (i.e., volume produced) may vary in these. Some pitcher plant species produce little of their own fluid and instead largely rely on filling up with rainwater; this includes *Sarracenia purpurea*, *Nepenthes ampullaria*, and many *Heliamphora* spp. These species appear to invest less in fluid production, but do not occur in dry environments. Little is known regarding fluid production as a trait, and the selective forces thereof. Some *Nepenthes* produce a sticky, viscoelastic fluid, which has a benefit in increasing prey retention (Gaume and Forterre 2007; Bonhomme, Pelloux-Prayer, et al. 2011; Bazile et al. 2015; Kang et al. 2021), however even watery fluid can have a retention function due to surface tension-lowering compounds that can be plant- or microbially-produced (Juniper et al. 1989; Armitage 2016b). Plant-produced viscoelastic fluid comprised of polysaccharides may have relatively low metabolic costs as compared to waxes requiring long-chain polycarbonates (Bonhomme, Pelloux-Prayer, et al. 2011).

Many pitcher plants synthesize a complex cocktail of digestive enzymes that are secreted into the fluid (Saganová et al. 2018; Adamec et al. 2021). Evidence suggests that the proteins present in the digestive fluid of some pitcher plants may be species-specific and could correlate with trapped items (Biteau et al. 2013; Rottloff et al. 2016; Saganová et al. 2018). Inducible enzyme production may reduce the metabolic costs relative to constitutive production (Pavlovič and Saganová 2015). Furthermore, it is speculated by Rottloff et al. (2016), that even though a particular protein is present in the secretome of pitcher plants, fluid pH may influence their activity, possibly rendering them inactive. The exact metabolic costs of the compounds secreted by the pitcher are under-explored, but some species appear to “outsource” their digestive function to mutualistic microbes or animals they interact with (Lam et al. 2017; Lam, Lim, et al.

2018; Lam, Chou, et al. 2019; Schöner et al. 2017), presumably offsetting those costs. *Nepenthes ampullaria* and *N. bicalcarata*, for example, may save energy (likely in the form of ATP, see An et al. 2001) by not acidifying the fluid environment to the same extent as other species in favor of outsourcing digestion (Moran et al. 2010; Lam, Chong, et al. 2019; Lam and Tan 2020; Freund et al. 2022; Gilbert et al. 2022). Examining the physiological costs involved in the production of pitcher fluid compounds, the active acidification and overall regulation of the fluid environment, as well as the consequent assimilation of nitrogen and other nutrients would present a fuller picture of the payoffs involved in carnivory investment.

The quantity and identity of prey (“diet” or “prey spectrum”) can also be considered as a trait or rather the consequence of a constellation of pitcher traits, and thus may also vary among and within species. Considering that carnivory is the primary function of pitchers, there are surprisingly few data on prey capture by pitcher plants. Overall, data on prey capture only exist for *Sarracenia*, *Heliamphora*, *Brocchinia*, and *Nepenthes*, with no documented data from *Darlingtonia*, *Cephalotus*, or *Catopsis berteroniana* (Figure 2). For most studies, taxonomic identification is only to the level of order, and collections made in a single day. This misses variation at finer taxonomic resolutions and variation in prey capture over time, and likely skews prey capture data towards less digestible prey (e.g., beetles and ants). The prey spectra among these pitcher plant lineages are broadly similar, comprising mainly ants (Formicidae), but the quantity and taxonomic composition of varies considerably within and between taxonomic groups of pitcher plants (Kato et al. 1993; Moran 1996; Adam 1997; Rembold et al. 2010). This prey capture has been demonstrated to contribute between 10-80% of the total nitrogen content of pitchers/plants (Ellison and Gotelli 2001). For *Sarracenia*, total prey capture has been quantified for 11 species and hybrids at 43 sites in total, and populations at different sites vary in the amount and composition of prey (Supplemental Data). For example, the number of prey items in *Sarracenia purpurea* pitchers varied by 20 times between 6 sites in Britain and Ireland, where the species has naturalized (Whatmore et al. 2022). In two neighboring *Darlingtonia* populations in Plumas Co., California, average prey biomass in pitchers collected at shaded sampling sites was approximately half that of pitchers collected in sunny habitats, and was positively associated with pitcher leaf size in both habitats (Armitage 2017).

In *Nepenthes*, prey spectra can differ amongst sympatric species (Chin et al. 2014). A reasonable hypothesis is that divergence in the genus may be driven by nutrient competition (Pavlovič 2012; Thorogood et al. 2017), though direct empirical tests investigating competition are rare (but see Lam, Lai, et al. 2018). Several species in Borneo have overlapping distributional ranges and have evolved specializations linked to nutrient sources including particular insect groups, mammalian faecal capture (Clarke et al. 2009; Greenwood et al. 2011; Schöner et al. 2017), and leaf litter (Moran et al. 2003; Pavlovič et al. 2011). This diversity in pitcher function appears to be the result of an adaptive radiation driven by dietary shifts, analogous to well-known examples in animals, such as the diverse beak shapes of Darwin’s finches (Thorogood et al. 2017). However, the trapping mechanisms of most of the ca. 200 documented species have never been observed. Recent work has used a mathematical modelling approach to provide a theoretical basis for how prey capture may be influenced both by peristome shape and relative size (Moulton et al. 2023). This work suggests prey capture success is linked to geometric complexities, and hints at a fine-tuning of peristome size to optimize capture likelihood for a given shape and size. For example, species such as *N. veitchii* produce a conspicuously broad, oblique peristome. The model predicts that optimal levels of peristome flaring are consistent with those observed in nature, suggesting that these features confer a selective advantage in the capture-versus-construction tradeoff. *N. veitchii* often forms a distinct tree-climbing habit such that a portion of the peristome touches the vertical axis of the supporting tree. A flared peristome may act as a prey shuttle into the pitfall trap. By contrast, the model predicts that for the production of peristome 'teeth' (prominent spine-like, parallel features in for example *N. macrophylla, N. diabolica, N. villosa* and *N. hamata*), the cost significantly outweighs the benefit. Therefore, these structures – which have evolved independently – probably serve an unidentified function, for instance, prey retention. This potential function could be determined by considering the prominent 'fangs' of *N. bicalcarata*, which have been shown to contribute to prey capture (Merbach et al. 1999; Bonhomme, Gounand, et al. 2011; Thornham et al. 2012); other species with flanges terminating in enlarged toothy projections may function similarly. In *N. hamata*, the highly ordered aquaplaning promoting microtopography may be restricted to the flanges and teeth, with less ordered microtopography in flatter areas (U. Bauer, *pers. obs.*).

Despite some empirical data on the relationship between pitcher morphology and prey spectra in the genus *Nepenthes*, a similar level of detail is lacking for the other pitcher plant taxa, which also display a striking range of variation in pitcher morphology and physiology. For instance, in *Sarracenia*, the size and position of the lid varies from being reflexed away from the pitcher mouth (e.g., *S. purpurea*) to entirely obscuring its entrance (e.g., *S. minor*). Whatmore et al. (2022) found that pitchers with wider mouths caught more prey, while Cresswell (1993) also found that larger *Sarracenia purpurea* pitchers caught more prey. Dupont et al. (2023) showed that both pitcher size and quantity of VOCs are correlated with quantity and diversity of prey. Together, these studies show there are complex interactions between pitcher form and prey spectrum. Climatic and other environmental conditions as well as the faunal composition in particular habitats may also drive functional constraints. In considering current data on pitcher plant prey spectra, one notable dimension is the degree to which different taxa specialize on ants. At the genus level, *Nepenthes* specialize more on ants on average (~60% of diet) compared to *Sarracenia* (~40% of diet comprised by ants), and both are dwarfed by *Brocchinia* and *Heliamphora* that both have upwards of 90-95% ant prey (Figure 2). Within *Nepenthes*, with the exception of the termite-specialist *N. albomarginata*, the species that do not have ants as the majority of their diet tend to be species from higher elevations like montane *N. kinabaluensis*, *N. lowii*, *N. macrophylla*, *N. muluensis*, *N. sandakanensis*, *N. tentaculata*, and *N. villosa* (Figure 2). Cliff-dwelling *N. campanulata* also has <50% ant relative abundance. Well-known consequences of elevational gradients on ant abundance could partly explain the general reduction of ants in the diets of high elevation species (Szewczyk and McCain 2016). However, more data from understudied pitcher plant lineages are needed to understand the apparent high degree of ant-specialization in the tepui-dwelling *Heliamphora* and *Brocchinia* species.

Budgetary Constraints on Photosynthetic Function

Contrary to the common misconception that carnivorous plants (CPs) are fully heterotrophic, relying solely on nutrients obtained from animal prey, all CPs conduct photosynthesis as their primary source of energy and carbon. In fact, CPs allocate a significant portion of the resources derived from photosynthesis towards trap construction and associated carnivorous functions, such as extrafloral nectar production and digestive enzyme secretion, generating a return on investment from carnivory. In pitcher plants, the photosynthetic cost of functional pitchers might be much higher than that of other CPs with simpler traps, such as sticky glandular traps, because of expensive pitcher construction and maintenance costs along with the photosynthetic inefficiency associated with their tubular shape. This suggests that pitcher plants must delicately balance the trade-off between photosynthesis and carnivory.

In optimal environments (sunny, moist, and nutrient-poor) where photosynthesis is not limited, the trade-off between photosynthesis and carnivory enables pitcher plants to enhance their overall fitness (i.e., through increased photosynthesis and relative growth rate) by obtaining additional nutrients from prey. However, in conditions or environments where the investment in carnivory outweighs the benefits, pitcher plants typically respond by reducing their allocation towards carnivory (e.g. reduction in trap size or quantity). In some instances, they might even completely forgo their carnivorous functions (e.g. production of flattened, non-carnivorous pitchers for photosynthesis or complete pitcher abortion as in Bazile et al. (2012)). Hence, the tradeoff between photosynthesis and carnivory present constraints which shape the evolution and ecology of pitcher plants.

