Evolutionary ecology of carnivorous plants

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After more than a century of being regarded as botanical oddities, carnivorous plants have emerged as model systems that are appropriate for addressing a wide array of ecological and evolutionary questions. Now that reliable molecular phylogenies are available for many carnivorous plants, they can be used to study convergences and divergences in ecophysiology and life-history strategies. Cost–benefit models and demographic analysis can provide insight into the selective forces promoting carnivory. Important areas for future research include the assessment of the interaction between nutrient availability and drought tolerance among carnivorous plants, as well as measurements of spatial and temporal variability in microhabitat characteristics that might constrain plant growth and fitness. In addition to addressing evolutionary convergence, such studies must take into account the evolutionary diversity of carnivorous plants and their wide variety of life forms and habitats. Finally, carnivorous plants have suffered from historical overcollection, and their habitats are vanishing rapidly. A major focus of future research on this exciting group of plants should be directed towards strategies for their conservation and management.

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Carnivorous plants have fascinated evolutionary ecologists, botanists and horticulturists for centuries. Early investigators were reluctant to accept that plants could consume insects and other small invertebrates[1]; Darwin[2] provided the first detailed experimental evidence for carnivory in several genera. Since then, approximately 600 species of carnivorous plants have been identified in six angiosperm subclasses, including both monocotyledons and eudicotyledons[3,4]. Twentieth-century botanists focused on describing the anatomical specializations and physiological mechanisms associated with botanical carnivory[1,5] and identifying commonalities among the carnivorous plants. In the mid-1980s, Givnish[6] proposed a general cost–benefit model to explain the restriction of most carnivorous plants to well-lit, nutrient-poor, waterlogged habitats. Although common ecological factors have led to some evolutionary convergence, focus on ecological similarities has obscured important evolutionary differences. Recent research on carnivorous plants has highlighted these differences, which illustrate the richness of ecological and evolutionary questions that can be approached with these plants. New research on carnivorous plant phylogeny informs interpretations of cost–benefit analyses for the evolution of carnivory in plants, use of captured prey, tradeoffs between attracting pollinators versus prey, and overall ecological effects of the carnivorous syndrome[1]. Recent studies also have successfully modeled the demography of some carnivorous plant populations, elucidating how changes in fitness affect population dynamics. As with other groups of plants, such as mangroves[7] and alpine plants[8] that exhibit broad evolutionary convergence because of strong selection in stressful habitats, detailed investigations of carnivorous plants at multiple biological scales can illustrate clearly the importance of ecological processes in determining evolutionary patterns.

Phylogenetic diversity among carnivorous plants

Phylogenetic relationships among carnivorous plants have been obscured by reliance on morphological characters[1] that show a high degree of similarity and evolutionary convergence among carnivorous taxa[9] (Fig. 1). For example, flypaper (sticky) traps have evolved independently in five eudicot families (Lentibulariaceae, Roridulaceae, Byblidaceae, Droseraceae and Dioncophyllaceae), and pitfall traps have arisen in three eudicot families (Sarraceniaceae, Nepenthaceae and Cephalotaceae) and one monocot family (Bromeliaceae). Most researchers have followed Darwin's lead in considering the flypaper traps of *Roridula, Byblis* and the Droseraceae (*sensu stricto*) to be homologous[2]. As recently as the late 1980s, researchers thought that all extant carnivorous plants were derived from a common ancestor[1]. However, modern molecular data support multiple, polyphyletic origins of the carnivorous plants, and even flypaper traps within the traditionally recognized family Droseraceae (including the sundew genera *Drosera* and *Drosophyllum*) appear to be homoplasic. Phylogenetic analysis based on sequences of the chloroplast *MatK* gene suggest that Droseraceae is polyphyletic and that *Drosophyllum* should be moved into its own family[10].

