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DARWIN REVIEW

Energetics and the evolution of carnivorous plants—Darwin's 'most wonderful plants in the world'

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Abstract

Carnivory has evolved independently at least six times in five angiosperm orders. In spite of these independent origins, there is a remarkable morphological convergence of carnivorous plant traps and physiological convergence of mechanisms for digesting and assimilating prey. These convergent traits have made carnivorous plants model systems for addressing questions in plant molecular genetics, physiology, and evolutionary ecology. New data show that carnivorous plant genera with morphologically complex traps have higher relative rates of gene substitutions than do those with simple sticky traps. This observation suggests two alternative mechanisms for the evolution and diversification of carnivorous plant lineages. The 'energetics hypothesis' posits rapid morphological evolution resulting from a few changes in regulatory genes responsible for meeting the high energetic demands of active traps. The 'predictable prey capture hypothesis' further posits that complex traps yield more predictable and frequent prey captures. To evaluate these hypotheses, available data on the tempo and mode of carnivorous plant evolution were reviewed; patterns of prey capture by carnivorous plants were analysed; and the energetic costs and benefits of botanical carnivory were re-evaluated. Collectively, the data are more supportive of the energetics hypothesis than the predictable prey capture hypothesis. The energetics hypothesis is consistent with a phenomenological cost–benefit model for the evolution of botanical carnivory, and also accounts for data suggesting that carnivorous plants have leaf construction costs and scaling relationships among leaf traits that are substantially different from those of non-carnivorous plants.

Key words: Carnivorous plants, competition, construction costs, cost–benefit model, Darwin, energetics, niche overlap, phylogeny, prey capture, universal spectrum of leaf traits.

Introduction

> '*This plant, commonly called Venus' fly-trap, from the rapidity and force of its movements, is one of the most wonderful in the world.*'
>
> (C. Darwin, *Insectivorous plants*, p. 231)[1]

Carnivorous plants have evolved multiple times among the angiosperms (Fig. 1), and the degree of morphological and physiological convergence across carnivorous taxa is remarkable. Molecular sequence data have revealed the

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Abbreviations: A_{mass}, mass-based photosynthetic rate in nmol CO_2 g^{-1} s^{-1}; ANOVA, analysis of variance; *atp*B, chloroplast gene encoding the β chain of membrane-bound ATP synthase; C-value, amount of DNA in a haploid nucleus [in millions of base pairs (Mbp)]; *cox*I, mitochondrial gene encoding subunit 1 of cyctochrome *c* oxidase; ITS, internal transcribed spacer; J_{Chao}, the Chao–Jaccard abundance-weighted index of similarity; nrITS, nuclear ribosomal ITS; *mat*K, chloroplast gene believed to encode a maturase, it is located within the *trn*K intron; *PIE*, probability of interspecific encounter, used here as a measure of specialization on prey by carnivorous plants; PRT1, nuclear gene encoding peptide transferase 1; *rbc*L, chloroplast gene encoding ribulose-bisphosphate carboxylase; *rps*16, a non-coding chloroplast intron; RRTree, software for comparing sequence divergence rates among related lineages (by extension, it has also come to mean the statistical relative-rate test between groups of sequences on a phylogenetic tree); *trn*K, a non-coding chloroplast intron; it includes the *mat*K exon; *trn*F and *trn*L, two other non-coding chloroplast introns; *trn*L-F, intergenic spacer between the *trn*L and *trn*F introns.

[1] All quotations from Darwin's *Insectivorous plants* are from the second (1898) edition.

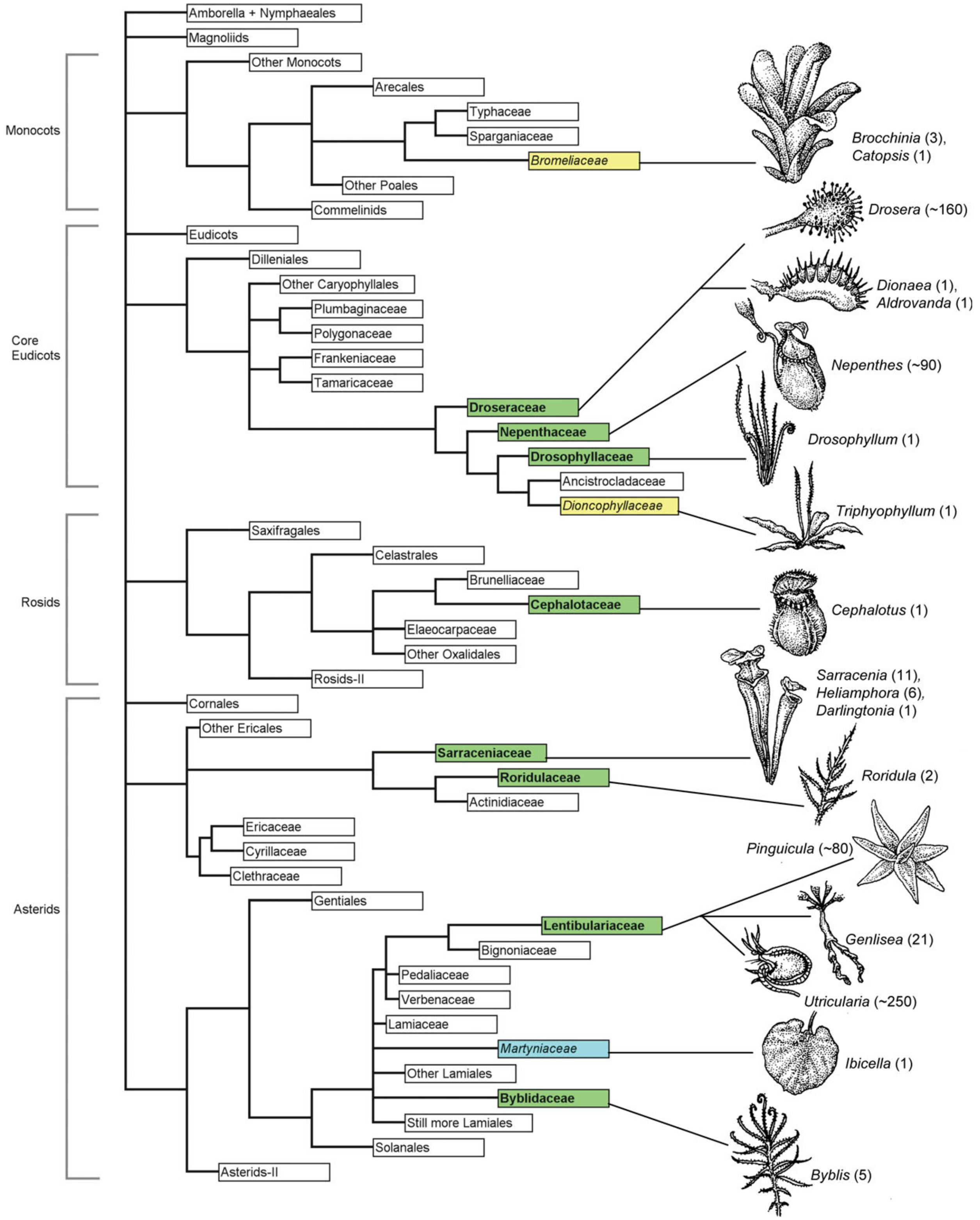

Fig. 1. Positions of carnivorous plant families in the current overall angiosperm phylogeny (Stevens, 2007; relationships within the Lamiales from Müller *et al.*, 2006). Families that are exclusively carnivorous are set in bold and highlighted in green; families with only one (Dioncophyllaceae) or two (Bromeliaceae) carnivorous genera are set in italic and highlighted in yellow; and the family (Martyniaceae) with the possibly carnivorous *Ibicella lutea* v.Eselt. is set in italic and highlighted in blue. Representative traps of each genus are illustrated (drawings by Elizabeth Farnsworth), and the number of species in each genus is given in parentheses. The phylogenetic tree was drawn using the MrEnt software package (Zuccon and Zuccon, 2006); branch lengths are drawn only to emphasize the location of carnivorous families and otherwise are not meaningful (*i.e.,* do not signify time since divergence or any other metric of relatedness).

phylogenetic history of the angiosperms (Stevens, 2007) and have yielded a better understanding of the patterns of evolution of carnivorous plants. The availability of reliable phylogenies, new observations and experiments, cost–benefit models (Givnish *et al.*, 1984; Laakkonen *et al.*, 2006), and contemporary statistical methods have allowed carnivorous plants to emerge as model systems that can be used to address a wide range of questions arising from plant molecular genetics to physiology and evolutionary ecology (Ellison and Gotelli, 2001; Ellison *et al.*, 2003).

Charles Darwin laid the foundation for modern research on carnivorous plants. In *Insectivorous plants*, Darwin (1875) applied his then relatively new conception of homology to illustrate evolutionary and functional convergence across seemingly unrelated taxa. He provided the first detailed descriptions of the structures by which eight genera of plants could entrap insects. With careful observations and clever experiments, Darwin determined for the first time that these plants directly dissolved animal protein using enzymes whose action was similar to pepsin and other proteases (see also Hepburn *et al.*, 1919, 1927). He further showed that dissolved nutrients were directly absorbed by carnivorous plants and that captured prey contributes significantly to plant growth (Darwin, 1875).

Drawing on >125 years of subsequent research, this review surveys recent progress in three areas of inquiry that Darwin initiated in *Insectivorous plants*: (i) the tempo and mode of carnivorous plant evolution; (ii) patterns and processes of prey capture; and (iii) the energetic costs and benefits of botanical carnivory. These three research fronts are unified by stable phylogenetic placement of carnivorous taxa, new data on gene evolution in carnivorous plants (Jobson and Albert, 2002; Müller *et al.*, 2004), and the refinement by Laakkonen *et al.* (2006) of the cost–benefit model for the evolution of botanical carnivory originally formulated by Givnish *et al.* (1984).

Current understanding of the phylogenetic placement of carnivorous plants re-affirms the occurrence of convergence in trapping mechanisms. Genomic data suggest biochemical, physiological, and ecological mechanisms that could have led to the rapid diversification of at least some carnivorous plant lineages. New analyses of published data on prey capture permit the evaluation of the degree of specialization among carnivorous plant genera and link evolutionarily convergent traits with the ecologically important process of predation. The use of carbon to measure both costs and benefits of carnivory allows carnivorous plants to be placed into the 'universal spectrum of leaf traits' (Wright *et al.*, 2004, 2005) that reflects fundamental trade-offs associated with the allocation of carbon to structural tissues and photosynthesis (Shipley *et al.*, 2006).

The tempo and mode of carnivorous plant evolution

'*By comparing the structure of the leaves, their degree of complication, and their rudimentary parts in the six genera* [Drosophyllum, Roridula, Byblis, Drosera, Dionaea, *and* Aldrovanda], *we are led to infer that their common parent form partook of the characters of* Drosophyllum, Roridula, *and* Byblis.'

(*Insectivorous plants*, p. 289)

'*It stands accordingly to reason that the carnivorous plants are quite as old as angiospermy, as an independent angiospermous group bound with still older groups eventually beyond the limits of angiospermy.*'

(Croizat, 1960: 129)

In *The origin of species*, Darwin (1859) asserted the importance of homology—the similarity of traits resulting from shared ancestry—for understanding evolutionary relationships. Although the importance of homologous traits (including sequences of DNA, genes, and proteins) in reconstructing phylogenies is widely recognized, actually identifying them remains a challenge. Nowhere is this challenge more evident than in the history of the placement of carnivorous plants in angiosperm phylogenies (Juniper *et al.*, 1989). A proper interpretation of patterns of prey capture, gene sequence data, and the evolution of carnivory all rely on firm knowledge of the phylogenetic placement of carnivorous plants and on stable nomenclature. Therefore, this review begins with a survey of current knowledge of carnivorous plant systematics, focused on how recent syntheses of molecular and morphological data illuminate the two most disparate hypotheses for the evolution and diversification of carnivorous plants: Darwin's (1875) hypothesis that the specialization and evolutionary novelty of carnivorous plants indicated convergence in independent lineages, and Croizat's (1960) hypothesis that carnivory evolved once near the base of the angiosperm lineage.

Darwin asserted that all of the species with sticky-leaf (or 'flypaper') traps in the genera *Drosera*, *Byblis*, *Roridula*, and *Drosophyllum*, along with the snap-trapping Venus' flytrap (*Dionaea muscipula* Ellis) and the water-wheel plant (*Aldrovanda vesiculosa* L.) were closely related (19th century botanists placed all six genera in the Droseraceae, the sundew family). In *Insectivorous plants*, he discussed in detail the apparent homology of the sessile glands that they use to digest prey. He also asserted that neither the butterworts (*Pinguicula*) (or the other Lentibulariaceae: *Genlisea* and *Utricularia*) nor the Asian pitcher plants (*Nepenthes*) were 'at all related to the Droseraceae' (*Insectivorous plants*, p. 292). Darwin appears to have had little familiarity with the American pitcher plants (*Sarracenia*, *Darlingtonia*, and *Heliamphora*), nor did he discuss the Australian pitcher plant *Cephalotus follicularis* Labill. (Cephalotaceae),[2] but it is safe to say that he recognized at least three lineages of carnivorous plants: his

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[2] *Sarracenia* is mentioned in passing only on the penultimate page of *Insectivorous plants*. In a letter to W Thiselton-Dyer (letter 724 in F Darwin, 1903), he refers to Asa Gray's examination of *Sarracenia*. In a letter to JD Hooker (letter 726 in F Darwin, 1903), he writes of hoping that Hooker will resume work on *Cephalotus* and *Sarracenia* and provide comparative data for Darwin's ongoing studies of *Utricularia*.