In a manipulative field experiment on *Sarracenia alata*, Segala and Horner (2023) tested the combined effects of light availability and prey capture on pitcher morphology, including leaf mass and pitcher aperture diameter, with greater diameters being important for effective prey capture (Heard 1998; Bhattarai and Horner 2009). Shading led to a reduction in pitcher diameter, revealing that not only do unusually high nutrient levels (N) tip the payoff balance away from carnivory and towards photosynthesis, but reduced energy from light (C) can also do the same. Segala and Horner (2023) also found that the prevention of prey capture led to a trend of reduced pitcher height. Further, the interaction between shading and feeding treatments was significant; shading significantly reduced leaf mass in fed plants while shading had no effect on leaf mass in unfed plants. This shows that a lack of nutrient availability may diminish the ability of the plants to respond to changes in light availability.

Budgetary Constraints on Carnivorous Function

The leaf economics spectrum focuses on trade-offs among traits for the optimal allocation of nutrients for harvesting of light and carbon dioxide by a leaf, and these trade-offs would be expected to apply to pitcher plants. Because they are also nutrient harvesting organs, the principles of the root economics spectrum may also play a role: that there is a tradeoff between nutrient exploration and resource conservation. Understanding how the strategies for managing the tradeoff between photosynthesis and prey capture are played out in different ecological situations provides useful insights into pitcher plant evolution and ecology. These may also constrain the reproductive ecology of pitcher plants, potentially limiting the suite of strategies which would be successful. Very little is known in this area, nevertheless, traps often seem to fall somewhere on the leaf economic spectrum between low investment/short life span and high investment/durable. Construction costs seem to play a role, but there is not just one economically viable solution. Larger traps tend to be more sturdy, long-lived and costly (i.e. reinforced with lignin). This might be due to the demand to be able to withstand higher forces, both from fluid mass inside the trap, higher wind drag, and also potentially larger prey. Lignin and other structural polysaccharides may in fact not be costly to CPs that grow in wet sunny habitats and are limited by N and P, not by photosynthesis. Several studies have examined concentrations of nutrients including N, P, K, and trace elements in the tissues of both pitchers and laminae in several species of *Nepenthes* (Osunkoya et al. 2007, 2008; Brearley and Mansur 2012; Van der Ent et al. 2015; Brearley 2021; Mansur et al. 2021, 2022, 2024); such data can provide pivotal insight into understanding these budgetary considerations to pitcher functions when combined with data on prey capture.

Environmental Constraints on Carnivory Traits

A clade-wide study of *Nepenthes* (94 species included) by Moran et al. (2013) used ecological niche models to identify the relationship between bioclimatic covariates such as annual mean, min, and max temperatures and precipitation with particular classes of pitcher traits (peristome size, wax presence/absence, viscoelastic fluid). They found that humidity and seasonality were strong predictors of trapping traits such that pitchers could be classified based on morphology as belonging to ‘wet’ or ‘dry’ syndromes, with those species bearing highly-specialised pitchers to be most associated with perhumid climates of equatorial Southeast Asia, possibly due either to increased selection against novel, ‘riskier’ traits at the clade’s distribution margins, or through increased hybridization among *Nepenthes* species in the more speciose Malay Archipelago. In a phylogenetic comparative analysis across the genus (85 species included), Gilbert et al. (2018) also found that species with higher elevational distributions (‘highland’ species) tended to produce shorter laminae, shorter pitchers (both upper and lower), and had larger peristome ribs than did lowland species, though there are many exceptions to these trends. In concert, these results suggest that interspecific differences in trapping traits may be partially attributable to climatic drivers but further experimental work is needed to separate population genetic and ecological contributions to intraspecific pitcher trait plasticity.

Another important study by Gaume et al. (2016) examined interspecific differences in the pitcher traits of six sympatric *Nepenthes* species and how these differences relate to prey capture. They found compelling evidence for prey partitioning in this system such that each species in the community had a pitcher phenotype specialized on a different subset of the local insect community. While it is tempting to attribute these differences to ecological character displacement driven by resource competition, without data on the strength of resource competition among pitcher plants with similar traits, the ecological and evolutionary processes structuring these patterns remain vague. Another important outcome of this study was to demonstrate the extent of intraspecific variation in morphological characters of the seven focal Bornean species. Here, much more variation was observed in *N. bicalcarata* and *N. rafflesiana* pitchers than in *N. ampullaria, N. albomarginata, N. hemsleyana,* or *N. gracilis.* However, the extent of intraspecific pitcher variation (both within and among lower and upper pitchers) was not clearly associated with a broader spectrum of captured prey. Instead, they found more variation at the interspecific level; specifically, prey diversity was positively correlated with pitcher mouth diameter, production of sweet odor, and fluid acidity, with *N. rafflesiana* var. *typica* and *N. r.* var. *gigantea* being the most generalist species.

In a Singapore field study of *N. gracilis*, which exhibits polymorphism in pitcher color, Gilbert et al. (2018) found a strong negative relationship between canopy cover and red pigmentation. This correlation between pigmentation and light environment was also suggested to be relevant more to interactions with herbivores rather than prey or for photoprotection.

To our knowledge, no studies have conducted similar trait-environment analyses on wild populations of *Heliamphora* or *Cephalotus.* However, both genera can be found growing across marked environmental gradients. In the case of *Heliamphora*, species can be found at the base and tops of tepui mountains where climatic conditions are considerably different. Likewise, *Cephalotus follicularis* can be found growing in habitats directly adjacent to the ocean to more inland habitats; these may differ in soil mineral characteristics and osmotic conditions. How these species' traits respond to such gradients remains an open question.

Environmental Constraints on Spatial Distribution

Plants' phenotypic traits are shaped in part by their local environments. That is, it may be more advantageous to possess certain traits at one end of an ecological gradient than the other, and can manifest as either intra- or interspecific trait variation. Such ecological gradients are ubiquitous in nature and span scales ranging from centimeters to thousands of kilometers. Pitcher plants growing over such gradients are challenged to balance the budgetary constraints imposed in the previous section alongside the additional constraints of specific ecological pressures arising from both the abiotic and biotic components of the local environment. Such phenotype - environment correlations have been documented both within and among species across the vascular plant phylogeny (Bruelheide et al. 2018), yet information specific to pitcher plants' morphological tradeoffs and variation over ecological gradients remains scarce. Most pitcher plant species are relegated to extremely small geographic ranges, and within these minute ranges, local populations tend to be further fragmented into infrequent patches of favorable habitat. Therefore, a reasonable *a priori* hypothesis might be that pitcher plants — owing to the constraints detailed in the previous sections — are prevented from expressing the levels of phenotypic plasticity or capacity for adaptive trait divergence that allow them to tolerate even moderate levels of environmental variation. If so, this has important consequences for pitcher plant species' range dynamics and vulnerability to a nonstationary climate.

In this section, we will attempt to understand the determinants of pitcher plants' local and regional distributions from the perspective of their morphological traits. To do so, we will first review literature on phenotype - environment correlations in pitcher plants. We will then contrast pitcher plant taxa in terms of habitat breadth and geographic range size with the goal of identifying potential axes of phenotypic variation and tradeoffs giving rise to these distributional trends.

The North American pitcher plant *Sarracenia purpurea* shows marked phenotypic variation across its large geographic range (Schnell 1979), and is probably the most well-studied pitcher plant species from the perspective of ecological trait variation. Factors implicated in pitcher leaf trait variation (primarily in size and color) include geographic location (Whatmore et al. 2022), light availability (Yoon et al. 2019), prey/nutrient availability (Farnsworth and Ellison 2008; Yoon et al. 2019), nitrogen deposition (Ellison and Gotelli 2002), substrate pH (Karberg and Gale 2013), wetland habitat type (Bott et al. 2008), and regional climate (Freedman et al. 2021). To date, only one study has combined multiple environmental factors to determine the most relevant environmental axes driving phenotypic variation in the species (Ellison et al. 2004). Here, authors measured six morphological traits on *S. purpurea/S. rosea* pitcher leaves from 39 locations spanning the entire native range of this species complex, and regressed these traits against principal axes representing aggregated climatic or pore-water chemical variables. The authors detected weakly-significant positive relationships between precipitation and pitcher size, shape, and peristome thickness. Pitchers from warmer sites tended to be taller and thinner than those from colder, more northern sites, and pitcher keel size was marginally positively correlated with increased dissolved nutrients in pore water. Overall, relationships between morphology and site characteristics — including climate — were relatively weak and much variation in pitcher morphology among sites remained unexplained. One further study assessed latitudinal variation in germination characteristics of *S. purpurea* which, while not directly related to prey trapping adaptations, showed no clear association with latitude (Ellison and Gotelli 2001).

Studies on spatial variation in pitcher morphology have also been carried out in other Sarraceniaceae. Comparing the morphology of *Sarracenia alata* growing at three neighboring sites in Louisiana, Green (2006) found significant differences in pitcher height, hood area, and funnel diameter between populations growing in a depression bog and a hillside seepage bog. These differences were associated with increased prey biomass by the larger hillside pitchers. In *Darlingtonia californica*, pitcher size peaks occuring at intermediate elevations, with the smallest pitchers at the lowest and highest elevation sites (Ellison and Farnsworth 2005). While this comparison was only conducted on 5 populations ranging from 411 to 1241 meters above sea level, anecdotal evidence from further *D. californica* populations ranging from sea level to 2000 meters elevation generally accord with this trend (D. Armitage, *pers. obs.*). At high elevations, the small sizes of pitchers are likely due in part to exposed, windy environments and short growing season. At sea level, while *D. californica* pitchers tend to be smaller, on average, than those at mid-elevations, there are also exceptions, and possibly have to do with habitat quality, which is more variable among low elevation populations. These size differences may also be genetic, rather than environmental, given that one introduced population of *D. californica* in a sub-optimal coastal habitat in Mendocino County, California maintained the large stature of its source population from the Northern Sierra Nevada mountains.