Current placements of carnivorous families within broader angiosperm phylogenies have been determined using chloroplast *rbcL* (Refs 3,11,12), *MatK* (Ref. 10) and *ORF2280* (Ref. 13) sequences, nuclear ribosomal 18S RNA (Ref. 14) and internal transcribed spacer (ITS) sequences[11]. For carnivorous taxa in three families within the Caryophyllidae, phylogenetic analyses suggest a monophyletic origin (Fig. 2)[10]. Molecular techniques have also resolved relationships among the Sarraceniaceae, Roridulaceae and Byblidaceae, which had been grouped on the basis of morphological analyses as sister taxa within the Rosidae[14]. The consensus tree based on *rbcL*, ITS and 18S RNA sequences places the Sarraceniaceae and

Fig. 1. Photographs of carnivorous plant taxa, illustrating evolution within clades and convergent characters across clades. (a) *Drosera binata*; (b) *Nepenthes rafflesiana*; (c) *Byblis filifolia*; (d) *Sarracenia purpurea*; (e) *Pinguicula vulgaris*; (f) *Utricularia radiata*. All photographs by Aaron M. Ellison.

Roridula as sister taxa closely related to the Ericales[3,11,14], but locates *Byblis* near the Solanaceae within the Asteridae[14]. This conclusion supports recent morphological analysis of the phylogenetic position of *Byblis* based on its embryology[15]. The two remaining eudicot families of carnivorous plants, Lentibulariaceae and Cephalotaceae, have been placed respectively in the Lamiidae and Geraniales, based on *rbcL* sequences[3].

Sequence data also provide insights into the origins and evolution of carnivorous structures, with some surprises. Although carnivory has long been considered to be a highly derived character[9], within the carnivorous clade of the Caryophyllidae (Fig. 2) carnivory is a basal trait within the Droseraceae (flypaper traps; Fig. 1a) that is retained in the Nepenthaceae (as pitfall traps; Fig. 1b), but is lost in the derived Ancistrocladaceae and Dioncophyllaceae (except in *Triphyophyllum peltatum*)[10]. In other unrelated families, more elaborate carnivorous structures, such as bladders and pitfalls, also evolved from ancestors possessing simpler, flypaper type traps [i.e. *Roridula* (flypaper) – Sarraceniaceae (pitfall; Fig. 1d); *Drosera* (flypaper) – *Nepenthes* (pitfall); *Byblis* (flypaper; Fig. 1c); and the butterworts *Pinguicula* (flypaper; Fig. 1e) – *Utricularia* (bladder; Fig. 1f)][3].

The adaptive value of carnivory

The multiple, independent evolution of carnivory in diverse plant families suggests that it is an adaptation to the low nutrient, bright, waterlogged habitats in which carnivorous plants occur[6]. Thus, the nutritional benefits of carnivory have been a traditional focus of research[16]. Givnish[6] proposed a cost–benefit model that predicts that carnivory is adaptive only in nutrient-poor environments that are well lit and moist (Box 1). This model requires both high light and wet conditions, because the photosynthetic costs to carnivory are thought to exceed the benefits in either shady or dry habitats. Benzing[17] recently extended this model by allowing for explicit tradeoffs between light, moisture and nutrient availability through litter (Box 1). Benzing's model can provide a synthetic framework for recent data showing that carnivorous taxa vary in the amount of nutrients obtained through carnivory and in the production of carnivorous structures. Testing these models requires detailed measurements of the contribution of carnivory to the nutrient budget of the plant, photosynthetic rates of carnivorous and noncarnivorous organs, the relationship between nutrient uptake and photosynthesis, and production rates of carnivorous organs.