'Droseraceae', the Lentibulariaceae, and the (Asian) pitcher plants (Nepenthaceae).

In contrast to Darwin, Croizat (1960) asserted a common origin for all carnivorous plants and placed them close to the base of the entire angiosperm lineage.[3] Croizat (1960) asserted that the Lentibulariaceae, and in particular *Utricularia*, was the basal angiosperm group, with morphological evolution proceeding from the relatively amorphous *Utricularia* with its vestigial leaves, stems, and roots that are barely distinguishable from one another, to plants with more differentiated characters including cladodes, shoots, and leaves. In Croizat's view, *Nepenthes* was derived directly from *Utricularia*.[4] Although the scant fossil record of carnivorous plants does suggest a long evolutionary history for at least some taxa (Thanikaimoni and Vasanthy, 1974; Li, 2005; Heubl *et al.*, 2006), modern phylogenetic analyses of molecular markers and DNA sequences suggest that carnivorous plants are highly derived, polyphyletic taxa. Contrary to Croizat's (1960) assertions, carnivorous plants do not represent a monophyletic ancestral Ur-angiosperm, nor are the vestigial structures of *Utricularia* evolutionary precursors to the more familiar morphological characters of higher plants.

Progress in resolving familial relationships

> '[*C*]*onstructive discussion is out of the question, and attempts made at demonstrating, e.g., that* Utricularia *is "derivative" forthwith disqualify their proponents as essentially ill informed.*'
>
> (Croizat, 1960: 120)

Carnivorous plants can be found in four of the major angiosperm lineages (the Monocots, Core Eudicots, Rosids, and Asterids), and in five orders: Poales, Caryophyllales, Oxalidales, Ericales, and Lamiales (Fig. 1). Convergence of carnivorous plants and their traps is most apparent at the ordinal level, whereas gene sequences have distinguished between convergence and homology within orders, families, and genera.

Over 95% of the >600 species of carnivorous plants are currently placed within the Caryophyllales and Lamiales (Fig. 1). New combined analyses based on sequences of the *trn*K intron and its associated *mat*K gene, additional chloroplast genes (*atp*B, *rbc*L), and nuclear 18S rDNA have clarified relationships among carnivorous families within the Caryophyllales (Heubl *et al.*, 2006). These analyses simultaneously confirm one of Darwin's notions of homology,[5] but dispel another:[6] *Aldrovanda vesiculosa* and *Dionaea muscipula* are sister taxa, and this clade of snap-trappers is a sister group to the sundews (*Drosera*) with their sticky leaves (Cameron *et al.*, 2002; Rivadavia *et al.*, 2003).

Three other carnivorous families—Nepenthaceae, Drosophyllaceae, and Dioncophyllaceae—are also clearly rooted within the Caryophyllales (Fig. 1). All three of these families are in a large clade linked to the Droseraceae by a common ancestor, presumably one with flypaper traps. Contrary to Darwin's hypothesis that *Nepenthes* was 'not at all related to the Droseraceae' (*Insectivorous plants*, p. 292), this genus (i.e. its monogeneric family, the Nepenthaceae) is the sister group of the Droseraceae (Fig. 1). The dewy pine *Drosophyllum lusitanicum* Link is now firmly established in its own family (Drosophyllaceae), and carnivory appears to have been re-derived in the Dioncophyllaceae by the flypaper-trapping *Triphyophyllum peltatum* (Hutch. & Dalz.) Airy Shaw (Cuenoud *et al.*, 2002; Heubl *et al.*, 2006).

Carnivory also had more than one independent origin in the Lamiales (Müller *et al.*, 2004, 2006; Fig. 1). As in the Caryophyllales, evolution of the trap structure in carnivorous Lamiales has proceeded from flypaper traps in *Pinguicula* to the more complex, unidirectionally twisted 'eel' traps in *Genlisea* and the bladder traps of *Utricularia* with their unique suction mechanism (Lloyd, 1942; Guisande *et al.*, 2007). At least half of all described carnivorous species are in these three genera, which historically were linked based on shared floral characters (Taylor, 1989). Contemporary molecular analysis unites them based on shared sequences in the *trn*L and *rps*16 introns, *rbc*L, the functional *cox*I and *mat*K genes, and 5.8S rDNA (Jobson and Albert, 2002; Jobson *et al.*, 2003; Müller *et al.*, 2004, 2006; Cieslak *et al.*, 2005). Despite Croizat's posthumous protestations to the contrary, both genetic and morphological data support the monophyly of the Lentibulariaceae, with *Pinguicula* sister to a *Genlisea–Utricularia* clade. However, contrary to Albert *et al.* (1992), it is clear that the other carnivorous family in this order, the Byblidaceae (*fide* Płachno *et al.*, 2006), is neither directly ancestral to the Lentibulariaceae nor even closely related to it (Fig. 1).

The three remaining carnivorous dicot families—Roridulaceae, Sarraceniaceae, and Cephalotaceae—illustrate variations on the convergent theme of trap evolution. Based on *rbc*L and 18S rDNA analyses, the African endemic Roridulaceae (two species) was considered to be the sister to the American Sarraceniaceae (three genera, 27 species) in the Ericales (Albert *et al.*, 1992; Conran and Dowd, 1993). However, the current placement of these two families in the

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[3] '*The "carnivorous ancestor" can of course be figured, as I have, in function of a morphogenetic and phylogenetic average quantified to fit everything – by tendency – between the Podostemonaceae/Lentibulariaceae and the Sarraceniaceae/Dioncophyllaceae.*' (Croizat, 1960: 256).

[4] '*The difference in all these regards between* Nepenthes*, and* Utricularia *and other lentibulariaceous genera is in every respect one of degree, not at all one of kind. The "runner" which in the latter aggregate becomes by easy steps under our own eyes "cladode" and "leaf" (cf., e.g.,* U. alpina/Pinguicula vulgaris*) is by now fully fixed as "foliage" in* Nepenthes*. …the interrelations between "foliage" and "stem" turn out to be far more complicated in* Nepenthes *than they are in the simplest forms of the Lentibulariaceae [i.e., Utricularia].*' (Croizat, 1960: 181-182).

[5] '*these octofid projections* [of the footstalk, backs of leaves, and spikes of *Dionaea*] *are no doubt homologous with the papillae on the leaves of* Drosera rotundifolia' (*Insectivorous plants*, p. 233).

[6] '*The circumferential part of the leaf of* Aldrovanda *thus differs greatly from that of Dionaea; nor can the points on the rim be considered as homologous with the spikes round the leaves of* Dionaea*, as these latter are prolongations of the blade, and not mere epidermic productions. They appear also to serve for a widely different purpose.*' (*Insectivorous plants*, p. 263).

overall angiosperm phylogeny (Stevens, 2007) reverses this, and has the Sarraceniaceae with its pitcher traps sister to a clade containing the sticky-leaved Roridulaceae and the non-carnivorous Actinidicaceae. If this placement is confirmed, it would represent one instance among carnivorous plant lineages of morphologically more complex traps (here, pitchers) being ancestral to simpler sticky traps. Similarly, the Australian endemic *Cephalotus follicularis* (Cephalotaceae) has no apparent sticky-leaved ancestor (Fig. 1).

Within the monocots, carnivory has also evolved at least twice in the Bromeliaceae genera *Brocchinia* (*B. hectioides* Mez, *B. reducta* Baker, and possibly *B. tatei* L.B. Smith) (Givnish, *et al.*, 1984; Benzing *et al.*, 1985) and *Catopsis berteroniana* (Schultes & Schultes) Mez (Frank and O'Meara, 1984). As with *Cephalotus*, there is no apparent sticky-leaved sister group to these bromeliads with pitcher traps.

Progress in resolving generic and subgeneric relationships

> '*…at the present moment, I care more about* Drosera *than the origin of all the species in the world.*'
> (Darwin 1860, in a letter to Charles Lyell[7])

As the ordinal placement and systematics of carnivorous plant families have stabilized, attention has turned to resolving relationships among the genera and to resolving subgeneric relationships in the most speciose carnivorous genera—*Drosera*, *Nepenthes*, *Pinguicula*, *Genlisea*, *Utricularia*, and *Sarracenia*. In most cases, phylogenetic patterns based only on inferred homologous morphological traits have been misleading. However, when morphological data have been combined with molecular analyses, novel insights into the evolution and biogeography of these carnivorous plant genera have emerged.

Drosera: As mentioned above, *Drosera*, *Dionaea*, and *Aldrovanda* form a well-supported clade, with snap-trapping having evolved only once in the clade consisting of *Dionaea* and *Aldrovanda* (Cameron *et al.*, 2002; Rivadavia *et al.*, 2003). The infrageneric classification of *Drosera*, on the other hand, has gone through many revisions. All data point to the basal position of *D. regia* Stephens, a South African narrow endemic, in the monophyletic *Drosera* clade. Beyond that conclusion, however, there is little concordance among different proposed phylogenies and subgeneric classifications.

Seine and Barthlott (1994) proposed a morphology-based classification of *Drosera* consisting of three subgenera and 11 sections, but this classification is not congruent with phylogenies based on molecular data alone (Rivadavia *et al.*, 2003; Williams *et al.*, 2004) or on combining molecular and morphological data (Rivadavia *et al.*, 2003). Further, different statistical analyses of *rbc*L data (e.g. using MacClade in Rivadavia *et al.*, 2003 and PAUP in Williams *et al.*, 1994) do not concur. For example, Williams *et al.* (1994) identified a 'capensis' clade consisting of South African and non-Australian temperate species, but this clade was not clearly identified by Rivadavia *et al.* (2003), who sequenced many more species than did Williams *et al.* (1994). Rivadavia *et al.* (2003) hypothesized that *Drosera* originated in southern Africa or in Australia; that South American species arose by dispersal from Australia; and that African species other than *D. regia* and *D. indica* L. were subsequently derived from South American ancestors. While shades of Croizat and Gondwanan vicariance could be inferred from this analysis, a Gondwanan origin of *Drosera* is not supported by the recent evolution of the Droseraceae (Rivadavia *et al.*, 2003). Clearly much more work remains to be done in this genus.

Nepenthes: About 90 species of *Nepenthes*, the sister group to the Droseraceae, occur throughout southeast Asia, with many endemics on Borneo and Sumatra. Biogeographic outliers (disjuncts) occur in India (*N. khasiana* Hook. f.), Sri Lanka (*N. distillatoria* L.), the Seychelles (*N. pervillei* Blume), and Madagascar (*N. madagascarensis* Poir. and *N. masoalensis* Schmid-Hollinger) (Meimberg *et al.*, 2001; Meimberg and Heubl, 2006). Morphology has been of limited use in resolving systematic relationships in this genus (Jebb and Cheek, 1997), but phylogenetic analysis of *Nepenthes* has improved dramatically as molecular data have accrued (Meimberg *et al.*, 2001; Meimberg and Heubl, 2006). Both chloroplast (*trn*K intron and *mat*K gene) and nuclear (PRT1 along with a non-plastid, translocated copy of *trn*K) genes have been used in phylogenetic reconstruction (Meimberg *et al.*, 2001; Meimberg and Heubl, 2006). These results suggest that the five western, biogeographically disjunct species listed above are ancestral to three clades consisting of the Indo-Malayan species. The relatedness and, more importantly, the biogeographic origins of these latter species suggest repeated colonizations and radiations by *Nepenthes* within the Indonesian islands throughout the Tertiary (Meimberg and Heubl, 2006).

Pinguicula: As with studies of *Drosera* and *Nepenthes*, the new cladistic analyses of *Pinguicula* do not agree with historical subgeneric classifications (Casper, 1966; Legendre, 2000). Based on sequencing of *trn*K/*mat*K and morphological analysis of 46 of the ~80 species of *Pinguicula*, Cieslak *et al.* (2005) found high levels of support for five discrete, geographically bounded lineages. This fundamental result supplanted and simplified earlier subgeneric and sectional classifications (three subgenera and 12 sections; Casper, 1966; Legendre, 2000). In Cieslak *et al.*'s (2005) new classification, the basal lineage appears to be tropical, with successive branchings of clades consisting of Eurasian species, East Asian species, the Eurasian *P. alpina* L., and a Central American/Mexican/Caribbean group (Cieslak *et al.*, 2005; Müller *et al.*, 2006). However, phylogenetic reconstruction based on sequencing nrITS1 and nrITS2 of 29 species of *Pinguicula* offered a different picture (Degtjareva *et al.*, 2006). Although both phylogenies found some support

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[7] Page 492 of the 1911 edition of *The life and letters of Charles Darwin*, edited by F Darwin.

for a derived Central American/Mexican/Caribbean clade, and the nrITS-based phylogeny was reasonably congruent with Casper's (1966) morphological classification, the remaining clades identified by the nrITS-based phylogeny were polyphyletic in the *trn*K-based phylogeny (Cieslak *et al.*, 2005). Resolving the infrageneric phylogeny of *Pinguicula* requires clearer definition of informative morphological and molecular characters as well as sequence data from a wider range of species.