Also, seed dispersal limitations may impose range restrictions on pitcher plants and prevent efficient habitat tracking. Seeds of *Sarracenia*, for example, travel an average of <10cm (Ellison et al. 2012), and while the hydrophobic seeds of Sarraceniaceae might have historically afforded them greater distance, the needed aquatic conditions for such extension are more fragmented now than during their pre-Eocene heyday (Ellison 2001). *Nepenthes* is dioecious, therefore colonization of both male and female seeds must establish in relatively close proximity in order for new populations to form (Baker 1955). Germination data of *Cephalotus* suggests that recruitment occurs within a narrow range of environmental conditions (Just et al. 2019), indicating that the window of opportunity is short and restricted. However, like many other functional traits, data on seed traits and dispersal in pitcher plants are relatively sparse in the literature.

Relationship Between Elevational and Geographic Range in *Nepenthes*

Geographic ranges themselves (and the climate conditions they encompass) can also be considered traits of a species. Species in the Sarraceniaceae and Nepenthaceae tend to occupy small geographic ranges. Within each family, however, there are a small number of “outlier” species with range sizes that are at least one order of magnitude larger than is typical for the family, for example *Sarracenia purpurea* in North America and *Nepenthes mirabilis* in Southeast Asia. These outliers may be well-adapted to broader environmental conditions; however, this remains unexplored. Another possibility is that some species may have evolved in a time when their preferred niche was less fragmented such as the more ancestral lowland species *Nepenthes mirabilis* and *Nepenthes gracilis*. Many of the small-ranged *Nepenthes* species are endemic to one or a few isolated mountains, and although they sometimes occur there over relatively wide elevational gradients encompassing a range of climate zones, they do not occupy the lowland area that spans the space between mountain ranges. Some *Heliamphora* and many *Nepenthes* species only grow over exceedingly narrow climatic ranges. Highland species thus have greatly constrained niche space and may face greater loss of suitable habitat in the face of climate change (Schwallier et al. 2016; Gray et al. 2017; Clarke and Moran 2015).

While interspecific trait variation is one of the most apparent properties of pitcher plants, and evidence suggests that these traits at least partially covary with climate or other environmental factors, we can begin to assess whether traits of certain large-ranged ‘outlier’ species discussed above relate to their unique range sizes or environmental tolerances. Taking *Nepenthes* as an example, we can quantify the elevational range of each species as the difference between their highest and lowest observed distributions in the field (Moran et al. 2013). Species with larger elevational ranges could generally be considered to be more tolerant of climate variation than those with very narrow elevational ranges. Since environmental tolerance is also a key determinant of geographic ranges (particularly over latitude), we can also rank *Nepenthes* species by their geographic range sizes, which might also positively covary with environmental breadth. To do so, we first pulled all georeferenced occurrence records of *Nepenthes* from various natural history databases (GBIF), and used them to fit species distribution models (SDMs) which correlate species presences with local climate variables and output a map of habitat suitability (Phillips et al. 2006). By constraining these suitability maps to convex polygons of each species’ observed distribution, we can then estimate the overall geographic range sizes of each species (Kass et al. 2022). While this is not a perfect way to estimate the range sizes of species with such limited numbers of occurrence records, it suffices for this illustrative comparative analysis. We asked whether the observed elevational distributions of *Nepenthes* species were associated with range sizes, with the expectation that taxa with elevational ranges should also have wide geographic ranges as well. Those species displaying the highest elevational and geographic ranges are anticipated to be few in number, but potentially possess some unique set of traits that might confer wide environmental tolerances.

We found a significant, positive relationship between elevational and geographic range size (Figure 3). Here, species such as *N. maxima*, *N. reinwardtiana*, *N. ampullaria*, *N. mirabilis,* and *N. tentaculata* can be classified as having both the largest geographic ranges and larger than average elevational extents. What common traits, then, might these species share with one another? While there are no single, obvious similarities distinguishing these species from the rest, all do display remarkably high morphological variability in terms of growth form, pitcher coloration, pitcher size, and peristome/operculum shape. However, these variants are typically relegated to very specific localities, rather than appearing repeatedly in similar environments on different landmasses, indicating they may not represent locally-adapted ecotypes but rather arise as an evolutionary consequence of these species' large, fragmented ranges.

Intraspecific trait variation arising from phenotypic plasticity is anticipated to be an advantageous trait for widely-distributed species. Since few studies have simultaneously assessed intraspecific trait variation in different pitcher plant taxa (but see Chomicki et al. 2024, which examined trapping related traits in 40+ species), this prediction is difficult to assess. One study to do so measured the morphological traits of 8 sympatric *Nepenthes* species on Mt. Kinabalu and Mt. Trusmadi in Sabah (Borneo) which included the small-ranged *N. burbidgeae, N. rajah, N. macrophylla,* and *N. villosa* and larger-ranged *N. lowii, N. stenophylla, N. reinwardtiana,* and *N. tentaculata* (Chin et al. 2010). Re-analysis of the authors' data reveal weakly negative trends between the first principal coordinate of pitcher morphology (including pitcher width, depth, height, volume, and orifice depth and explaining 83% of variance), and both log geographic range size and elevational breadth (Figure 3). The two species with the largest geographic/elevational ranges (*N. tentaculata* and *N. reinwardtiana*) in this study were also those with the smallest pitchers. There were, however, no relationships between range sizes and trait variation, as measured by the coefficient of variation. Further, for all morphological traits measured, interspecific variation was, on average, 2.5 times greater than intraspecific variation. This suggests that pitcher traits may be constrained more strongly by species-specific factors such as genetic background, rather than being free to converge on phenotypic optima in a common environment. Future work may take a macroecological perspective by integrating the frequency distributions of quantitative pitcher and leaf traits in *Nepenthes* to assess whether sympatric communities are non-random subsets of this distribution and to identify more morphological correlates of elevational and geographic range sizes.

Future Directions: Where to go from here?

Similar to other plant organs, pitcher leaves of carnivorous plants show a broad trait spectrum (variation), both within and among independent lineages. The key to understanding the general ecological drivers and constraints to pitcher traits is leaf economy, which has been successfully explored and applied to other plant organs before and thus applies to pitchers as well. However, given that very little databased trait data exist for pitcher plants, biologists must first focus on collecting trait data in a standardized and premeditated way. More specifically, the community must decide on which traits to collect, and by which methodology. Answers to these related questions, therefore, must engage with the observed or hypothesized tradeoffs either in accordance with, or contradicting, the LES. That is, to best understand developmental, functional, budgetary, or ecological constraints on pitcher leaves, which traits must we focus on collecting and comparing? This task and line of questioning has recently been posed for aquatic carnivorous plants as well (Rossano et al. 2024).

Beyond the constraints discussed thus far, pitcher plants bring novel considerations, which can greatly expand our understanding of factors shaping leaf construction writ large, whether carnivorous or not. One important insight is that leaves have multiple functions, not just photosynthesis. In the case of pitcher leaves, many key traits function in carnivory: attracting, trapping, and digesting prey and assimilating prey-derived nutrients. A perhaps underappreciated detail is that while roots are generally considered to be the assimilatory organs of non-carnivorous plants, leaves in general do have some capacity to uptake nutrients—even without specially adapted absorptive glands—such as via the stomata (Harrison et al. 2000). The predominance of this absorptive function may exist as a gradient across all plants, with carnivorous plants and other specialized plants like tank bromeliads at one end of the extreme. Incorporating this realization into a generalized economic spectrum model may not only improve our understanding of pitcher traits, but better contextualize variation in leaf traits overall.

Some insights may be more restricted to pitcher plants, such as traits that are most important to the trapping of prey. However, even these findings have broader implications for contemplating an expanded model of leaf trait evolution. Consider the springboard trapping mechanism; this is to our knowledge unique to pitcher plants and serves illustrative example of how complex traits (relying on multiple interdependent components for its function) can evolve from existing trait variation (Chomicki et al. 2024). Additionally, springboard trapping raises a novel point, which is that certain traits may not be strictly dependent on material construction, but rather the same tissue arranged in different ways may achieve novel biomechanical properties. Much leaf trait work has framed tradeoffs and constraints in terms of construction costs, as we have also done here. However, leaves are not simply static objects, and mechanical properties may come into play even outside of carnivorous contexts as all leaves must deal with wind, rain, and the movements of herbivores. Leaf biomechanics clearly matter in trapping strategies, but plants may also exploit the ways leaves are set in motion for the benefit of photosynthesis, e.g. shedding water to preserve photosynthetic efficiency. Thus, to fully understand global leaf trait variation space, simply measuring morphological and biochemical features in isolation may not suffice; more studies should investigate biomechanical features. All in all, many specific questions remain regarding pitcher traits (Box 3), but a lot of recent progress has been made and future directions have been identified. Ultimately, we believe it is possible to create an integrated model of leaf traits that can compare pitchers alongside "typical" leaves; expanding LES with these novel insights promises to greatly advance our knowledge even beyond this singular group of plants.

Acknowledgements

We thank editor Gitte Petersen for the invitation to write this review. KJG was supported by United States Department of Agriculture National Institutes of Food and Agriculture grant 2019-67012-37587.

Data Availability

Supplemental data and associated code will be made available on the Michigan State University Github repository (https://gitlab.msu.edu/gilbe334/pitcher-economic-spectrum).

References

Adam JH. **1997**. Prey spectra of Bornean *Nepenthes* species (Nepenthaceae) in relation to their habitat. *Pertanika Journal of Tropical Agricultural Science* **20**: 121–134.

Adamec L, Matušíková I, Pavlovič A. **2021**. Recent ecophysiological, biochemical and evolutional insights into plant carnivory. *Annals of Botany* **128**: 241–259.

An C-I, Fukusaki E-I, Kobayashi A. **2001**. Plasma-membrane H+-ATPases are expressed in pitchers of the carnivorous plant *Nepenthes alata* Blanco. *Planta* **212**: 547–555.

Annis J, Coons J, Helm C, Molano-Flores B. **2018**. The Role of Red Leaf Coloration in Prey Capture for Pinguicula planifolia. *Southeastern Naturalist* **17**: 433–437.

Arber A. **1941**. On the morphology of the pitcher-leaves in *Heliamphora*, *Sarracenia*, *Darlingtonia*, *Cephalotus*, and *Nepenthes*. *Annals of Botany* **5**: 563–578.