Genlisea and *Utricularia*: In contrast to the ongoing systematic confusion in *Pinguicula*, sequence data from *mat*K, *trn*K, *rbc*L, *rps*16, and *trn*L-F (Jobson *et al.*, 2003; Müller *et al.*, 2004, 2006) generally have supported the infrageneric grouping of the 21 species of *Genlisea* based on differences in the way capsules dehisce (Fischer *et al.*, 2000). The South American subgenus *Tayloria* is sister to a clade consisting of three African species and five additional South American species. The African species do not form a natural clade, as the East African/Madagascan species *G. margaretae* Hutchinson is more closely related to the South American species than it is to the remaining African species (Fischer *et al.*, 2000; Müller *et al.*, 2006).

The ~220 species of *Utricularia* have been organized into three subgenera and ~21 sections. Analysis of *trn*L-F, *rps*16, and *trn*K sequence data (Jobson *et al.*, 2003; Müller and Borsch, 2005) suggested a refinement of the three subgenera *Polypompholyx*, *Bivalvia*, and *Utricularia*. Taylor's (1989) 34 sections based on morphology were, with three exceptions (sections *Iperua*, *Setiscapella*, and *Psyllosperma*), upheld as monophyletic. Current analysis suggests a single terrestrial origin for bladderworts in South America; the aquatic and epiphytic habits of *Utricularia* species appear to have been re-derived multiple times within the genus (Jobson *et al.*, 2003; Müller and Borsch, 2005; Müller *et al.*, 2006).

Greilhuber *et al.* (2006) reported the remarkable result that many species of *Genlisea* and *Utricularia* have very small nuclear genome sizes. In fact, they found that *Genlisea margaretae* (C-value = 63 Mbp), *G. aurea* St. Hil. (64 Mbp), *Utricularia gibba* L. (88 Mbp), *U. blanchetii* A.DC. (135 Mbp), and *U. parthenopipes* P. Taylor (140 Mbp) have smaller C-values than that found for the previous record holder for the smallest angiosperm genome, *Arabidopsis thaliana* (L.) Heynh. (157 Mbp). Neither the functional significance nor the potential role in evolutionary diversification of this apparent genome simplification in *Genlisea* and *Utricularia* is known.

Sarracenia: Recent genetic analyses have revealed perhaps the most taxonomic surprises in the American pitcher plants (Sarraceniaceae). Three sets of phylogenetic reconstructions, one based only on the chloroplast *rbc*L gene (Albert *et al.*, 1992), another that used *rbc*L along with two nuclear ITS regions of rDNA (Bayer *et al.*, 1996), and a third that used ITS-2 along with the 26S rRNA gene (Neyland and Merchant, 2006), have all supported the monophyly of the Sarraceniaceae. Older analyses of biogeographical (Croizat, 1960; McDaniel, 1971; Maguire, 1978), palynological (Thanikaimoni and Vasanthy, 1972), and morphological (Macfarlane, 1893; deBuhr, 1977; Maguire, 1978; Juniper *et al.*, 1989) data have traditionally grouped the North American genera *Sarracenia* and *Darlingtonia* together and posited that the South American genus *Heliamphora* was either sister to, or derived from, a *Sarracenia–Darlingtonia* clade. In contrast, all of the molecular data suggest that *Darlingtonia* is sister to a derived *Sarracenia–Heliamphora* clade. This result is concordant with Renner's (1989) hypothesis that modern-day Sarraceniaceae are derived from a widespread common ancestor (or ancestral stock).

These results do not settle the long-standing debate about whether the common ancestor of modern Sarraceniacae was Neotropical (South America) or subtropical (southeast North America) (Bayer *et al.*, 1996; Neyland and Merchant, 2006). However, these results do help in resolving species-level relationships within the genus *Sarracenia*. Three distinct clades now seem plausible in this genus: one consisting of *S. psittacina* Michx., *S. minor* Walt., and *S. flava* L.; another consisting of *S. rubra* Walt. (*sensu lato*), *S. alata* Wood, *S. oreophila* (Kearney) Wherry, and *S. leucophylla* Raf.; and a third consisting of *S. purpurea* L. (*sensu lato*).

Neither Bayer *et al.* (1996) nor Neyland and Merchant (2006) provide support for separation of the *S. rubra* complex into the separate species and subspecies *S. jonesii* Wherry, *S. alabamensis* Case & Case, *S. rubra* ssp. *gulfensis* Schnell, *S. rubra* ssp. *wherryi* (Case & Case) Schnell, and *S. rubra* ssp. *rubra* Walt. (Case and Case, 1974, 1976; Schnell, 1977, 1979*b*; Godt and Hamrick, 1998). Although the *S. rubra* complex is clearly derived within the genus (Romeo *et al.*, 1977), the molecular data provide no apparent discrimination among them. The repeated failure to distinguish them as distinct taxa raises questions about the separate listing of *S. jonesii* and *S. alabamensis* as endangered species in the USA.

In contrast to the lack of taxonomic differentiation within *S. rubra*, there do appear to be significant differences among named taxa within *S. purpurea*. This species was divided by Gleason and Cronquist (1991) into two varieties (considered to be subspecies by Schnell, 2002), *S. purpurea purpurea* (Raf.) Wherry and *S. purpurea venosa* (Raf.) Wherry; the latter has been further subdivided into three varieties: *venosa* (Raf.) Fernald; *montana* Schnell & Determann; and *burkii* Schnell (Schnell, 1979*a*, 1993; Schnell and Determann, 1997) or two varieties (*venosa*, *montana*) and the separate species *S. rosea* Naczi, Case & Case (Naczi *et al.*, 1999). The ITS-2 and 26S rRNA analyses confirmed an earlier study based on allozymes (Godt and Hamrick, 1999); all data clearly separate *S. purpurea venosa* var. *burkii* from the other named varieties of *S. purpurea venosa* and *S. purpurea purpurea*, and support its elevation to *S. rosea* (Neyland and Merchant, 2006). Because *S. rosea* is endemic to the Florida panhandle, additional data on its distribution, demography, and threats to its persistence are immediately needed to determine if it should be a candidate for listing as threatened or endangered at either the state or federal level.

Furthermore, both the allozyme work (Godt and Hamrick, 1999) and the molecular analysis (Neyland and

Merchant, 2006) linked the two varieties of *S. purpurea venosa* more closely to each other than to *S. purpurea purpurea*; and the three taxa diverge from each other by about as much as *S. rosea* diverges from the *S. purpurea* clade (Neyland and Merchant, 2006). Thus, either the three other subspecies/varieties of *S. purpurea* each should be raised to species status (as tentatively suggested by Neyland and Merchant, 2006), or they should be considered as a single species with broad geographic variability (as suggested by Gleason and Cronquist, 1991; Ellison *et al.*, 2004).

Rates of genetic change and new hypotheses arising from carnivorous plant genomics

As phylogenetic hypotheses have stabilized and as more gene sequence data have accrued for carnivorous plant species, comparative analyses of evolutionary rates of the different taxa have become possible. Initial attention has focused on the Lentibulariaceae because of the extreme specialization in trap morphology within the derived genera *Utricularia* and *Genlisea*. Jobson and Albert (2002) found that relative rates of nucleotide substitutions (based on RRTree computations: Robinson-Rachavi and Huchon, 2000) in seven loci (*trn*L/*mat*K intron, *trn*L second exon, *trn*L-F spacer, *rps*16 intron, *cox*1, and 5.8S RNA) occurred 4–14 times faster in *Utricularia* than in *Pinguicula*. Similarly, Müller *et al.* (2004) reported that *Genlisea* and *Utricularia* have relative rates of nucleotide substitutions (relative to an *Amborella*+Nymphaeales outgroup) in *mat*K that are 63% higher than they are in *Pinguicula*.[8] Müller *et al.* (2004) also found that substitution rates of *Genlisea* and *Utricularia* were higher than those of 292 other angiosperm taxa, and that four other carnivorous plant genera—*Pinguicula*, *Drosera*, *Nepenthes*, and *Sarracenia*—had substitution rates more in line with those of other angiosperms (Fig. 2).

Two hypotheses have been suggested to account for the high rates of molecular evolution observed in *Utricularia* and *Genlisea*. First, Jobson and Albert (2002) hypothesized that a single or small number of changes in regulatory genes could have led to rapid morphological evolution in *Utricularia*. In particular, Jobson *et al.* (2004) focused on the *cox*I subunit of cytochrome *c* oxidase. They showed that a unique motif of two contiguous cysteine residues in *cox*I has been subject to strong selection, and this novel structure of *cox*I in *Utricularia* could help to provide the additional metabolic energy required to reset *Utricularia* traps.

As Darwin and Croizat both noted, *Utricularia* shows little differentiation between stems, shoots, and leaves. Such 'relaxed' morphology is often observed in aquatic and epiphytic habitats, where neutral buoyancy (in the water) or other supporting structures (for epiphytes) obviate the need for structural tissues (such as large stems or wood). Thus, the combination of a unique molecular mutation in a key metabolic pathway and the relaxed morphological requirements of aquatic and epiphytic habitats has been hypothesized to be the driver of morphological diversity in this genus (Jobson *et al.*, 2004; Laakkonen *et al.*, 2006). We refer to this hypothesis as the 'energetics hypothesis'.

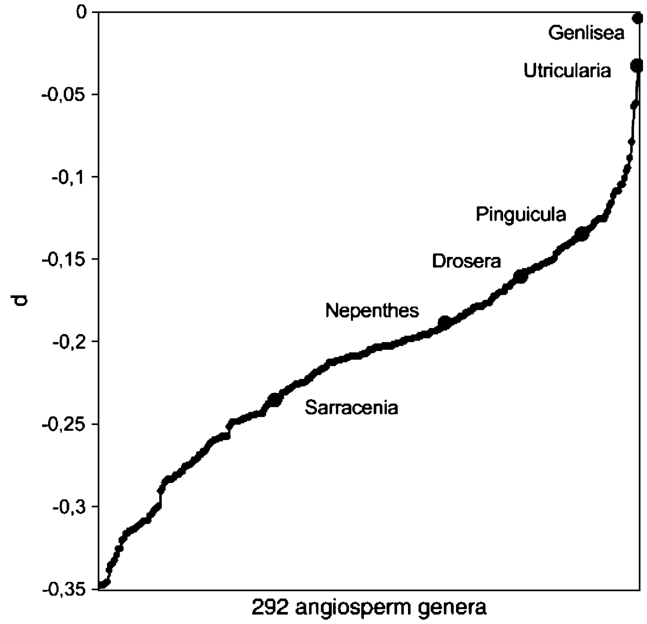

Fig. 2. Relative rates of gene substitution in carnivorous plant genera relative to the basal angiosperm (*Amborella*+Nymphaeales). Angiosperm taxa are arrayed on the *x*-axis from smallest to largest rates of *mat*K substitution rates. The relative substitution rate on the *y*-axis is calculated as the difference between *K*(*Genlisea*, outgroup)–*K*(other taxon, outgroup), where *K*(taxon, outgroup)=the maximum likelihood estimate of substitutions per site between the taxon and the outgroup (Müller, 2005). A rough estimate of the percentage difference in substitution rates between two carnivorous plant taxa can be found as $100 \times 1 - \frac{CP_1 - CP_2}{CP_1}$, where CP_i is the relative substitution rate of carnivorous plant species *i* (see text footnote 8 for caveats in using this estimator). Figure reprinted from Müller (2004) with permission of the author and the publisher, Georg Thieme Verlag KG.

Alternatively, Müller *et al.* (2004) pointed to the extreme specialization of the traps in *Genlisea* and *Utricularia* relative to the sticky leaves of *Pinguicula* and *Drosera* and the pitfalls of *Nepenthes* and *Sarracenia* as paralleling the differences in genetic substitution rates (Fig. 2). Like Jobson *et al.* (2004), Müller *et al.* (2004) suggested that high mutation rates in *Utricularia* and *Genlisea* are related to relaxed morphological constraints. However, Müller *et al.* (2004) further argued that morphological evolution in carnivorous plants was achievable because they can directly take up large biosynthetic building blocks, such as amino acids, peptides, and nucleotides, that the plants obtain from capturing and dissolving prey. Importantly, Müller *et al.* (2004) suggested that *Utricularia* and *Genlisea* have more predictable and frequent captures of prey in their habitats relative to the other carnivorous genera, and that there is a positive feedback between this reliable supply of prey and

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[8] This percentage comparison assumes similar molecular clocks and may be biased by using the basal angiosperm (*Amborella*+Nymphaeales) as the outgroup in the analysis (Kai Müller, personal communication to A Ellison, 5 March 2008).

further morphological evolution. We refer to this hypothesis as the 'predictable prey capture hypothesis'.

These two hypotheses were formulated for carnivorous Lentibulariaceae (*Genlisea* and *Utricularia* relative to *Pinguicula*), but the general pattern of complex traps being derived relative to simple (sticky-leaf) traps (Fig. 1) suggests that these hypotheses could apply across carnivorous plant lineages. Although the broader application of these hypotheses to other carnivorous plant lineages is necessarily speculative, testing between the energetics and predictable prey capture hypotheses nonetheless could provide further insights into factors driving the evolution of carnivorous plants. These analyses are the focus of the subsequent sections of this paper.

Pattern and process in prey capture by carnivorous plants

'*Now it would manifestly be a great disadvantage to the plant* [Dionaea muscipula] *to waste many days in remaining clasped over a minute insect, and several additional days or weeks in afterwards recovering its sensibility; inasmuch as a minute insect would afford but little nutriment. It would be far better for the plant to wait for a time until a moderately large insect was captured, and to allow all the little ones to escape; and this advantage is secured by the slowly intercrossing marginal spikes, which act like the large meshes of a fishing-net, allowing the small and useless fry to escape*.'
(*Insectivorous plants*, pp. 251–252).

The available phylogenetic data suggest that in all carnivorous lineages except perhaps the Sarraceniaceae/Roridulaceae clade (Fig. 1), complex traps (pitchers, eel traps, bladders) are derived relative to sticky-leaved, flypaper traps (Ellison and Gotelli, 2001). Müller *et al.* (2004) hypothesized that carnivorous genera with rapidly evolving genomes (*Genlisea* and *Utricularia*) have more predictable and frequent captures of prey than do genera with more slowly evolving genomes; by extension it could be hypothesized that, in general, carnivorous plants with more complex traps should have more predictable and frequent captures of prey than do those with relatively simple traps. Increases in predictability and frequency of prey capture could be achieved by evolving more elaborate mechanisms for attracting prey, by specializing on particular types of prey, or, as Darwin suggested, by specializing on particular (*e.g.,* large) sizes of prey. In all cases, one would expect that prey actually captured would not be a random sample of the available prey. Furthermore, when multiple species of carnivorous plants co-occur, one would predict, again following Darwin,[9] that interspecific competition would lead to specialization on particular kinds of prey.

The accumulated contents of carnivorous plant traps can provide an aggregate record of the prey that have been successfully 'sampled' by the plant. Over the past 80 years, many naturalists, botanists, and ecologists have gathered data on prey contents of carnivorous plants from around the world. Such samples can be used to begin to test the hypothesis that carnivorous plant genera differ in prey composition and to look for evidence of specialization in prey capture. Here these data are summarized and synthesized in a meta-analysis to test for differences in prey composition among carnivorous plant genera, and to look for evidence of specialization in prey capture.

The data

Prey capture data were gathered from 30 studies that were published (in the literature or in otherwise unpublished MSc and PhD theses) between 1923 and 2007. These studies encompass 87 records of prey capture for 46 species of carnivorous plants in eight genera: *Drosera* (13 species), *Dionaea* (one species), *Triphyophyllum* (one species), *Nepenthes* (11 species), *Pinguicula* (seven species), *Utricularia* (five species), *Sarracenia* (seven species), and *Brocchinia* (one species). The geographic scope of these data is similarly broad, encompassing all continents on which carnivorous plants occur. Each record (prey composition of a single plant taxon at a single locality) was treated as an independent observation, and no distinction was made in terms of within- and between-species variability within each plant genus. Most studies contained from dozens to thousands of individual prey items; the one record of *Drosera rotundifolia* measured by Judd (1969) in southwestern Ontario, Canada that contained only six individual prey items was excluded from the analysis. Using designations in the original publications, prey were classified into 43 taxonomic groups. For insects, these taxonomic groups were usually orders, although virtually all authors distinguished ants from other Hymenoptera, and this distinction was retained in the analysis. There were a few coarser classifications (e.g. 'Other insects', 'Mollusca'), but prey in these categories were very rare.

In the majority of the studies, the original data consisted of counts of individual prey, usually pooled from traps of several plants. Some studies of *Pinguicula* and other sticky-leaved plants recorded the number of prey per leaf area, whereas others summarized data as percentages of captures per trap or as numbers of individuals per trap. For the purposes of the present analyses, all of the observations were converted to the proportion of prey collected for each species within a study. Most carnivorous plants consume a wide range of prey; a notable documented exception is *Nepenthes albomarginata* Lobb ex Lindl., which, based on field observations (Kato *et al.*, 1993; Merbach *et al.*, 2002) and stable isotope analysis (Moran *et al.*, 2001), appears to prey almost exclusively on termites. Among other terrestrial carnivorous plants, captured prey is dominated by ants and

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[9] '*As species of the same genus have usually, though by no means invariably, some similarity in habits and constitution, and always in structure, the struggle will generally be more severe between species of the same genus, when they come into competition with each other, than species of distinct genera*.' [*The origin of species*, p. 64, 1996 Oxford University Press printing of the 2nd edition (1859)].

flies (Fig. 3), whereas captured prey of aquatic *Utricularia* spp. is dominated by Cladocera (mean=37% of prey) and cyclopoid copepods (mean=36% of prey).[10]

Do different carnivorous plant genera specialize on particular prey?

Methods of data analysis: The first question considered was whether there was any indication of specialization by different carnivorous plant genera. A specialist would be one whose prey consisted of many individuals of only a few prey taxon, whereas a generalist predator would have prey consisting of relatively few individuals spread among many different prey taxon. A useful index of specialization is Hurlbert's (1971) probability of an interspecific encounter (*PIE*):

$$PIE = \frac{N}{N-1} \times 1.0 - \sum_{i=1}^{S} (p_i)^2$$

in which S is the number of prey taxa, p_i is the proportion of prey taxon i in the sample, and N is the total number of individual prey items in the sample. *PIE* ranges from 0 to 1, and can be calculated for data measured in disparate units such as counts, percentages, or densities (Gotelli, 2008).

In this analysis, *PIE* has a simple and direct statistical interpretation: if an investigator randomly sampled two individual prey items from the same trap (or set of traps that are pooled for a species in a site), what are the chances that they represented two different prey taxa? A value of *PIE* close to 1 implies that the carnivorous plant genus was not a prey specialist because any two randomly sampled prey items would probably be from different prey taxa. In contrast, a value of *PIE* close to 0 implies specialization on a single prey taxon because any two randomly sampled prey items would probably be the same. Note that the value of *PIE* contains no information about the *identity* of the prey taxa, only the numbers of prey taxa and the relative distribution of individuals among them. Thus, two carnivorous plant genera might have identical values of *PIE*, but share no prey taxa in common.

In addition to *PIE*, the proportion of prey items represented by ants (Formicidae) and the proportion represented by flies and mosquitoes (Diptera), two of the most important prey taxa for most carnivorous plants, were also analysed. *PIE* and the proportion of ants and flies were arcsine-square root transformed prior to analysis (Gotelli and Ellison 2004). A one-way ANOVA was used to compare the response variables among the different genera of carnivorous plants, without distinguishing among within- and between-species variation within a genus. Statistical analyses were conducted using R version 2.6.1.[11]

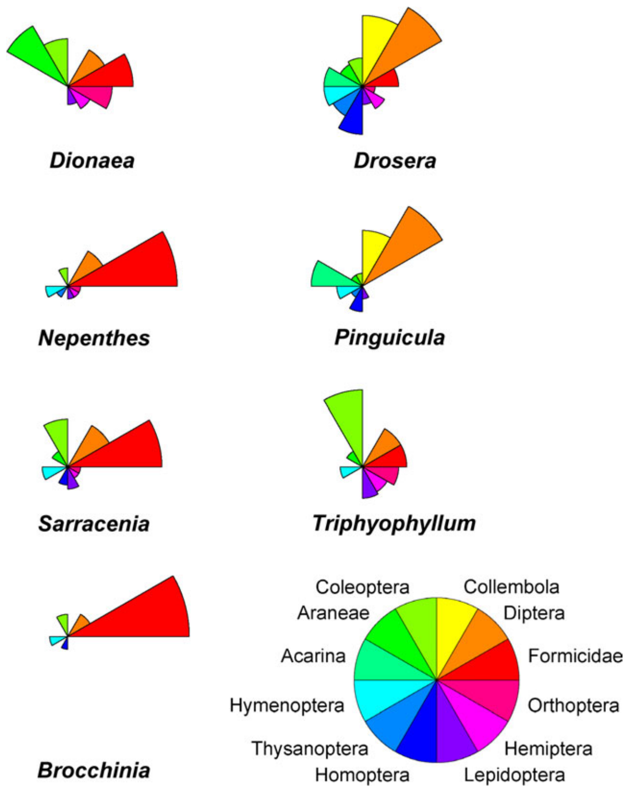

Fig. 3. Prey spectra of terrestrial carnivorous plant genera. The slices of each 'star' plot are scaled to the average proportion of each prey taxon (order except for ants—family Formicidae). Only the 12 most common prey orders are shown. The key to the colours is given in the lower right of the figure.

Results: The analysis of prey capture spectra using *PIE* suggests that different carnivorous plant genera differ significantly in their relative degree of taxonomic specialization, at least at the ordinal level of prey diversity ($F_{7,79}$=2.03, P=0.009). The analysis included a low outlier for *Drosera erythrorhiza* Lindl. (Watson *et al.*, 1982) in which 10 826 of 10 911 prey items counted (99.2%) were Collembola (*PIE*=0.015), and only one sample for the genus *Triphyophyllum* (Green *et al.*, 1979), the most generalist taxa measured (*PIE*=0.802). However, removal of these two taxa from the analysis did not alter the qualitative conclusion; *PIE* still differed among genera ($F_{6,78}$=3.84, P=0.002). The most specialized carnivorous plant genera in the analysis were the pitcher plants *Brocchinia* (*PIE*=0.189), *Nepenthes* (*PIE*=0.452), and *Sarracenia* (*PIE*=0.491), and the most generalized genera were *Triphyophyllum* (*PIE*=0.802) and *Utricularia* (*PIE*=0.713; Fig. 4A).

Differences among genera in the capture of particular prey taxa were also very strong. Genera differed dramatically in the proportion of ants and flies captured (ants, $F_{7,79}$=36.01, $P < 10^{-15}$; flies, $F_{7,79}$=8.29, P=1.5$\times 10^{-7}$). The pitcher plants *Brocchinia*, *Nepenthes*, and *Sarracenia* had the highest proportions of ants in their diets (90, 73, and 55%, respectively), reflecting their higher

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[10] The raw data and complete list of studies from which the data were drawn are available as data set HF-111 from the Harvard Forest data archive: http://harvardforest.fas.harvard.edu/data/p11/hf111/hf111.html.

[11] http://www.r-project.org/

specialization values (low *PIE*). Captures of ants were much less frequent for the sticky traps of *Drosera* (3.4%) and *Pinguicula* (0.5%), and for the aquatic, bladder-trapping *Utricularia* (0%). Flies predominated in the diets of *Drosera* (44%) and *Pinguicula* (52%) (Fig. 4C), but were uncommon prey for *Utricularia* (3%) and *Sarracenia* (14%). A notable outlier was a single study of *Sarracenia purpurea* by Judd (1959), in which 690 of 1095 prey (63%) were Diptera (not identified to suborders or families by Judd, 1959).

Collectively, these results illustrate that different genera of carnivorous plants do indeed selectively capture different prey taxa. In some cases, the differences simply reflect habitat differences: ants and adult flies are unavailable to aquatic *Utricularia* or terrestrial *Utricularia* with subterranean traps. However, the statistical significance of differences in captures of flies and ants by pitchers (*Sarracenia* and *Nepenthes*) and sticky traps (*Drosera* and *Pinguicula*) is not dependent on the inclusion of *Utricularia* in the analysis, but rather do appear to reflect the different morphological specializations in these genera.