Armitage DW. **2016a**. The cobra's tongue: Rethinking the function of the "fishtail appendage" on the pitcher plant *Darlingtonia californica*. *American Journal of Botany* **103**: 780–785.

Armitage DW. **2016b**. Bacteria facilitate prey retention by the pitcher plant *Darlingtonia californica*. *Biology Letters* **12**: 20160577.

Armitage DW. **2017**. Linking the development and functioning of a carnivorous pitcher plant's microbial digestive community. *The ISME journal* **11**: 2439–2451.

Baker HG. **1955**. Self-compatibility and establishment after "long-distance" dispersal. *Evolution* **9**: 347–349.

Bauer U, Bohn HF, Federle W. **2008**. Harmless nectar source or deadly trap: *Nepenthes* pitchers are activated by rain, condensation and nectar. *Proceedings. Biological Sciences / The Royal Society* **275**: 259–65.

Bauer U, Clemente CJ, Renner T, Federle W. **2012**. Form follows function: morphological diversification and alternative trapping strategies in carnivorous *Nepenthes* pitcher plants. *Journal of Evolutionary Biology* **25**: 90–102.

Bauer U, Di Giusto B, Skepper J, Grafe TU, Federle W. **2012**. With a flick of the lid: a novel trapping mechanism in *Nepenthes gracilis* pitcher plants. *PloS ONE* **7**: e38951.

Bauer U, Scharmann M, Skepper J, Federle W. **2013**. "Insect aquaplaning"on a superhydrophilic hairy surface: how *Heliamphora nutans* Benth. pitcher plants capture prey. *Proceedings of the Royal Society B: Biological Sciences* **280**: 20122569.

Bazile V, Le Moguédec G, Marshall DJ, Gaume L. **2015**. Fluid physico-chemical properties influence capture and diet in *Nepenthes* pitcher plants. *Annals of Botany* **115**: 705–716.

Bazile V, Moran JA, Le Moguédec G, Marshall DJ, Gaume L. **2012**. A carnivorous plant fed by its ant symbiont: a unique multi-faceted nutritional mutualism. *PloS ONE* **7**: e36179.

Beaulac D, Walguamery J, Meyer R. **2002**. Baseline study of the hooded pitcher plant (*Sarracenia* minor): its utility as an indicator species of freshwater wetland habitats.

Bennett KF, Ellison AM. **2009**. Nectar, not colour, may lure insects to their death. *Biology Letters*: rsbl20090161.

Bhattarai GP, Horner JD. **2009**. The importance of pitcher size in prey capture in the carnivorous plant, *Sarracenia alata* Wood (Sarraceniaceae). *The American Midland Naturalist* **161**: 264–272.

Biteau F, Nisse E, Miguel S, Hannewald P, Bazile V, Gaume L, Mignard B, Hehn A, Bourgaud F. **2013**. A simple SDS-PAGE protein pattern from pitcher secretions as a new tool to distinguish *Nepenthes* species (Nepenthaceae). *American Journal of Botany* **100**: 2478–84.

Bohn HF, Federle W. **2004**. Insect aquaplaning: *Nepenthes* pitcher plants capture prey with the peristome, a fully wettable water-lubricated anisotropic surface. *Proceedings of the National Academy of Sciences of the United States of America* **101**: 14138–14143.

Bonhomme V, Gounand I, Alaux C, Jousselin E, Barthélémy D, Gaume L. **2011**. The plant-ant *Camponotus schmitzi* helps its carnivorous host-plant *Nepenthes bicalcarata* to catch its prey. *Journal of Tropical Ecology* **27**: 15–24.

Bonhomme V, Pelloux-Prayer H, Jousselin E, Forterre Y, Labat J-J, Gaume L. **2011**. Slippery or sticky? Functional diversity in the trapping strategy of *Nepenthes* carnivorous plants. *New Phytologist* **191**: 545–54.

Bott T, Meyer GA, Young EB. **2008**. Nutrient limitation and morphological plasticity of the carnivorous pitcher plant *Sarracenia purpurea* in contrasting wetland environments. *New Phytologist* **180**: 631–641.

Brearley FQ. **2021**. Nutrient and metal concentrations in *Nepenthes mcafarlanei* Hemsl. (Nepenthaceae) from a Malaysian montane forest. *Notulae Scientia Biologicae* **13**.

Brearley FQ, Mansur M. **2012**. Nutrient Stoichiometry of *Nepenthes* Species from A Bornean Peat Swamp Forest. *Carnivorous Plant Newsletter* **41**.

Bruelheide H, Dengler J, Purschke O, Lenoir J, Jiménez-Alfaro B, Hennekens SM, Botta-Dukát Z, Chytrý M, Field R, Jansen F, others. **2018**. Global trait-environment relationships of plant communities. *Nature Ecology & Evolution* **2**: 1906–1917.

Capó-Bauçà S, Font-Carrascosa M, Ribas-Carbó M, Pavlovič A, Galmés J. **2020**. Biochemical and mesophyll diffusional limits to photosynthesis are determined by prey and root nutrient uptake in the carnivorous pitcher plant *Nepenthes* x ventrata. *Annals of Botany* **126**: 25–37.

Chave J, Coomes D, Jansen S, Lewis SL, Swenson NG, Zanne AE. **2009**. Towards a worldwide wood economics spectrum. *Ecology Letters* **12**: 351–66.

Chin L, Chung AY, Clarke C. **2014**. Interspecific variation in prey capture behavior by co-occurring *Nepenthes* pitcher plants: evidence for resource partitioning or sampling-scheme artifacts? *Plant Signaling & Behavior* **9**: e27930.

Chin L, Moran JA, Clarke C. **2010**. Trap geometry in three giant montane pitcher plant species from Borneo is a function of tree shrew body size. *New Phytologist* **186**: 461–470.

Chomicki G, Burin G, Busta L, Gozdzik J, Jetter R, Mortimer B, Bauer U. **2024**. Convergence in carnivorous pitcher plants reveals a mechanism for composite trait evolution. *Science* **383**: 108–113.

Clarke CM, Bauer U, Ch'ien CL, Tuen AA, Rembold K, Moran JA. **2009**. Tree shrew lavatories: a novel nitrogen sequestration strategy in a tropical pitcher plant. *Biology Letters* **5**: 632–635.

Clarke C, Moran JA. **2015**. Climate, soils and vicariance-their roles in shaping the diversity and distribution of Nepenthes in Southeast Asia. *Plant and Soil*: 1–15.

Cresswell JE. **1993**. The morphological correlates of prey capture and resource parasitism in pitchers of the carnivorous plant *Sarracenia purpurea*. *American Midland Naturalist*: 35–41.

Dupont C, Buatois B, Bessiere J-M, Villemant C, Hattermann T, Gomez D, Gaume L. **2023**. Volatile organic compounds influence prey composition in *Sarracenia* carnivorous plants. *PLoS ONE* **18**: e0277603.

Ellison AM. **2001**. Interspecific and intraspecific variation in seed size and germination requirements of *Sarracenia* (Sarraceniaceae). *American Journal of Botany* **88**: 429–37.

Ellison AM, Adamec L. **2017**. *Carnivorous Plants: Physiology, Ecology, and Evolution*. Oxford University Press.

Ellison AM, Buckley HL, Miller TE, Gotelli NJ. **2004**. Morphological variation in *Sarracenia purpurea* (Sarraceniaceae): geographic, environmental, and taxonomic correlates. *American Journal of Botany* **91**: 1930–5.

Ellison AM, Butler ED, Hicks EJ, Naczi RFC, Calie PJ, Bell CD, Davis CC. **2012**. Phylogeny and biogeography of the carnivorous plant family Sarraceniaceae. *PloS one* **7**: e39291.

Ellison AM, Farnsworth EJ. **2005**. The cost of carnivory for *Darlingtonia californica* (Sarraceniaceae): evidence from relationships among leaf traits. *American Journal of Botany* **92**: 1085–93.

Ellison AM, Gotelli NJ. **2001**. Evolutionary ecology of carnivorous plants. *Trends in Ecology & Evolution* **16**: 623–629.

Ellison AM, Gotelli NJ. **2002**. Nitrogen availability alters the expression of carnivory in the northern pitcher plant, *Sarracenia purpurea*. *Proceedings of the National Academy of Sciences of the United States of America* **99**: 4409–12.

Van der Ent A, Sumail S, Clarke C. **2015**. Habitat differentiation of obligate ultramafic *Nepenthes* endemic to Mount Kinabalu and Mount Tambuyukon (Sabah, Malaysia). *Plant Ecology* **216**: 789.

Farnsworth EJ, Ellison AM. **2008**. Prey availability directly affects physiology, growth, nutrient allocation and scaling relationships among leaf traits in 10 carnivorous plant species. *Journal of Ecology* **96**: 213–221.

Foot G, Rice SP, Millett J. **2014**. Red trap colour of the carnivorous plant *Drosera rotundifolia* does not serve a prey attraction or camouflage function. *Biology Letters* **10**: 20131024.

Franck DH. **1976**. The morphological interpretation of epiascidiate leaves—An historical perspective—. *The Botanical Review* **42**: 345–388.

Freedman ZB, McGrew A, Baiser B, Besson M, Gravel D, Poisot T, Record S, Trotta LB, Gotelli NJ. **2021**. Environment-host-microbial interactions shape the *Sarracenia purpurea* microbiome at the continental scale. *Ecology*.

Freund M, Graus D, Fleischmann A, Gilbert KJ, Lin Q, Renner T, Stigloher C, Albert VA, Hedrich R, Fukushima K. **2022**. The digestive systems of carnivorous plants. *Plant Physiology* **190**: 44–59.

Fu C-N, Wicke S, Zhu A-D, Li D-Z, Gao L-M. **2023**. Distinctive plastome evolution in carnivorous angiosperms. *BMC Plant Biology* **23**: 660.