Are they really specialists? Comparisons of captured prey and available prey

Although the frequencies of prey collected in carnivorous plant traps are rarely equiprobable, a predominance of a single prey taxon, such as ants, need not indicate specialization because some taxa simply may be more abundant than others. In five published studies (Watson *et al.*, 1982; Zamora 1990, 1995; Antor and García, 1994; Harms 1999), the investigators not only collected prey from carnivorous plants but also used passive traps in the habitat to sample available prey. Watson *et al.* (1982) used life-sized and -shaped cardboard models of *Drosera erythrorhiza* coated with Hyvis 10 (a tacky inert compound based on polymerized butane) to assess prey available to *Drosera erythrorhiza* in the field. Zamora (1990) used life-sized and -shaped paper or wooden models to assess prey available to *Pinguicula nevadense* (Lindbg.) and *P. vallisneriifolia* Webb., respectively. Antor and García (1994) used sticky cards in one year (1990) and sticky, life-sized, leaf-shaped models in another year (1991) to assess prey available to *Pinguicula longifolia* Ram. ex. DC ssp. *longifolia*. Harms (1999) used grab samples to determine prey available to *Utricularia intermedia* Hayne, *U. minor* L. and *U. vulgaris* L.

The appropriate null hypothesis is that the carnivorous plant is a passive trap: the relative abundance of the different prey categories does not differ from the relative abundance of prey in the environment. The alternative hypothesis is that some prey taxa are selectively attracted or captured by the plant. Under the alternative hypothesis, there should be a significant difference in the relative proportions of prey caught and the relative proportions of prey available.

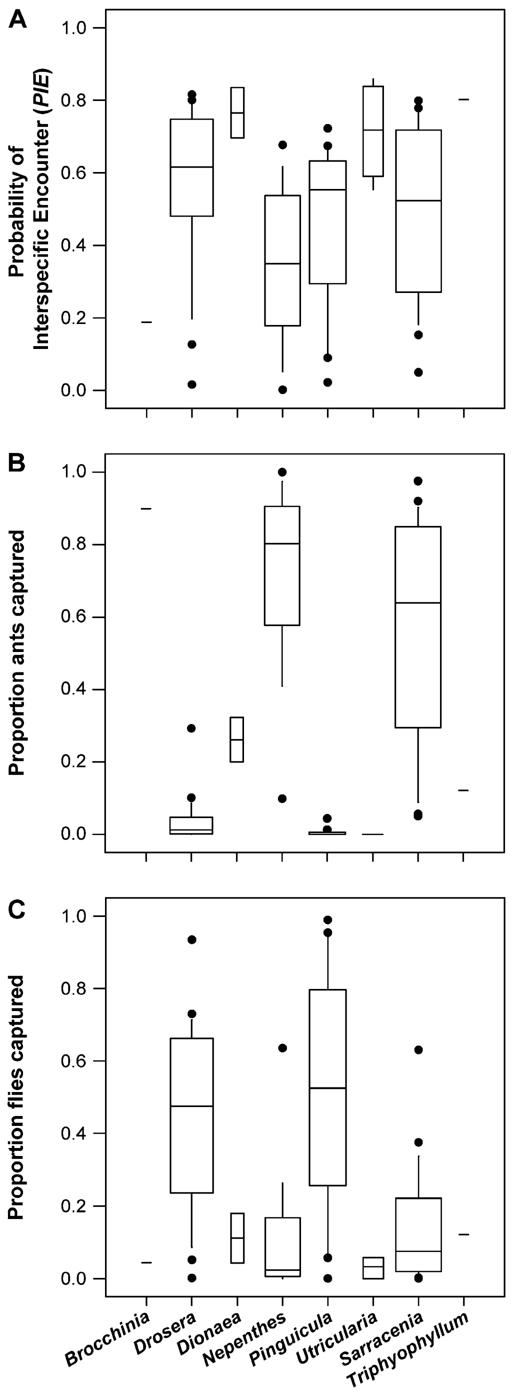

Fig. 4. Results of the analysis of prey capture by seven carnivorous plant genera. (A) Probability of interspecific encounter (*PIE*), or the probability that two prey items drawn at random from a trap are from different taxa. High values of *PIE* indicate less specialization on particular prey orders than do low values of *PIE*. (B) Proportion of ants in the prey captured by each genus. (C) Proportion of flies in the prey captured by each genus. For each variable, boxes illustrate the median (horizontal line), upper, and lower quartiles (limits of the box), upper and lower deciles (limits of the vertical lines), and extreme values (individual points). The width of the box is proportional to the square-root of the sample size. Note that for *Brocchinia* and *Triphyophyllum* the sample size is only equal to 1 each, so there is no distribution from which to draw a box. The values for those two species are indicated by a single horizontal line.

Methods of data analysis: To quantify the similarity of the prey captured by plants to the prey collected in passive traps, we used the Jaccard index, J (Jaccard, 1901):

$$J = \frac{a}{a + b + c}$$

in which a is the number of shared species between two samples (plant traps and passive traps), and b and c are the number of unique species in each of the two samples. The Jaccard index was modified recently by Chao *et al.* (2005) to incorporate relative abundance and to account statistically for undetected shared species that might be present, but that did not occur in the samples. Like J, the Chao–Jaccard (or J_{Chao}) index ranges from 0.0 (no shared to species) to 1.0 (all species shared). J_{Chao} was calculated using the EstimateS software package (Colwell 2005); 1000 bootstrap replications were used to estimate parametric 95% confidence intervals for the point-estimates of J_{Chao}.

Results: In all cases, J_{Chao} was close to 1.0, indicating a very high similarity between prey captured by the plants and prey captured by inert traps or taken in a grab sample (Fig. 5). For each pairwise comparison (captures by plants versus prey available), the confidence interval bracketed 1.0 (Fig. 5), so the null hypothesis that these carnivorous plants were behaving as passive sampling traps could not be rejected. The occasional observations of mass captures of locally abundant insects (Oliver, 1944; Evans *et al.*, 2002) are in line with this conclusion, as is Folkerts's (1992) observation that the majority of ants captured by *Sarracenia minor*, *S. flava*, and *S. purpurea* in the southeast USA are the very abundant, non-native fire ant *Solenopsis invicta* Buren. These results do not necessarily imply that carnivorous plants are not 'specialized' in their diets. Rather, the observed degree of specialization is similar to that of a simple passive trap of similar size and shape. Unique coloration (e.g. Schaefer and Ruxton, 2008) or chemical attractants (e.g. Jaffe *et al.*, 1995; Moran, 1996) of some carnivorous plant genera do not appear to contribute much to the composition of captured prey. Rather, selectivity of a trap can be understood largely based on the simple geometry of its size, shape, and orientation. As a caveat, note that the majority of these results are for genera (*Pinguicula*, *Sarracenia*) that have traps that have relatively passive mechanisms for attracting prey.

Niche overlap among co-occurring carnivorous plants

Darwin (1859) speculated that competition between species is more severe within a genus. If this is true, co-occurring congeners should partition important ecological resources, such as space, food, or time (Schoener, 1974). Such partitioning should be reflected in relatively low niche overlap between pairs of species. For carnivorous plants, this question can be phrased as whether co-occurring congeners show any evidence of partitioning or specialization on different categories of prey. Folkerts (1992) provided prey utilization data on five *Sarracenia* species that co-occur in the southeastern USA. Porch (1989), Thum (1986), van Achterberg (1973), and Verbeek and Boasson

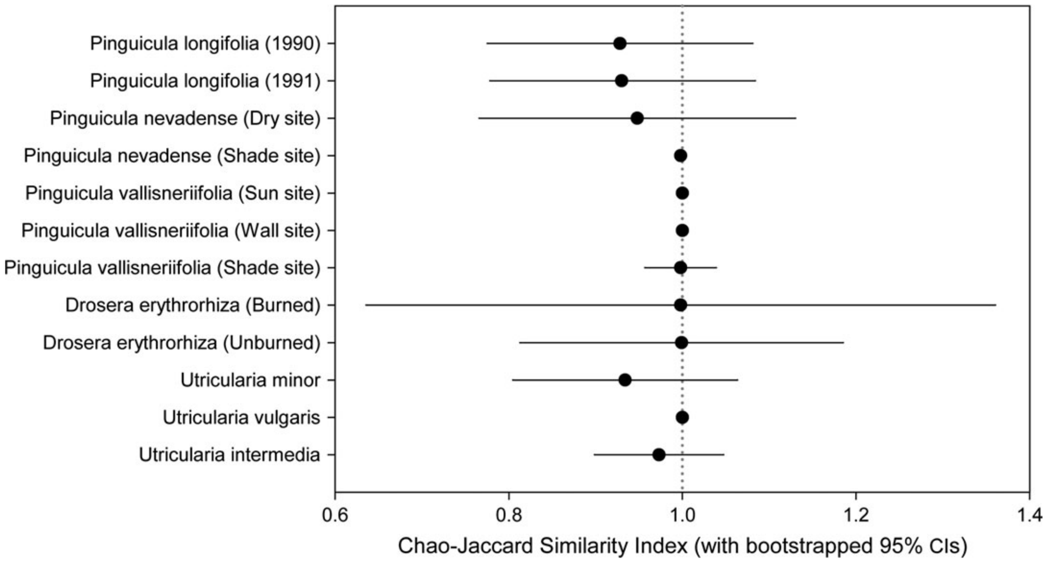

Fig. 5. Results of the similarity analysis for four studies in which prey abundances were measured in carnivorous plants and in artificial traps in, or grab samples from, the same habitat. Prey taxon categories used were the same as in the original study, and microhabitat differences were retained in separate analyses. The value plotted is the Chao–Jaccard abundance-based similarity index J_{Chao} adjusted for unobserved taxa (Chao *et al.*, 2005); 95% parametric confidence intervals are derived from 1000 bootstrap samples. If the interval includes 1.0 (grey vertical dotted line), then the J_{Chao} value does not differ from that expected given the null hypothesis that the distribution of prey captures by the plants is not different from that in the traps.

(1993) provided data on co-occurring species of *Drosera* in, respectively, the southeastern USA, Germany, The Netherlands, and southwestern Australia. These same data were part of the prey utilization analyses described above, but here these data are isolated for more detailed analysis of niche overlap.

Methods of data analysis: How much niche overlap would be expected by chance, in the absence of any competition? The EcoSim software (Gotelli and Entsminger, 2007) was used to quantify niche overlap using Pianka's (1973) index of overlap in resource use:

$$O_{12} = \frac{\sum_{i=1}^{n} p_{1i} p_{2i}}{\sqrt{\sum_{i=1}^{n} \left(p_{1i}^{2}\right)\left(p_{2i}^{2}\right)}}$$

where p_{1i} and p_{2i} are the proportion of prey used by species 1 and species 2, respectively. O_{12} ranges from 0.0 (no shared prey) to 1.0 (identical prey utilization), and is calculated for each pair of species in an assemblage. For assemblages with more than two species, the average of all pairwise values of O_{ij} was calculated, where i and j index each species. Null model analysis (Gotelli and Graves, 1996) is a statistical method for randomizing ecological data to see whether patterns are more extreme than expected by chance. Thus, to determine whether our average value of O_{ij} differed from that expected under the null hypothesis that the niche overlap reflected only random interactions, the software 'reshuffled' the observed utilization values to generate expected overlap in a null community that was unstructured by competition. We used the 'RA-3' algorithm in EcoSim; it retains observed niche breadths within a species, but randomizes the particular prey categories that were used. This algorithm has good statistical properties (Winemiller and Pianka, 1990) and has been used in many other studies of niche overlap (reviewed in Gotelli and Graves, 1996).

Results: For the most species-rich assemblages [five species of *Sarracenia* (Folkerts, 1992) and five species of *Drosera* (Verbeek and Boasson, 1993)], niche segregation was not observed (Table 1). In the *Sarracenia* assemblage, the highest observed niche overlap was between *Sarracenia flava* and *Sarracenia purpurea* (overlap =0.99), and the lowest overlap was between *Sarracenia leucophylla* and *Sarracenia psittacina* (overlap=0.26). The average overlap for all 10 unique pairs was 0.637 (Table 1), which is about midway between complete segregation (0.0) and complete overlap (1.0). However, in the simulated 'null assemblages', the average niche overlap was only 0.197, and the observed overlap in the real *Sarracenia* community was larger than that found in 998 out of 1000 simulation trials. Thus, the real five-species *Sarracenia* assemblage (and all pairwise comparisons) showed significantly more niche overlap than expected by chance (P=0.002), directly contradicting the hypothesis of niche segregation in sympatry.

Similar results were found for five species of co-occurring *Drosera* at the Fitzgerald River site in southwestern Australia (Verbeek and Boasson, 1993). Observed pairwise niche overlaps ranged from 0.65 (*D. menziesii* versus *D. paleacea*) to 0.92 (*D. glanduligera* versus *D. paleacea*). The average overlap for the pooled assemblage was 0.534, >96% of the 1000 simulations (Table 1). This result again suggested significantly more niche overlap than expected by chance (P=0.04).

The high overlap in both cases was clear from an inspection of the raw data. Except for *S. leucophylla*, which favoured Diptera, all co-occurring *Sarracenia* primarily captured ants (Folkerts 1992). The relatively modest morphological differences between co-existing species of *Sarracenia* did not translate into appreciable differences in composition of prey captured, suggesting that competition for limiting resources was not regulating species co-existence. Similarly, among co-occurring *Drosera* at Fitzgerald River, prey composition was dominated by Collembola, Homoptera, and Diptera (Verbeek and Boasson, 1993).

No evidence of interspecific competition was found among the *Sarracenia* assemblages composed of two or three species (Folkerts, 1992), or among the two- or three-species assemblages of *Drosera* in the southeastern USA, Germany, The Netherlands, and at Murdoch University (van Achterberg, 1973; Thum, 1986; Porch, 1989; Verbeek and Boasson, 1993) (Table 1). In all cases, the observed niche overlap was significantly greater than expected (Table 1), which was the opposite of the pattern that would be predicted by competitive segregation of prey.

The two caveats to these results are that prey were identified only to orders and that the analysis assumed that all prey categories were equally abundant. Finer taxonomic resolution of prey could reveal less overlap among prey. If the assumption of equal abundance of prey categories is violated, the analytic method used tends to overestimate the amount of niche overlap because the results are dominated by common taxa. In contrast, when independent estimates of prey abundance are available, values of prey actually used can be rescaled to downweight the importance of common prey (for further discussion of statistical issues associated with measures of niche overlap, see Gotelli and Graves, 1996). Unfortunately, the studies used here for assessing niche overlap did not include independent estimates of prey availability.

Rates and efficiency of prey capture by pitcher plants and bladderworts

'*From an examination which I made to-day on a leaf of the* S. flava *about half grown, I am led to suspect that the surface, where the fly stands so unsteadily, and from which it finally drops down to the bottom of the tube, is either covered with an impalpable and loose powder, or that the extremely attenuated pubescence is loose. This surface gives to the touch*

Table 1. Summary of null model analysis of niche overlap in prey utilization by congeneric carnivorous plants

Each row gives a different study and the number of co-existing congeneric species. Observed is the observed average pairwise niche overlap. Expected is the mean value of average pairwise niche overlap in 1000 randomizations of the resource utilization data. The *P*-value is the upper tail probability of finding the observed pattern if the data were drawn from the null distribution.

			Niche overlap		
Genus	**Site**	**Species**	**Observed**	**Expected**	***P***
Sarracenia[a]	Okaloosa County, Florida, USA	5	0.637	0.197	0.002
Sarracenia[b]	Santa Rosa County, Florida, USA	2	0.996	0.128	0.038
Sarracenia[c]	Turner County, Georgia, USA	3	0.634	0.235	0.013
Sarracenia[d]	Brunswick County, North Carolina, USA	3	0.975	0.128	0.001
Drosera[e]	Baldwin County, Alabama, USA	3	0.880	0.241	0.001
Drosera[f]	Santa Rosa County, Florida, USA	2	0.868	0.256	0.001
Drosera[g]	Walton County, Florida, USA	2	0.738	0.205	0.031
Drosera[h]	Chiemsee, S. Bavaria, Germany	2	0.708	0.226	0.045
Drosera[i]	Eastern Netherlands	3	0.796	0.168	0.001
Drosera[j]	Fitzgerald River, SW Australia	5	0.534	0.486	0.043
Drosera[k]	Murdoch University, SW Australia	3	0.801	0.614	0.001

[a] *S. flava*, *S. leucophylla*, *S. rubra*, *S. purpurea*, *S. psittacina*.
[b] *S. flava*, *S. psittacina*.
[c] *S. flava*, *S. minor*, *S. psittacina*;
[d] *S. flava*, *S. purpurea*, *S. rubra*;
[e] *D. filiformis* Raf. var. *tracyi* (Macf. ex Diels) Diels, *D. intermedia* Hayne, *D. capillaris* Poir.
[f] *D. intermedia*, *D. capillaris*
[g] *D. filiformis* var. *tracyi*, *D. capillaris*.
[h] *D. rotundifolia* L., *D. intermedia*
[i] D. rotundifolia, *D. intermedia*, *D. anglica* Huds.
[j] *D. menziesii* R.Br. ex. DC, *D. drummondii* Lehm. [= *D. barbigera* Planch.], *D. glanduligera* Lehm., *D. paleacea* DC, *D. erythrorhiza* Lindl.
[k] *D. pallida* Lindl., *D. stolonifera* Endl., *D. menziesii*.

the sensation of the most perfect smoothness. The use of a good microscope will determine this point.'

(Macbride, 1818: 52)

The statistical analysis of the prey spectra (Figs 3 and 4) revealed that at relatively coarse taxonomic resolution (genera of plants, orders of prey), carnivorous plants act as opportunistic sit-and-wait predators, capturing prey in proportion to their availability (Fig. 5), and rarely competing with co-occurring congeners (Table 1). Additional evidence from several species of pitcher plants and bladderworts, however, suggests that these taxa do have some adaptations to increase the rates and efficiency of capture of specific prey items, at least under certain environmental conditions.

Detailed observations of *Sarracenia purpurea* using video cameras (Newell and Nastase, 1998) and of *Darlingtonia californica* Torrey using multiple observers (Dixon *et al.*, 2005) found that fewer than 2% of ants visiting *S. purpurea* or wasps visiting *D. californica* were successfully captured by the plants. These observations were made under sunny and relatively dry field conditions. Similar rates of ant captures by *Nepenthes rafflesiana* Jack. (Bohn and Federle, 2004; Bauer *et al.*, 2008) were observed under sunny and dry conditions. However, when the pitcher lip (peristome) of *N. rafflesiana* was wetted by rain, condensation, or secretion of nectar by the extrafloral nectaries lining the peristome, it became, like that of Macbride's (1818) *Sarracenia flava*, a nearly frictionless surface. Foraging ants that contacted the wetted peristome 'aquaplaned' and slipped into the pitcher in very large numbers (Bauer *et al.*, 2008); capture rates by *N. rafflesiana* under humid or wet conditions often reached 100% of foraging ants (Bauer *et al.*, 2008). As the other pitcher plants—*Cephalotus* and all the Sarraceniaceae—also have extrafloral nectaries ringing the peristome (Vogel, 1998; Płachno *et al.*, 2007), it is not unreasonable to hypothesize that these taxa also have peristomes that could be wetted to increase prey capture rates. Hopefully, we will not have to wait another 200 years for a good microscopist to test this hypothesis for the other groups of pitcher plants!

Adaptations to enhance prey capture by bladderworts have also been postulated. The suction trap (described in detail by Lloyd, 1942; Guisande *et al.*, 2007) of *Utricularia* is a highly specialized structure that is activated when a passing animal touches a trigger hair (Lloyd, 1942 illustrated it as a 'better mousetrap'). When triggered, the trap opens inward, the prey is sucked in to the water-filled trap, the door closes, and the prey is digested and absorbed. Finally, the water is pumped out and the trap is reset. This energy-intensive process appears to be facilitated by the evolutionary change in *cox*I described above (Jobson *et al.*, 2004).

Beginning with Darwin (1875) investigators have hypothesized that periphyton growing on the hairs and bristles surrounding the trap attract zooplankton that graze their way down to the trigger hairs. This hypothesis was verified experimentally for *U. vulgaris* by Meyers and Strickler (1979) and for *U. foliosa* L. (Díaz-Olarte *et al.*, 2007). However, the presence and species composition of periphyton on hairs and bristles of *Utricularia* appear to depend on local environmental conditions (Díaz-Olarte *et al.*, 2007), not on a direct facilitation of periphyton growth by *Utricularia* (cf. Ulanowicz, 1995). Determining causal relationships between environmental conditions, morphological structures, and prey capture rates and efficiency by *Utricularia* remains an active area of research.

Do fly-traps really catch only large prey?

> [Of 14 *Dionaea* leaves sent to Darwin by William M. Canby], '*[f]our of these had caught rather small insects, viz. three of them ants, and the fourth a rather small fly, but the other ten had all caught large insects, namely five elaters, two chrysomelas, a curculio, a thick and broad spider, and a scolopendra....But what most concerns us is the size of the ten larger insects. Their average length from head to tail was 0.256 of an inch, the lobes of the leaves being on average 0.53 of an inch in length, so that the insects were very nearly half as long as the leaves within which they were enclosed. Only a few of these leaves, therefore, had wasted their powers by capturing small prey, though it is probable that many small insects had crawled over them and been caught, but had then escaped through the bars.*'
>
> (*Insectivorous plants*, p. 252)

Our analyses suggest that carnivorous plants are not selective predators with respect to prey composition. However, is there any evidence that, as Darwin hypothesized, they capture only relatively large prey? Here the data are limited to two small collections of prey contents of the Venus' fly-trap, *Dionaea muscipula* (Darwin, 1875; Jones, 1923). In both cases, some assumptions had to be made to reconstruct the data and test the hypothesis that *Dionaea* prey are unusually large.

Darwin (1875) provided the average size of only the 10 largest prey (0.256 inch=6.5 mm); the sizes of the four smaller prey items (three ants and a fly) were not reported. Jones (1923) gave a bit more detail for 50 dissected *Dionaea* leaves, each with one prey item: of the 50 prey items recovered, 'only one was less than 5 mm in length, and only seven, less than 6 mm; ten were 10mm or more in length, with a maximum of 30 mm' (Jones 1923: 593). Jones also reported that the average length of the prey was 8.6 mm, and the normal minimum observed was 6.4 mm (approximately the average length of Darwin's subsample).

Based on Jones's (1923) reported size intervals, prey size distributions were simulated using R version 2.6.1 as being drawn from a mixture of three normal distributions [$\mathcal{N}(5.5, 0.25)$, $\mathcal{N}(20, 5)$, and $\mathcal{N}(8, 1)$][12], with sample sizes respectively equal to 7 ('less than 6 mm', but more than 5 mm), 10 ('10mm or more in length, with a maximum of 30 mm'), and 32 (the remainder, unenumerated by Jones, but by inference being between 6 and 10 mm long), plus one outlier (4 mm), corresponding to the one 'less than 5 mm in length'). This mixture gave a skewed distribution of prey sizes with mean=9.3 mm, and a median=7.6 mm. Darwin's distribution of prey was similarly simulated as a mixture of two normals: $\mathcal{N}(6.5, 1)$ and $\mathcal{N}(5.5, 0.25)$ with sample sizes of 10 and 4, respectively. Because Darwin gave no information on the size of the four small prey items, the sample of small prey sizes in this mixture was drawn from the same distribution as Jones's small prey. This mixture gave a skewed distribution of prey sizes with mean=6.0 mm and a median=5.8 mm. The two distributions are shown in Fig. 6.

The relevant question is whether either of these data sets support the hypothesis that the average size of prey that *Dionaea* captures is at least half the length of a 13.5 mm leaf (Darwin's '0.53 of an inch'). A plausible way to determine this is to create replicate bootstrapped samples (i.e. with replacement) of the available data and use these bootstrapped samples to estimate the population mean and confidence intervals (Efron, 1982).

The `sample` function in R was used to create 10 000 bootstrapped samples of both Darwin's and Jones's prey size data. The estimated mean of the small population from which Darwin drew his sample was 6 mm (95% CI=5.70–6.38), which fails to support the hypothesis that *Dionaea* catches prey that is on average half as large as the trap (6.75 mm). In contrast, the estimated population mean of Jones's larger sample was 9.3 mm (95% CI=7.92–10.86), a result that is more in line with Darwin's expectation.

What do they do with all that prey? The energetics of botanical carnivory

> '*Ordinary plants…procure the requisite inorganic elements from the soil by means of their roots....[T]here is a class of plants which digest and afterwards absorb the animal matter, namely, all the* Droseraceae, Pinguicula, *and, as discovered by Dr. Hooker*, Nepenthes.'
>
> (*Insectivorous plants*, p. 365)

Based on his detailed observations of feeding behaviour and nutrient absorption, Darwin discussed *how* carnivorous structures might have evolved in plants. Later authors (e.g. Lloyd, 1942; Juniper *et al.*, 1989) generally followed his lead. Little attention was paid to *why* botanical carnivory might evolve until Givnish *et al.* (1984) proposed a cost–benefit model to explain why carnivorous plants are most common in habitats that are bright and wet but very low in nutrients. Givnish *et al.*'s (1984) model postulated a trade-off between the nutrients gained by capturing animals and the energy foregone by constructing photosynthetically inefficient traps instead of leaves. Givnish *et al.* (1984) asserted that carnivory would be expected to evolve if the increased nutrients provided by carnivory gave plants possessing carnivorous structure an energetic advantage relative to co-occurring non-carnivorous plants. This model was elaborated by Benzing (2000), who additionally

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[12] The notation $\mathcal{N}(\mu, \sigma)$ means a normal distribution with mean = μ and standard deviation = σ. We used the R function `rnorm(...)` to generate our size distributions.