Fukushima K, Fujita H, Yamaguchi T, Kawaguchi M, Tsukaya H, Hasebe M. **2015**. Oriented cell division shapes carnivorous pitcher leaves of *Sarracenia purpurea*. *Nature Communications* **6**: 6450.

Fukushima K, Narukawa H, Palfalvi G, Hasebe M. **2021**. A discordance of seasonally covarying cues uncovers misregulated phenotypes in the heterophyllous pitcher plant *Cephalotus follicularis*. *Proceedings of the Royal Society B* **288**: 20202568.

Gaume L, Bazile V, Huguin M, Bonhomme V. **2016**. Different pitcher shapes and trapping syndromes explain resource partitioning in *Nepenthes* species. *Ecology and Evolution*.

Gaume L, Forterre Y. **2007**. A viscoelastic deadly fluid in carnivorous pitcher plants. *PloS ONE* **2**: e1185.

Gaume L, Gorb S, Rowe N. 2002. Function of epidermal surfaces in the trapping efficiency of *Nepenthes alata* pitchers. *New Phytologist* **156**: 479–489.

Gaume L, Perret P, Gorb E, Gorb S, Labat J-J, Rowe N. 2004. How do plant waxes cause flies to slide? Experimental tests of wax-based trapping mechanisms in three pitfall carnivorous plants. *Arthropod Structure & Development* **33**: 103–111.

GBIF.org (2023) GBIF Occurrence Download https://doi.org/10.15468/dl.vwcwjp

Ghazalli MN, Tamizi AA, Esa MIM, Besi EE, Nikong D, Nordin ARM, Zaini AZ. 2019. The systematic significance of leaf epidermal micro-morphology of ten *Nepenthes* species (Nepenthaceae) from Peninsular Malaysia. *Reinwardtia* **18**: 81–96.

Gilbert KJ, Goldsborough T, Lam WN, Leong F, Pierce NE. 2022. A semi-detritivorous pitcher plant, *Nepenthes ampullaria* diverges in its regulation of pitcher fluid properties. *Journal of Plant Interactions* **17**: 956–966.

Gilbert KJ, Nitta JH, Talavera G, Pierce NE. 2018. Keeping an eye on coloration: ecological correlates of the evolution of pitcher traits in the genus *Nepenthes* (Caryophyllales). *Biological Journal of the Linnean Society* **123**: 321–327.

Di Giusto B, Grosbois V, Fargeas E, Marshall DJ, Gaume L. 2008. Contribution of pitcher fragrance and fluid viscosity to high prey diversity in a *Nepenthes* carnivorous plant from Borneo. *Journal of Biosciences* **33**: 121–136.

Di Giusto B, Guéroult M, Rowe N, Gaume L. 2009. The waxy surface in *Nepenthes* pitcher plants: variability, adaptive significance and developmental evolution. *Functional Surfaces in Biology*. Springer, 183–203.

Givnish TJ, Burkhardt EL, Happel RE, Weintraub JD. 1984. Carnivory in the bromeliad *Brocchinia reducta*, with a cost/benefit model for the general restriction of carnivorous plants to sunny, moist, nutrient-poor habitats. *American Naturalist*: 479–497.

Gray LK, Clarke C, Wint GW, Moran JA. 2017. Potential effects of climate change on members of the Palaeotropical pitcher plant family Nepenthaceae. *PloS ONE* **12**: e0183132.

Green ML. 2006. The relationship between prey capture and characteristics of the carnivorous pitcher plant, *Sarracenia alata* Wood.

Greenwood M, Clarke C, Lee CC, Gunsalam A, Clarke RH. 2011. A unique resource mutualism between the giant Bornean pitcher plant, *Nepenthes rajah*, and members of a small mammal community. *PloS ONE* **6**: e21114.

Harrison A, Schulze E-D, Gebauer G, Bruckner G. 2000. Canopy uptake and utilization of atmospheric pollutant nitrogen. *Carbon and nitrogen cycling in European forest ecosystems*:

171–188.

Hatcher CR, Ryves DB, Millett J. **2020**. The function of secondary metabolites in plant carnivory. *Annals of Botany* **125**: 399–411.

Heard SB. **1998**. Capture rates of invertebrate prey by the pitcher plant, *Sarracenia purpurea* L. *The American Midland Naturalist* **139**: 79–89.

Ho WW, Nathan Kutz J, Ng J, Riffell JA. **2016**. Rapid Floral and Pitcher Scent Diversification in Carnivorous Pitcher Plants (Sarraceniaceae). *bioRxiv*: 079947.

Huda MHN, Meekiong K, Elias H. **2022**. Leaf Anatomical Characteristics of *Nepenthes* Species in Western Sarawak, Borneo. *Malaysian Applied Biology* **51**: 201–210.

Jaffe K, Michelangeli F, Gonzalez JM, Miras B, Ruiz MC. **1992**. Carnivory in pitcher plants of the genus *Heliamphora* (Sarraceniaceae). *New Phytologist* **122**: 733–744.

Joel D, Juniper B, Dafni A. **1985**. Ultraviolet patterns in the traps of carnivorous plants. *New Phytologist* **101**: 585–593.

Juniper BE, Robins RJ, Joel DM. **1989**. *The carnivorous plants*. London, etc.: Academic Press.

Jürgens A, El-Sayed AM, Suckling DM. **2009**. Do carnivorous plants use volatiles for attracting prey insects? *Functional Ecology* **23**: 875–887.

Just MP, Merritt DJ, Turner SR, Conran JG, Cross AT. **2019**. Seed germination biology of the Albany pitcher plant, *Cephalotus follicularis*. *Australian Journal of Botany* **67**: 480–489.

Kang V, Isermann H, Sharma S, Wilson DI, Federle W. **2021**. How a sticky fluid facilitates prey retention in a carnivorous pitcher plant (*Nepenthes rafflesiana*). *Acta Biomaterialia* **128**: 357–369.

Karberg JM, Gale MR. **2013**. Influence of surface water mineral nutrition on the plasticity of *Sarracenia purpurea* in *Sphagnum* fens, marl wetlands, and sand savannahs. *Wetlands* **33**: 631–639.

Kass JM, Guénard B, Dudley KL, Jenkins CN, Azuma F, Fisher BL, Parr CL, Gibb H, Longino JT, Ward PS, others. **2022**. The global distribution of known and undiscovered ant biodiversity. *Science advances* **8**: eabp9908.

Kato M, Hotta M, Tamin R, Itino T. **1993**. Inter-and intra-specific variation in prey assemblages and inhabitant communities in *Nepenthes* pitchers in Sumatra. *Tropical Zoology* **6**: 11–25.

Kattge J, Bönisch G, Díaz S, Lavorel S, Prentice IC, Leadley P, Tautenhahn S, Werner GD, Aakala T, Abedi M, others. **2020**. TRY plant trait database-enhanced coverage and open access. *Global Change Biology* **26**: 119–188.

Lam WN, Chong KY, Anand GS, Tan HTW. **2017**. Dipteran larvae and microbes facilitate nutrient sequestration in the *Nepenthes gracilis* pitcher plant host. *Biology Letters* **13**: 20160928.

Lam WN, Chong KY, Anand GS, Tan HT. **2019**. In situ proteolytic activity in *Nepenthes gracilis* pitcher plant traps is affected by both pitcher-extrinsic and pitcher-intrinsic factors. *International Journal of Plant Sciences* **180**: 179–185.

Lam WN, Chou YY, Leong FWS, Tan HTW. **2019**. Inquiline predator increases nutrient-cycling efficiency of *Nepenthes rafflesiana* pitchers. *Biology Letters* **15**: 20190691.

Lam WN, Lai HR, Lee CC, Tan HT. **2018**. Evidence for pitcher trait-mediated coexistence between sympatric *Nepenthes* pitcher plant species across geographical scales. *Plant Ecology & Diversity*: 1–12.

Lam WN, Lim RJY, Wong SH, Tan HTW. **2018**. Predatory dipteran larva contributes to nutrient sequestration in a carnivorous pitcher plant. *Biology Letters* **14**: 20170716.

Lam W-N, Tan HTW. **2020**. The Pitcher Plants (*Nepenthes* Species) of Singapore.Lam WN and Tan HTW ed. National University of Singapore, Singapore, 75–98.

Lessware OC, Mantell JM, Bauer U. **2024**. Carnivorous *Nepenthes* pitcher plants combine common developmental processes to make a complex epidermal trapping surface. *Annals of Botany*: mcae147.

Liu S, Smith SD. **2023**. Replicated radiations in the South American marsh pitcher plants (*Heliamphora*) lead to convergent carnivorous trap morphologies. *American Journal of Botany* **110**: e16230.

Mansur M. **2017**. Potensi serapan CO2 pada beberapa jenis kantong semar (*Nepenthes* spp.) dataran rendah. *Berita Biologi* **16**: 47–57.

Mansur M, Brearley FQ, Esseen PJ, Rode-Margono EJ, Tarigan MRM. **2021**. Ecology of *Nepenthes clipeata* on Gunung Kelam, Indonesian Borneo. *Plant Ecology & Diversity* **14**: 195–204.

Mansur M, Salamah A, Mirmanto E, Brearley FQ. **2022**. Nutrient concentrations in three *Nepenthes* species (Nepenthaceae) from North Sumatra. *Reinwardtia* **21**: 55–62.

Mansur M, Salamah A, Mirmanto E, Brearley FQ. **2024**. Ecology of *Nepenthes* on Mount Talang, West Sumatra, Indonesia. *Tropical Ecology*: 1–10.

McPherson S, Robinson A, Fleischmann A. **2009**. *Pitcher plants of the Old World*. Redfern Natural History Productions Dorset.

McPherson S, Wistuba A, Fleischman A, Nerz J. **2011**. Sarraceniaceae *of South America*. Redfern Natural History Productions.

Merbach M, Zizka G, Fiala B, Maschwitz U, Booth W. **2001**. Patterns of nectar secretion in five *Nepenthes* species from Brunei Darussalam, Northwest Borneo, and implications for ant-plant relationships. *Flora* **196**: 153–160.