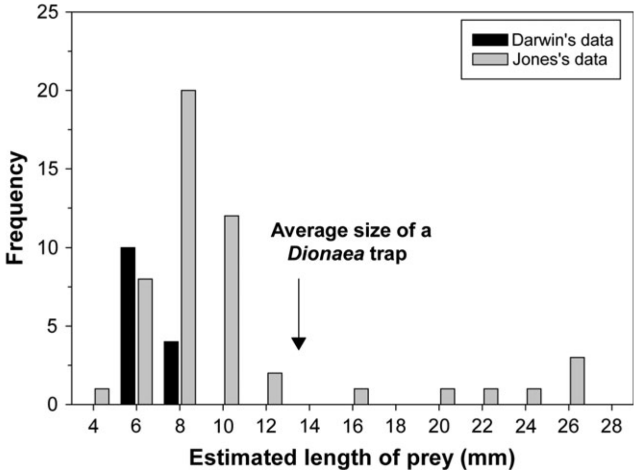

Fig. 6. Simulated frequency distributions of sizes of prey captured by the Venus' fly-trap, *Dionaea muscipula*, described by Darwin (1875; black bars) and Jones (1923; grey bars). The arrow indicates the average size of the *Dionaea* traps studied by Darwin (Jones did not report trap size).

considered decaying litter as a nutrient source and a third axis of selection. Both models were initially derived from studies of carnivorous bromeliads, but the cost–benefit framework has been used to interpret results from a wide range of observational and experimental studies on many carnivorous plant species (reviewed by Ellison and Gotelli, 2001; Ellison, 2006).

The benefits of carnivory

Givnish *et al.* (1984) identified three ways in which nutrients acquired through carnivory could result in energetic benefits to the plants. First, photosynthesis could increase with increasing nutrient uptake (following prey capture and digestion). This photosynthetic benefit could be realized through either an increase in the total mass of leaves the plant can support or an increased A_{mass}. Secondly, the excess nutrients derived from carnivory could be disproportionately allocated to reproduction. This allocation to reproduction should be measurable either as a positive relationship between prey captured and seeds produced or as an increase in nutrient content within the seeds. Thirdly, if carnivorous plants could extract carbon from prey, they could bypass photosynthesis as a means of producing sugars. This last benefit could be most important for aquatic carnivorous plants, as CO_2 used for photosynthesis is often limiting because it must be obtained by diffusion from the surrounding water (Adamec, 1997*a*, 1997*b*, 2006).

Most studies on the benefits of carnivory have found that plants significantly increase growth (in terms of leaf mass or total biomass) in response to prey additions (see Table 1 of Ellison, 2006). However, detailed measurements of photosynthesis of carnivorous plants in response to prey or nutrient additions—the primary measure of the first hypothesized benefit of carnivory—have generated more equivocal results. Méndez and Karlsson (1999) reported no significant increase in photosynthetic rates of *Pinguicula villosa* L., *P. vulgaris* L., or *Drosera rotundifolia* when they were provided supplemental prey. Adamec (2008) found that the photosynthetic rate of *Aldrovanda vesiculosa* increased following prey additions, but that of *Utricularia australis* decreased following prey additions. However, for both species, supplemental prey caused an increase in growth rates (Adamec, 2008). Wakefield *et al.* (2005) also reported no significant change in photosynthetic rates of *Sarracenia purpurea* pitchers fed additional prey in a field study, although tissue N and P concentrations did increase with feeding level. Nutrient storage in new *Sarracenia* pitchers (Butler and Ellison, 2007) or reproductive structures (see below) are alternative sinks for excess nutrients derived from prey captured by existing pitchers. For example, in a greenhouse study of prey addition to 10 species of *Sarracenia*, A_{mass} increased in new pitchers, and photosystem II stress (as measured by fluorescence) decreased with prey additions (Farnsworth and Ellison, 2008).

The second postulated benefit of carnivory has also been demonstrated. Temperate-zone *Pinguicula* species, which exhibit reproductive pre-formation (buds set in year *y* flower and produce seeds in year *y*+1; Worley and Harder, 1999), increased vegetative reproduction in the year of prey additions and also increased sexual reproduction in subsequent years (Thorén and Karlsson, 1998; Worley and Harder, 1999). In *P. vallisneriifolia*, neither flower set nor fruit set changed with prey additions, but seed set (measured as seed:ovule ratio) did increase (Zamora *et al.*, 1997). A similar increase in seed:ovule ratio in response to prey availability and inorganic nutrient addition was observed in *Sarracenia purpurea* (Ne'eman *et al.*, 2006), which also makes pre-formed buds (Shreve, 1906). Three other *Pinguicula* species (*P. alpina*, *P. villosa*, and *P. vulgaris*) all preferentially allocated nitrogen to reproductive structures (Eckstein and Karlsson, 2001). Both fruit set and seed set of *Drosera intermedia* and *D. rotundifolia* were positively correlated with prey captured (Thum, 1989; Stewart and Nilsen, 1992). Experimental prey additions subsequently confirmed these correlative results (Thum, 1988).

In summary, increases in plant growth, nutrient storage, and reproduction in response to increased prey have been documented in a number of carnivorous plant species, although evidence for elevated photosynthetic rates is weak. To date, there is only scant evidence for Givnish *et al.*'s (1984) third prediction, that of heterotrophic uptake of C from prey. Fabian-Galan and Savageanu (1968) found that ^{14}C from labelled *Daphnia* fed to both *Aldrovanda vesiculosa* and *Drosera capensis* L. was incorporated into leaf and stem tissues and into new growing tips of these carnivorous plants. Similarly, *Drosera erythrorhiza* stored ^{14}C from labelled flies in new growth (Dixon *et al.*, 1980). Additional evidence for facultative heterotrophy in carnivorous plants is most likely to be found in aquatic carnivorous plants (Adamec, 1997*a*, 1997*b*, 2006), as dissolved CO_2 can limit photosynthetic rates in submerged plants.

The costs of carnivory

The costs of carnivory have been assessed much less frequently than the benefits, perhaps because measuring energy foregone is more difficult than measuring increased growth, photosynthetic rates, or seed set. However, the existing measurements do suggest that the costs can be substantial. Among carnivorous plants with flypaper traps, carbon and nutrients (in proteins) must be allocated to construction of specialized leaf glands, sticky mucilage, and digestive enzymes. Pate (unpublished data, as cited in Pate, 1986, p. 320) reported that Australian *Drosera* spp. allocated 3–6% of net photosynthate to the production of mucilage for leaf glands. In shaded conditions when light levels fell well below photosynthetic saturation, *Pinguicula vallisneriifolia* reduced its mucilage production, presumably because it lacked sufficient carbon (Zamora *et al.*, 1998). At the opposite extreme, when nutrients were added to the soil, *Drosera rotundifolia* reduced its mucus gland production (Thorén *et al.*, 2003). This result was attributable to the avoidance of the costs of carnivory when nutrients were obtained at a lower carbon cost.

Similar plasticity has been observed in *Utricularia* spp. and *Sarracenia* spp. When prey or dissolved nutrients were plentiful, the number of carnivorous bladders declined significantly in *U. macrorhiza* Le Conte (Knight and Frost, 1991), *U. vulgaris* (Friday, 1992), and *U. foliosa* (Guisande *et al.*, 2000, 2004). Bladder traps are photosynthetically inefficient, and Knight (1992) calculated that *U. macrorhiza* of a given mass without bladders would grow 1.2–4.7× faster than *U. macrorhiza* of the same mass with bladders. Likewise, *Sarracenia purpurea* produced non-carnivorous leaves (phyllodia) when inorganic nutrients were added to levels comparable with atmospheric inputs from anthropogenic sources, and these phyllodia photosynthesized ~25% faster than did carnivorous pitchers (Ellison and Gotelli, 2002). Similar results were obtained for *S. purpurea* and eight other species of *Sarracenia* fed supplemental prey (Farnsworth and Ellison, 2008). The related *Darlingtonia californica* had absolute levels of A_{mass} of carnivorous plants that were 30–50% lower than predicted from scaling relationships between leaf nitrogen content and A_{mass} of non-carnivorous plants (Ellison and Farnsworth, 2005), and similar departures from the universal spectrum of leaf traits have been observed for other species of *Sarracenia* (Farnsworth and Ellison, 2008).

Photosystems of carnivorous plants do appear to be nutrient limited. Fluorescence measurements of greenhouse-grown *Sarracenia* species suggested significant 'stress' of photosystem II at low levels of prey capture, and this stress was alleviated by prey additions (Farnsworth and Ellison, 2008). Observations of spectral reflectance also implied low chlorophyll content and similar photosystem stress in *Nepenthes rafflesiana* in the field (Moran and Moran, 1998). Overall photosynthetic nitrogen use efficiency (μmol CO_2 mol N s^{-1}; Aerts and Chapin, 2000) is 50% lower for carnivorous plants than for non-carnivorous plants (P=1.3×10^{-14}, *t*-test; Fig. 7); and photosynthetic phosphorus use efficiency is 60% lower for carnivorous plants than for non-carnivorous plants (P=5.5×10^{-7}, *t*-test; Fig. 7). These data on photosynthetic nutrient use efficiency further support the hypothesis that carnivorous plants are outliers with respect to scaling relationships between tissue nutrient content and A_{mass} that have been compiled for thousands of non-carnivorous species (Wright *et al.*, 2004, 2005). However, the data for non-carnivorous plants come from a wide range of habitats and plant life-forms. It is not known whether carnivorous plants have higher photosynthetic nutrient use efficiencies than co-occurring non-carnivorous plants. However, there is no evidence to suggest that carnivorous plants and non-carnivorous plants are actually competing for nutrients (Brewer, 1999*a*, 1999*b*, 2003).

Can carnivorous plants escape Hobson's Choice?

Where to elect there is but one,
'*Tis Hobson's choice—take that, or none.*
(from *England's reformation*, by Thomas Ward; 1710)

The observations that carnivory appears to be energetically costly, that excess nutrients do not lead directly to increasing photosynthetic rates in existing leaves or traps, and that photosynthetic nutrient use efficiency of carnivorous plants is extremely low led Ellison and Farnsworth (2005) to suggest that botanical carnivory is an evolutionary Hobson's Choice—the last resort when nutrients are scarcely available from the soil. Two new lines of evidence challenge this interpretation, however.

First, two recent studies have shown that the actual energetic costs of constructing carnivorous traps are significantly lower than the energetic costs of constructing phyllodia of carnivorous plants (Osunkoya *et al.*, 2007; Karagatzides and Ellison, 2009) or leaves of non-carnivorous plants (Fig. 8). These data include not only 'passive' traps (flypaper traps of *Drosera*, pitfall traps of *Nepenthes* and *Sarracenia*) but also the 'active' snap-traps of *Dionaea*. Thus, carnivorous traps are relatively inexpensive structures that provide substantial nutrient gain for little energetic cost; thus, it would take very little photosynthetic gain to yield a substantial marginal benefit[13] from a small investment in carnivory.

Not all active traps are equally active, however. The snap-trap of the Venus' fly-trap uses a mechanical trigger (the mechanism of which is still poorly understood) passively to release elastic energy stored in the fully hydrated leaf (Forterre *et al.*, 2005). This relatively cheap trap is rarely reset; rather, after one (rarely two or three) captures, the trap senesces (Darwin, 1875). In contrast, *Utricularia*'s suction trap is used multiple times, and must be reset after it captures prey (Lloyd, 1942). Pumping out water is an energetically expensive process, and how *Utricularia* bears this cost has come to light only recently.

Jobson *et al.* (2004) found that the *cox*I gene in *Utricularia* has a markedly different structure—with two

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[13] The marginal benefit is the difference between the total photosynthetic increase resulting from nutrients gained from producing a new trap and the total photosynthetic cost of producing a trap as opposed to a phyllode or other photosynthetically more efficient structure.)

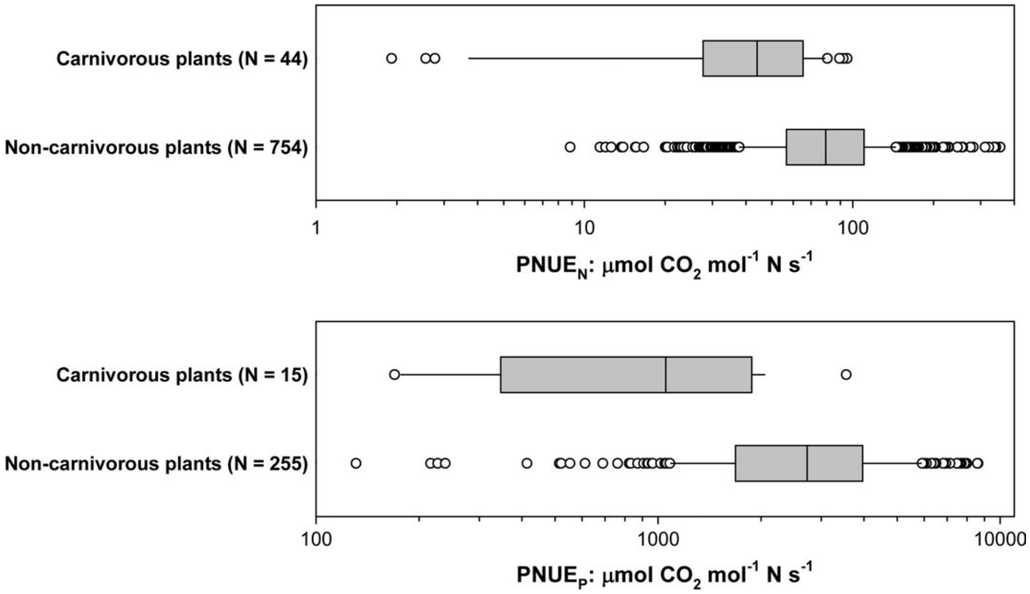

Fig. 7. Photosynthetic nitrogen and phosphorus use efficiency by carnivorous plants and non-carnivorous plants. Data for carnivorous plants from Weiss (1980), Knight (1992), Adamec (1997), Méndez and Karlsson (1999), Wakefield *et al.* (2005), Ellison and Farnsworth (2005), Farnsworth and Ellison (2008), and Karagtzides and Ellison (2008). Data for non-carnivorous plants from Wright *et al.* (2004) and Santiago and Wright (2007).

contiguous cysteines—from that seen in 99.9% of *cox*I sequences recorded from Archaea, bacteria, or eukaryotes. This dicysteine motif causes a conformational change that at least partly decouples this protein's electron transport function from its proton pumping function. Laakkonen *et al.* (2006) estimated that this conformational change optimizes power output when the bladder trap is reset. Although there is an associated respiratory cost to this change, this cost ought to be offset by gains due to carnivory. Laakkonen *et al.* (2006) modified Givnish *et al.*'s (1984) original cost–benefit model to replace photosynthetic costs with respiratory costs. The rapid rate of gene substitution rates in *Utricularia* (Müller *et al.*, 2004; see Fig. 2) further suggests that once this mutation arose in *cox*I, selective pressures on *Utricularia* were relaxed and 'runaway' morphological evolution occurred in this genus. Whereas this mutation in *cox*I has been completely or partially lost in *Genlisea*, its rapid rate of evolution has been attributed to the smaller energetic costs of the passive, albeit morphologically complex, eel traps in that genus (Jobson *et al.*, 2004). Measurements of construction costs of traps in *Pinguicula*, *Genlisea*, and *Utricularia* would shed additional light on the generality of this hypothesis.

Conclusions and directions for future research

The integration of three research areas—the tempo and mode of carnivorous plant evolution as revealed through molecular analysis; the dynamics of prey capture illuminated with rigorous statistical analysis; and the physiological energetics of botanical carnivory in the context of cost–benefit models—has dramatically improved our understanding of many of the questions that Darwin first raised in *Insectivorous plants*. This integration also permits the evaluation of existing hypotheses that may explain the evolution of carnivorous plants and the convergence of trap structures in a wide range of angiosperm lineages. The well-documented restriction of carnivorous plants to low-nutrient, high-light, and wet environments was explained phenomenologically by a cost–benefit model (Givnish *et al.*, 1984). Molecular data have revealed novel mutations and accelerated mutation rates in carnivorous plants, suggesting plausible alternative mechanisms underlying this phenomenological model (Jobson *et al.*, 2004; Müller *et al.*, 2004; Laakkonen *et al.*, 2006). Analyses of carnivorous plant nutrient physiology, trap and leaf construction costs, and overall physiological energetics support the hypothesis that mutations in *cox*I provide an energetic boost in the *Genlisea*–*Utricularia* clade. Statistical analyses support the hypotheses that carnivorous plants have evolved varying degrees of prey specialization (Fig. 4), although there is no evidence for niche partitioning among co-existing congeners (Table 1).

This review also raises unanswered questions and highlights research needs in the areas of carnivorous plant systematics and taxonomy, dynamics of prey capture, and physiological energetics. Priority areas include the following.

Systematics and taxonomy

1. By identifying a key configurational change in *cox*I, Jobson *et al.* (2004) found a plausible molecular and physiological pathway to botanical carnivory. Are there alternative pathways that overcome the energetic costs of carnivory in other carnivorous plant lineages, including others within unrelated carnivorous groups within the Lamiales?

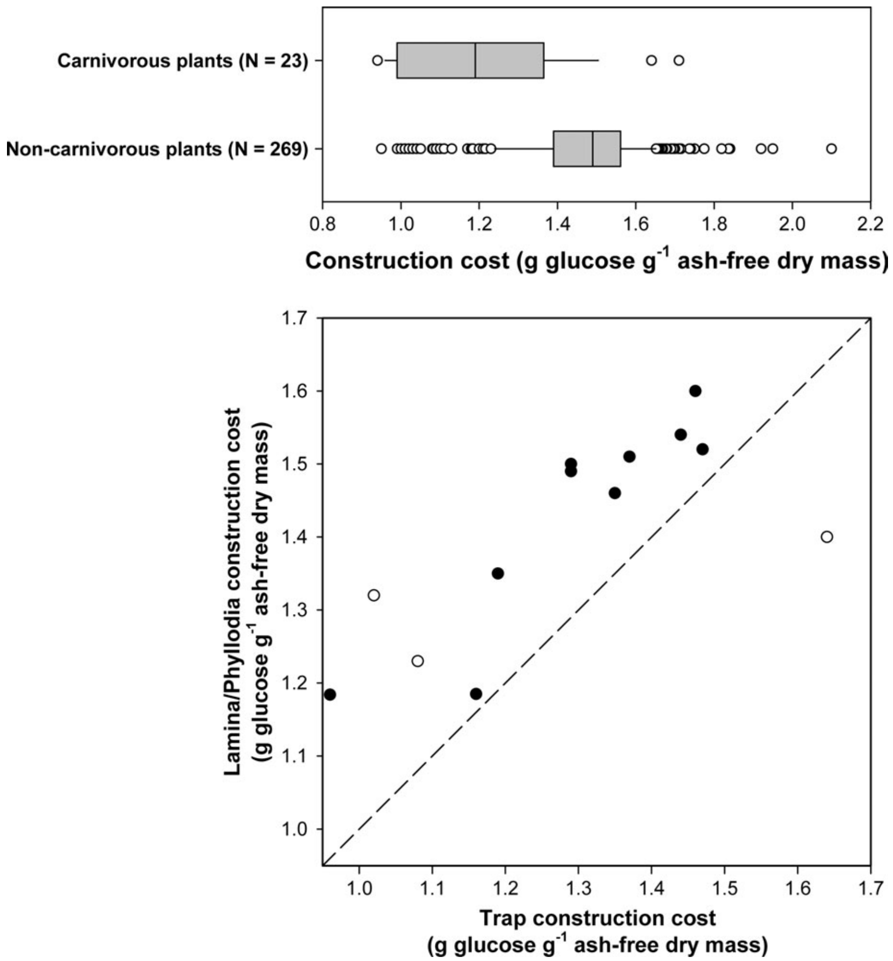

Fig. 8. Box plots illustrating leaf construction costs for traps of 23 carnivorous plants (data from Osunkoya *et al.*, 2007; Karagatzides and Ellison, 2008) and 269 non-carnivorous plants (data summarized in Karagatzides and Ellison, 2009)[15]. The scatter plot illustrates the difference between construction costs of traps and laminae of *Nepenthes* (filled symbols); or phyllodia and pitchers of three species of *Sarracenia* (open symbols) (data from Osunkoya *et al.*, 2007; Karagatzides and Ellison, 2009); the dotted line indicates the location where the construction costs of traps and laminae would be equal.

2. Molecular data have strongly supported infrageneric morphology-based classification systems for the speciose carnivorous genera of *Utricularia* and *Genlisea*, but do not agree with morphological-based classifications of *Drosera*, *Pinguicula*, or *Sarracenia*. Better integration of morphological and molecular data (*cf.* Williams *et al.*, 1994), along with full genomic sequences of representative carnivorous plant species, could help to resolve phylogenies of many groups of carnivorous plants
3. Complete genomic data also would allow for less biased estimates of mutation rates in carnivorous plants relative to non-carnivorous plants, and could provide an explanation for the remarkably low C-values found in *Utricularia* and *Genlisea* (Greilhuber *et al.*, 2006). C-values are well known to be correlated with cell size (Gregory, 2001), which in turn may be correlated with bladder size. Further analysis of the relationship between trap size (and prey capture rates; see, for example, Sanabria-Aranda *et al.*, 2006), cell size, and C-values of *Utricularia* would be illuminating.
4. The genetic analyses to date have suggested some biogeographical anomalies. Examples include repeated transoceanic dispersal events in *Drosera*; repeated colonizations of the Indonesian islands by *Nepenthes*; and evidence that *Darlingtonia* is sister to a *Sarracenia–Heliamphora* clade. As better distributional data and genetic data become available, these should be explicitly linked (using tools such as GeoPhyloBuilder[14]) to create formal phylogeographic hypotheses regarding the origin and diversification of carnivorous plants.

Dynamics of prey capture

1. Prey capture data should be better resolved taxonomically; existing, ordinal data clearly are quite coarse, but family-

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[14] https://www.nescent.org/wg_EvoViz/GeoPhyloBuilder.

[15] Data available from the Harvard Forest Data Archive, dataset HF-112: http://harvardforest.fas.harvard.edu/data/p11/hfX112/hf112.html.

(and lower) level data are harder to come by. Specialization and niche segregation may become more apparent if prey are sorted to finer taxonomic levels.

2. Measures of specialization, niche overlap, capture rate, and capture efficiency are all potentially biased without parallel measurements of available prey (*cf.* Gotelli and Graves, 1996) and prey size. Future studies of prey capture by carnivorous plants should also measure the relative abundance of potential prey in the surrounding habitat.
3. The dichotomy between 'passive' and 'active' traps needs to be rethought. Darwin observed movement by the tentacular glands in *Drosera* and hypothesized selectivity in size of prey captured by *Dionaea*. Macbride (1818) proposed the existence of a frictionless peristome in *Sarracenia*, and Federle and his colleagues (Bohn and Federle, 2004; Bauer *et al.*, 2008) found such frictionless surfaces in *Nepenthes*. The amount of friction, however, can be controlled either by environmental conditions (rain, fog) or by the plant itself (nectar secretion). Because hypotheses regarding the evolution and diversification of carnivorous plants depend, at least in part, on mechanisms and rates of prey capture, renewed attention should be focused on the activity of 'passive' traps, especially in the pitcher plants and in *Genlisea*.
4. Similarly, better assessment of the relative importance of environmental control and direct control by the plant itself of periphyton abundance on *Utricularia* traps and its role in prey capture will help to clarify exactly how active these traps are (Lloyd, 1942; Meyers, 1982). Such studies will also expand the focus of research on prey capture by carnivorous plants beyond simple predator–prey models (cf. Ulanowicz, 1995; Díaz-Olarte *et al.*, 2007).

Carnivorous plant energetics

1. The benefits of botanical carnivory are well established (Ellison, 2006). More importantly, an assessment of the relationship (or lack thereof) between changes in growth rate and underlying ecophysiological processes such as photosynthesis and respiration or tissue nutrient content and stoichiometry (see Shipley, 2006) would unify the currently discordant data on responses of carnivorous plants to experimental prey and nutrient additions.
2. Available data indicate that most responses to prey addition do not occur in the fed traps, but in traps and leaves that are subsequently produced (Butler and Ellison, 2007; Farnsworth and Ellison, 2008). Therefore, not only should future studies assess changes in A_{mass} in leaves produced subsequently to feeding, but they should also better delineate where nutrients are stored and how they are subsequently remobilized in current and future growing seasons. Stable isotopes can be used effectively for such studies (Butler and Ellison, 2007; Butler *et al.*, 2008).
3. Measurements of the costs of carnivorous structures have lagged well behind measurements of the benefits. Estimates of trap construction costs in the Lentibulariaceae and other carnivorous Lamiales are needed to complement existing data on Sarraceniaceae and carnivorous Caryophyllales.
4. Many derived lineages of carnivorous plants have separated traps from photosynthetic structures: phyllodia of *Nepenthes*, *Cephalotus*, and *Sarracenia*; leaves of *Utricularia* and *Genlisea*; and loss of carnivory in *Triphyophyllum* as the plant matures (Green *et al.*, 1979). Detailed analysis of construction costs of traps and photosynthetic structures in these genera will provide additional insights into the true costs of botanical carnivory.
5. How is the carbon derived from prey used by carnivorous plants? This last question is perhaps the most vexing and hearkens back to Darwin:

> '*Most, however, of the plants belonging to these four classes* [carnivorous plants that directly and indirectly digest prey, those that derive nutrients only from decaying litter, and parasitic plants] *obtain* ***part of their carbon*** [emphasis added] *like ordinary species, from the atmosphere. Such are the diversified means,* ***as far as at present known*** [emphasis added]*, by which higher plants gain their subsistence.*'
>
> (*Insectivorous plants,* p. 367)

Since Darwin's seminal publication, carnivorous plants have continued to provide general insights into the evolution and biogeography of plant lineages, the physiological ecology of nutrient uptake and use, and the evolution of leaf form. There is much yet to learn about these most wonderful plants in the world.

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