Merbach MA, Zizka G, Fiala B, Merbach D, Maschwitz U. **1999**. Giant nectaries in the peristome thorns of the pitcher plant *Nepenthes bicalcarata* Hooker f. *Ecotropica* **5**: 45–50.

Meriko L. **2018**. Struktur Stomata Daun Beberapa Tumbuhan Kantong Semar (*Nepenthes* spp.)[Structure of Leaves Stomata on Some Pitcher Plants (*Nepenthes* spp.)]. *Berita Biologi* **16**.

Millett J, Foot GW, Thompson JC, Svensson BM. Geographic variation in Sundew (*Drosera*) leaf colour: plant-plant interactions counteract expected effects of abiotic factors. *Journal of Biogeography*.

Moran JA. **1996**. Pitcher dimorphism, prey composition and the mechanisms of prey attraction in the pitcher plant *Nepenthes rafflesiana* in Borneo. *Journal of Ecology*: 515–525.

Moran JA, Booth WE, Charles JK. **1999**. Aspects of pitcher morphology and spectral characteristics of six Bornean *Nepenthes* pitcher plant species: implications for prey capture. *Annals of Botany* **83**: 521–528.

Moran JA, Clarke C, Gowen BE. **2012**. The use of light in prey capture by the tropical pitcher plant *Nepenthes* aristolochioides. *Plant Signaling & Behavior* **7**: 957–60.

Moran JA, Clarke C, Greenwood M, Chin L. **2012**. Tuning of color contrast signals to visual sensitivity maxima of tree shrews by three Bornean highland *Nepenthes* species. *Plant Signaling & Behavior* **7**: 1267–1270.

Moran JA, Clarke CM, Hawkins BJ. **2003**. From carnivore to detritivore? Isotopic evidence for leaf litter utilization by the tropical pitcher plant *Nepenthes ampullaria*. *International Journal of Plant Sciences* **164**: 635–639.

Moran JA, Gray LK, Clarke C, Chin L. **2013**. Capture mechanism in Palaeotropical pitcher plants (Nepenthaceae) is constrained by climate. *Annals of Botany*: mct195.

Moran JA, Hawkins BJ, Gowen BE, Robbins SL. **2010**. Ion fluxes across the pitcher walls of three Bornean *Nepenthes* pitcher plant species: flux rates and gland distribution patterns reflect nitrogen sequestration strategies. *Journal of Experimental Botany*: erq004.

Moulton DE, Oliveri H, Goriely A, Thorogood CJ. **2023**. Mechanics reveals the role of peristome geometry in prey capture in carnivorous pitcher plants (*Nepenthes*). *Proceedings of the National Academy of Sciences* **120**: e2306268120.

Nishi AH, Vasconcellos-Neto J, Romero GQ. **2012**. The role of multiple partners in a digestive mutualism with a protocarnivorous plant. *Annals of Botany* **111**: 143–150.

Osunkoya OO, Daud SD, Di-Giusto B, Wimmer FL, Holige TM. **2007**. Construction costs and physico-chemical properties of the assimilatory organs of *Nepenthes* species in northern Borneo. *Annals of Botany* **99**: 895–906.

Osunkoya OO, Daud SD, Wimmer FL. **2008**. Longevity, lignin content and construction cost of the assimilatory organs of *Nepenthes* species. *Annals of Botany* **102**: 845–853.

Osunkoya OO, Muntassir NA. **2017**. Comparative anatomy of the assimilatory organs of *Nepenthes* species. *Australian Journal of Botany* **65**: 67–79.

Paluvi N, Mukarlina RL. **2015**. Struktur Anatomi Daun, Kantung dan Sulur *Nepenthes gracilis* Korth. yang Tumbuh di Area Intensitas Cahaya Berbeda. *Protobiont* **4**: 103–107.

Pavlovič A. **2012**. Adaptive radiation with regard to nutrient sequestration strategies in the carnivorous plants of the genus *Nepenthes*. *Plant Signaling & Behavior* **7**: 295–297.

Pavlovič A, Kocáb O. **2022**. Alternative oxidase (AOX) in the carnivorous pitcher plants of the genus *Nepenthes*: what is it good for? *Annals of Botany* **129**: 357–365.

Pavlovič A, Masarovičová E, Hudák J. **2007**. Carnivorous syndrome in Asian pitcher plants of the genus *Nepenthes*. *Annals of Botany* **100**: 527–536.

Pavlovič A, Saganová M. **2015**. A novel insight into the cost-benefit model for the evolution of botanical carnivory. *Annals of Botany* **115**: 1075–1092.

Pavlovič A, Singerová L, Demko V, Hudák J. **2009**. Feeding enhances photosynthetic efficiency in the carnivorous pitcher plant *Nepenthes talangensis*. *Annals of Botany*: mcp121.

Pavlovič A, Slováková L, Šantrůček J. **2011**. Nutritional benefit from leaf litter utilization in the pitcher plant *Nepenthes ampullaria*. *Plant, Cell & Environment* **34**: 1865–1873.

Phillips SJ, Anderson RP, Schapire RE. **2006**. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* **190**: 231–259.

Poppinga S, Koch K, Bohn HF, Barthlott W. **2010**. Comparative and functional morphology of hierarchically structured anti-adhesive surfaces in carnivorous plants and kettle trap flowers. *Functional Plant Biology* **37**: 952–961.

Rembold K, Fischer E, Wetzel MA, Barthlott W. **2010**. Prey composition of the pitcher plant *Nepenthes* madagascariensis. *Journal of Tropical Ecology* **26**: 365–372.

De la Riva EG, Querejeta JI, Villar R, Pérez-Ramos IM, Marañón T, Galán Díaz J, de Tomás Marín S, Prieto I. **2021**. The economics spectrum drives root trait strategies in Mediterranean vegetation. *Frontiers in Plant Science* **12**: 773118.

Roddy AB, Martínez-Perez C, Teixido AL, Cornelissen TG, Olson ME, Oliveira RS, Silveira FA. **2021**. Towards the flower economics spectrum. *New Phytologist* **229**: 665–672.

Ross TG, Barrett CF, Soto Gomez M, Lam VK, Henriquez CL, Les DH, Davis JI, Cuenca A, Petersen G, Seberg O, others. **2016**. Plastid phylogenomics and molecular evolution of Alismatales. *Cladistics* **32**: 160–178.

Rossano B, Lubomír A, others. **2024**. Measuring standardized functional leaf traits of aquatic carnivorous plants-challenges and opportunities. *Perspectives in Plant Ecology, Evolution and Systematics*: 125826.

Rottloff S, Miguel S, Biteau F, Nisse E, Hammann P, Kuhn L, Chicher J, Bazile V, Gaume L, Mignard B, others. **2016**. Proteome analysis of digestive fluids in *Nepenthes* pitchers. *Annals of Botany* **117**: 479–495.

Saganová M, Bokor B, Stolárik T, Pavlovič A. **2018**. Regulation of enzyme activities in carnivorous pitcher plants of the genus *Nepenthes*. *Planta*: 1–14.

Schaefer HM, Ruxton GD. **2008**. Fatal attraction: carnivorous plants roll out the red carpet to lure insects. *Biology Letters* **4**: 153–5.

Schaefer HM, Ruxton GD. **2014**. Fenestration: a window of opportunity for carnivorous plants. *Biology Letters* **10**: 20140134.

Schnell D. **1979**. A critical review of published variants of *Sarracenia purpurea* L. *Castanea*: 47–59.

Schnell DE. **1980**. Notes on the biology of *Sarracenia oreophila* (Kearney) Wherry. *Castanea*: 166–170.

Schwallier R, Raes N, Boer HJ, Vos RA, Vugt RR, Gravendeel B. **2016**. Phylogenetic analysis of niche divergence reveals distinct evolutionary histories and climate change implications for tropical carnivorous pitcher plants. *Diversity and Distributions* **22**: 97–110.

Schöner CR, Schöner MG, Grafe TU, Clarke CM, Dombrowski L, Tan MC, Kerth G. **2017**. Ecological outsourcing: a pitcher plant benefits from transferring pre-digestion of prey to a bat mutualist. *Journal of Ecology* **105**: 400–411.

Segala MC, Horner JD. **2023**. The effects of light availability, prey capture, and their interaction on pitcher plant morphology. *Plant Ecology* **224**: 539–548.

Silva SR, Miranda VF, Michael TP, Płachno BJ, Matos RG, Adamec L, Pond SL, Lucaci AG, Pinheiro DG, Varani AM. **2023**. The phylogenomics and evolutionary dynamics of the organellar genomes in carnivorous *Utricularia* and *Genlisea* species (Lentibulariaceae). *Molecular Phylogenetics and Evolution* **181**: 107711.

Szewczyk T, McCain CM. **2016**. A systematic review of global drivers of ant elevational diversity. *PloS ONE* **11**: e0155404.

Thornham DG, Smith JM, Ulmar Grafe T, Federle W. **2012**. Setting the trap: cleaning behaviour of *Camponotus schmitzi* ants increases long-term capture efficiency of their pitcher plant host, *Nepenthes bicalcarata*. *Functional Ecology* **26**: 11–19.

Thorogood C, Bauer U, Hiscock S. **2017**. Convergent and divergent evolution in carnivorous pitcher plant traps. *New Phytologist*.

Whatmore R, Wood PJ, Dwyer C, Millett J. **2022**. Prey capture by the non-native carnivorous pitcher plant *Sarracenia purpurea* across sites in Britain and Ireland. *Ecology and Evolution* **12**: e9588.

Whitewoods CD, Gonçalves B, Cheng J, Cui M, Kennaway R, Lee K, Bushell C, Yu M, Piao C, Coen E. **2020**. Evolution of carnivorous traps from planar leaves through simple shifts in gene expression. *Science* **367**: 91–96.

Wicke S, Schäferhoff B, Depamphilis CW, Müller KF. **2014**. Disproportional plastome-wide increase of substitution rates and relaxed purifying selection in genes of carnivorous Lentibulariaceae. *Molecular Biology and Evolution* **31**: 529–545.

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JH, Diemer M, others. **2004**. The worldwide leaf economics spectrum. *Nature* **428**: 821–827.

Yoon JS, Riu YS, Kong S-G, others. **2019**. Regulation of Anthocyanin Biosynthesis by Light and Nitrogen in *Sarracenia purpurea*. *Journal of Life Science* **29**: 1055–1061.

Box 1: **Comparison of Different Lineages of Carnivorous Pitcher Plants**

The pitcher is one of a handful of divergent trapping structures that have evolved among carnivorous plants. In pitcher plants, the leaf has been modified into a tube-shaped pitfall trap. Insects attracted to the pitcher land on slippery rims which causes them to fall into a pool of digestive fluid. This strategy has evolved at least three times independently, in the families Sarraceniaceae (Ericales), Nepenthaceae (Caryophyllales), and Cephalotaceae (Oxalidales). In a broader sense, the pitfall strategy also applies to a handful of carnivorous bromeliad species (*Brocchinia reducta*, *B. hectioides*, *Catopsis beteroniana*) and the potentially carnivorous *Paepalanthus bromelioides* (Eriocaulaceae), also in the Poales. However, unlike in the case of pitcher plants *sensu stricto*, these pitfall traps consist of tanks created by multiple tightly overlapping leaves. In Sarraceniaceae, Nepenthaceae, and Cephalotaceae, pitcher traps are all formed by individual leaves. These ‘true pitcher plants’ have many similarities in the general structure of their pitchers, including a lid covering the trap opening (the operculum), a slippery rim (the peristome), the tubular pitcher body, and the glandular digestive zone at the bottom of the inner pitcher wall, which also contains the digestive fluid.

The pitcher plants *sensu lato* in Bromeliaceae and Eriocaulaceae create fluid-filled tanks with multiple closely appressed leaves. By examining these multi-leaved pitcher plants, we can still test the extent to which the LES applies to carnivorous pitcher plants. While developmental constraints of single-leaved pitchers are likely already low, the developmental constraints of creating a tank bromeliad pitcher may be even lower, as it requires no rolled leaf. However, the functional requirement to attract, trap, and digest prey, as well as convert carbon to sugar, remains. Although each individual leaf does not function as a pitcher, the individual leaves are still governed by functional constraints on the entire pitcher’s ability to catch prey. For example, individual leaves produce a crumbling wax layer on the inner wall that interferes with adhesion between insect feet and the pitcher surface (Gaume et al. 2004; Nishi et al. 2012). In contrast to single-leaved pitchers, there is likely between-leaf variability in leaf photosynthetic efficiency; those forming the tank are quite vertical, and reducing photosynthetic efficiency, but outer leaves are at a more typical angle for bromeliads and should have a more typical photosynthetic contribution to the plant. Thus, the net cost of each leaf is likely more variable in multi-leaved pitchers than in single-leaved species. Here we hypothesize similar functional constraints between single-leaved and multi-leaved pitchers, lower developmental constraints in multi-leaved pitchers, and budgetary constraints are more variable. Examining the various constraints on each leaf of a carnivorous bromeliad would test the limits of the LES.

Box 2: **Pitcher Traits in Large-Scale Plant Trait Databases**

Large-scale collaborative databasing efforts have potentiated a move toward trait-based ecology in the past two decades, which has provided new insights into ecosystem processes, trait evolution, and plant function. These databases provide free access to trait data allowing for a diversity of large-scale studies that seek to describe and explain the vast trait variation found globally. One example of such a plant trait database is TRY (Kattge et al. 2020), which is one particularly large and comprehensive database. As of the time of access, TRY contains 15,409,681 trait records from 305,594 species. This is a massive amount of data, however there are still gaps in our knowledge. One major gap concerns the tradeoffs involved in multi-function plant structures, such as those required for both carbon fixation and nutrient or water acquisition, for example the photosynthetic roots of epiphytic orchids or the prey trapping structures of carnivorous plants — the latter of which are the focus of this review.

To examine the state of trait data for these plants, we downloaded the data for all available pitcher plant species in the TRY database (Kattge et al. 2020); this yielded 135 species with a total of 143 available traits. In contrast, if a random subset of 135 non-carnivorous species is selected, its trait table yields an average of 418 total measured traits (Supplemental Data). This illustrates that, even considering the relatively small number of species, pitcher plants have not been subject to the same depth and breadth of trait measurements, relative to non-carnivorous plants within this database. Compared to other plant groups, either fewer traits have been recorded and uploaded for pitcher plants, and/or researchers have yet to determine a standardized set of trait measurements that would facilitate ease of entry into large databases. Consequently, cross-species trait comparisons are less frequent within pitcher plants as a group. This is surprising, given that leaf and pitcher trap trait variation in these clades can be very high and are often used for species delimitation. This presents an opportunity for a more consistent trait-based approach to pitcher plant biology, expanding our database of traits to better-understand these evolutionary enigmas, and how they fit into the existing framework.

Box 3: **Assorted Unanswered Questions and Future Directions**

Developmental

The low developmental costs of transforming a flat leaf to a pitcher are understood, however less is known regarding the developmental forces shaping intraspecific variation:

- Nepenthaceae produce dimorphic pitchers–what developmental programming regulates the production of upper versus lower pitchers in *Nepenthes*?
- What controls the geometry of the trap shape, i.e. more cylindrical versus rounder pitcher shapes?
- What controls the angle of the lid and orientation of the pitcher aperture?
- Are there any developmental costs to pitcher fluid formation? The total volume of fluid appears to be under genetic control–consider the stable difference in fluid volume between *Nepenthes rafflesiana* and the closely related *N. hemsleyana*, the latter of which produces a lower volume.

- Are there any developmental constraints/costs to pigment pattern formation, including transparent windows found in *Darlingtonia* and *Sarracenia minor*?
- What constraints are there related to the expression of genes and proteins related to carnivory within pitchers and non-pitcher tissues?

Functional

- Research on the functional ecology of pitcher trapping mechanisms have thus far focused on adult pitchers, however many pitcher plants including *Sarracenia*, *Heliamphora*, and *Nepenthes* have clear morphological differences in the juvenile pitchers produced by seedlings and earlier ontogenetic life stages of the plant. The size and shape of these juvenile pitchers may be suboptimal considering the functional constraints of the adult form pitchers. Do juvenile pitchers function for prey capture? How do the plants overcome these potential functional costs?
- To what extent do pitcher traits vary, within and between species? How does this variability impact prey capture characteristics?
- What factors go into the regulation of fluid production?

Budgetary

- How do carnivory-photosynthesis tradeoffs change during ontogeny?
- How does the carbon investment (LMA) of carnivorous pitcher plants compare to non-carnivorous leaves in both range (are most CPPs on the high LMA high LL end of the LES) and variability?

Ecological

- What is the ecological niche breadth of particular pitcher traits (e.g., trap size, pigmentation, peristomal structure)?
- What are the environmental cues that regulate pitcher expression in *Nepenthes*? Do these cues vary across environments?
- Given that the trapping tissues of *Cephalotaceae* and Sarraceniaceae are also their centers of photosynthesis, they must be continuously produced by the plant. In contrast, *Nepenthes* can withhold pitcher production but still meet its carbon demands in suboptimal environments. Do these fundamental differences manifest as increased levels of trait-environment correlations in the trapping structures of the former groups relative to the latter?
- If trait-environment correlations in pitcher morphology (and leaf) morphology are rare (as they appear to be) then what aspect of a species' phenotype permits it to have wider environmental tolerances or geographic distributions than small-ranged congeners?
- Similarly, does the spatial separation of trapping and photosynthetic tissues (e.g., in *Nepenthes*) permit a wider environmental distribution and more interspecific trap variation?

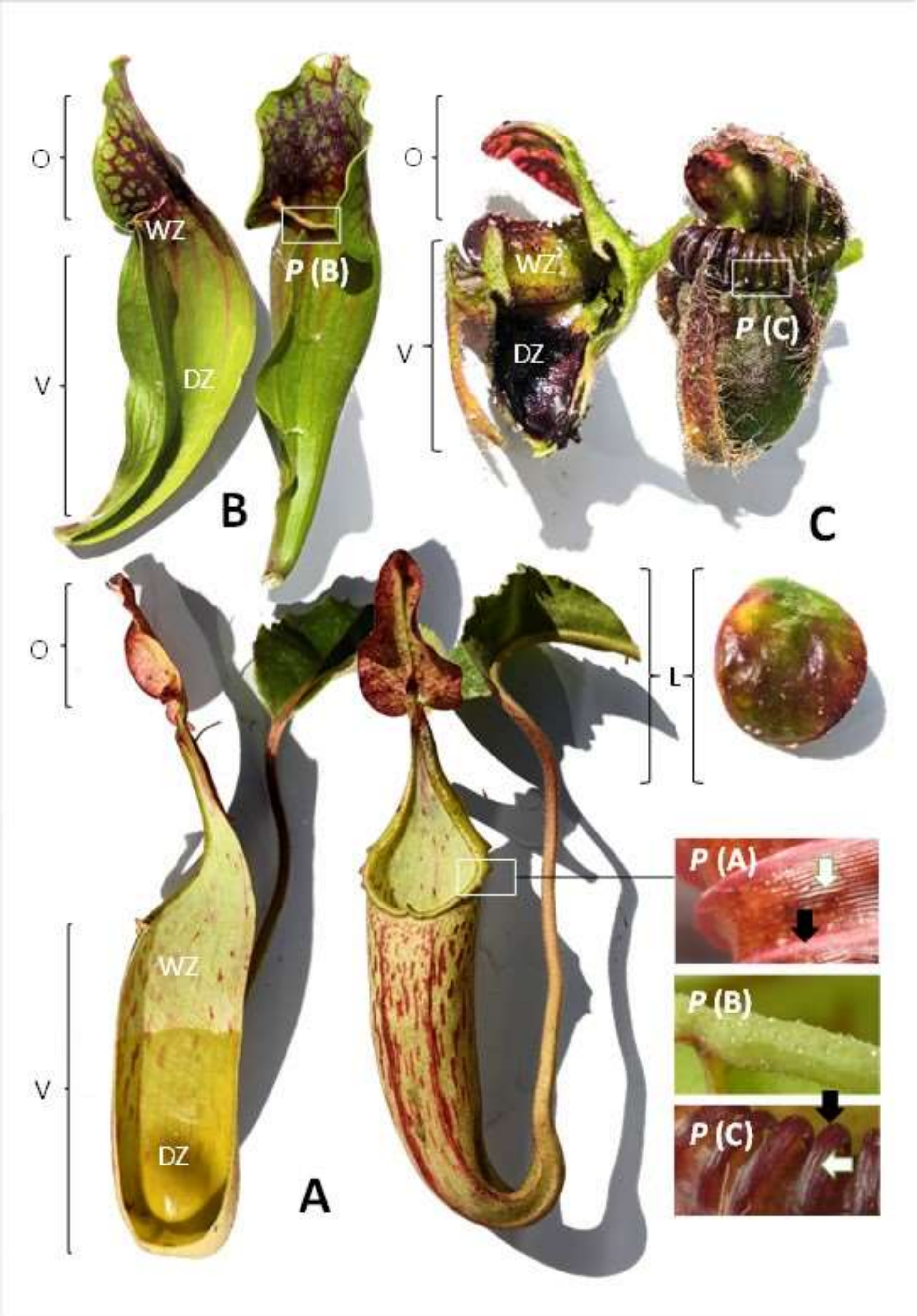

Figure 1. The convergent pitcher structures and surfaces of: A. *Nepenthes*, B. *Sarracenia*, and C. *Cephalotus*. DZ=Digestive Zone; L=photosynthetic (non-tubular) lamina of *Nepenthes* (left) and *Cephalotus* (right: note the lamina is not attached to the pitcher); WZ=Waxy Zone; V=Vessel; O=Operculum; P=Peristome (followed by the letter denoting the genus, as above); bottom right boxes show magnification of peristomes; note the primary ribs (black arrow) and secondary ribs (white arrow) present in *Nepenthes* and *Cephalotus* which are absent in *Sarracenia*.

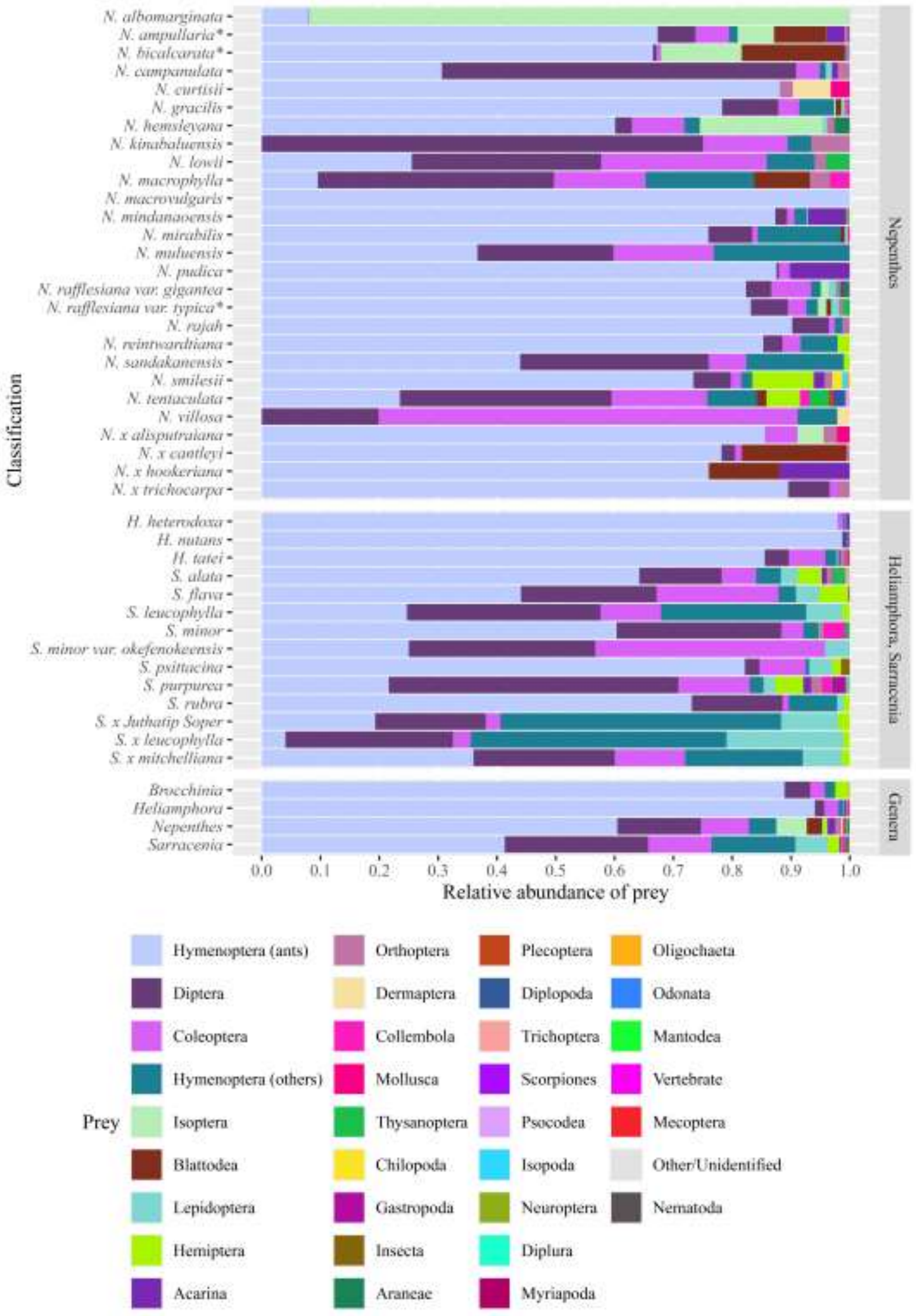

Figure 2. Relative prey abundance of *Nepenthes*, *Brocchinia*^, *Heliamphora*, and *Sarracenia* at the species and genera level. *Indicates prey captures include unquantified vegetation. ^*Brocchinia reducta* was the sole species of its genus included in analysis and, therefore, not included in the cross-species comparison

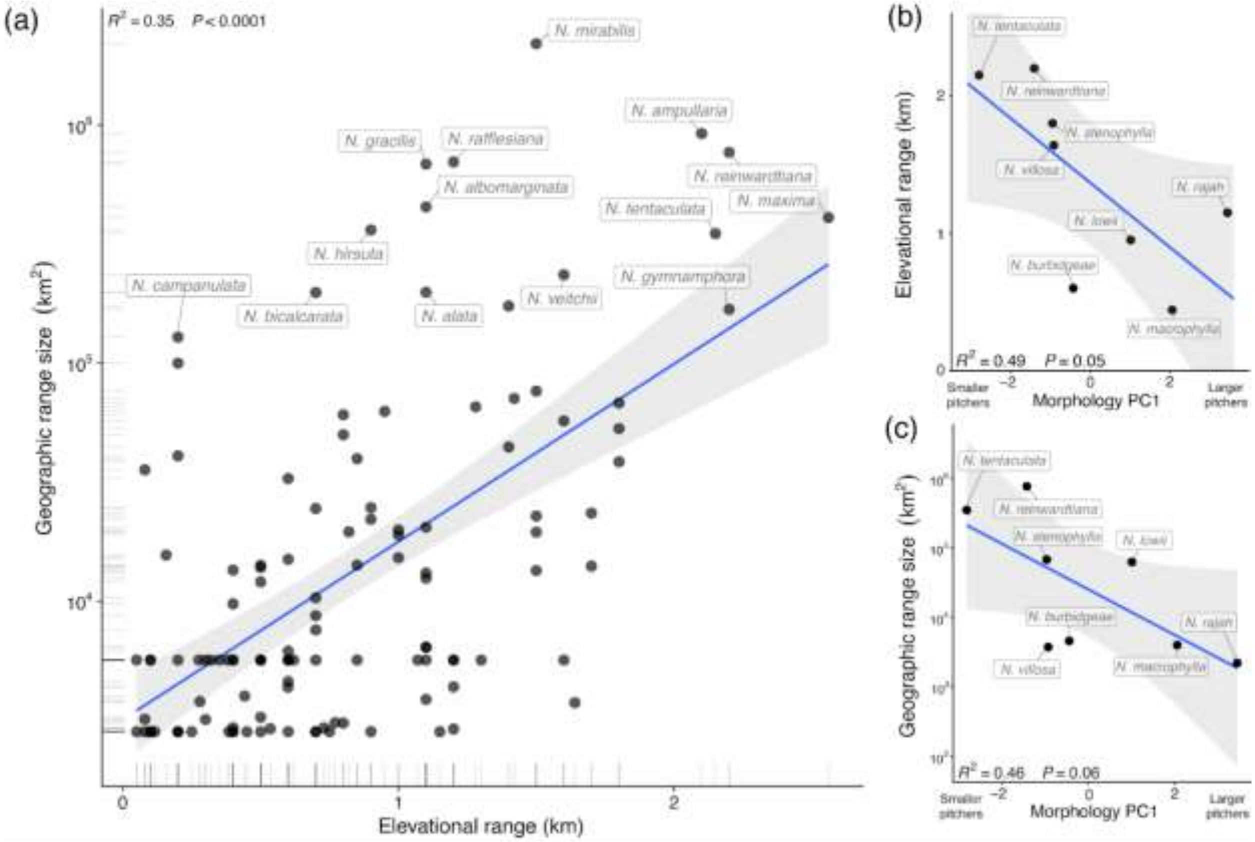

Figure 3 - (a) Relationship between elevational range and geographic range size for *Nepenthes* species. Here, elevation limits were obtained from Clarke and Moran (2015) and range limits were estimated by fitting ecological niche models (when $n \geq 5$) or 30 km-buffered convex hulls (when $n < 5$) to georeferenced occurrence data. Panels (b) and (c) show relationship between pitcher morphology and elevational/geographic range for sympatric *Nepenthes* species in Sabah (data from Chin et al., 2010).