Nutritional benefits of carnivory

Schulze *et al.*[18] used δ^{15} nitrogen (N) (Ref. 19) of soil and insects to show that carnivorous species differ significantly in their reliance on insect-derived nutrients (Table 1). In general, reliance on insect-derived N increases as carnivorous structures become more elaborate (from sticky leaves of *Drosera* spp. to the >1 m tall pitchers of the cobra lily *Darlingtonia californica*); the northern pitcher plant *Sarracenia purpurea* being a notable exception to this pattern[20]. Plants themselves vary through time in the relative contribution of insect-derived N to total plant N content. In the four genera of pitcher plants (*Cephalotus, Darlingtonia, Nepenthes* and *Sarracenia*), juveniles have nonfunctional pitchers, and derive their N from the soil and from insects captured by older pitchers[18]. By contrast, young functional pitchers that capture insects retain virtually all the nutrients that they derive from prey and do not shunt nutrients to nonfunctional pitchers[18]. Similarly, new bladders of the aquatic common bladderwort *Utricularia vulgaris* do not catch prey[21], but once functional bladders are produced in mid-summer, this species obtains ~50% of its N from captured prey and the remainder from the surrounding water[22].
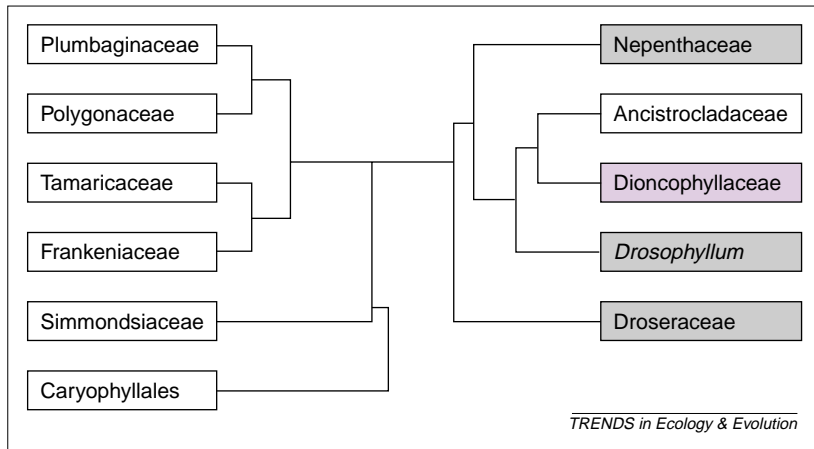
Fig. 2. Consensus tree from bootstrap analyses of *MatK* sequences for the Caryophyllidae, with emphasis on carnivorous taxa[10]. Families in which all members are carnivorous are shaded in dark grey. The Dioncophyllaceae (purple) has lost carnivory in all but one genus, the monospecific *Triphyophyllum peltatum*. This phylogeny, which agrees substantially with those derived from *rbcL* data[58], illustrates two general principles of carnivorous plant evolution: (1) that carnivory can be ancestral within a clade; and (2) that within a clade, sticky ('flypaper') traps are normally ancestral to other trap types (here, pitcher traps of the Nepenthaceae). Reproduced, with permission, from Ref. 10.

A small increase in the availability of insect-derived N (e.g. through supplemental feeding) can lead to a disproportionately large increase in the ability of carnivorous plants to harness soil N or reproduce[16]. Many carnivorous plants produce leaf and flower primordia for year $y+1$ in year y, and such 'preformation'[23] could have significant demographic consequences for carnivorous plants. Preformation also means that fertilization experiments must span multiple years to give reliable results on the effects of nutrients on growth and fitness of carnivorous plants[24,25].

Photosynthetic benefits and costs of carnivory
Although nutritional benefits of carnivory have been documented, the general predictions of the cost–benefit models for the evolution of carnivory have not been well tested because there are few measurements of the photosynthetic rates of carnivorous plants, and even fewer of the responsiveness of these rates to additional prey (Table 2). Overall, carnivorous plants have very low maximal photosynthetic rates (P_{max}), often 50% or more lower than co-occurring plant species[26,27]. In addition, P_{max} of butterworts (*Pinguicula* spp.) and sundews (*Drosera* spp.) do not respond to prey additions, suggesting that the cost-benefit analysis of carnivory based on carbon economy (i.e. P_{max}) alone[6] is insufficient to explain the evolution of carnivory in plants[27]. The increased vigor and sexual and asexual reproduction resulting from prey additions suggests that carnivory supplies substantial nutritional benefits independent of photosynthetic rate[27–29].

Nutrients, light and plasticity in the production of carnivorous organs
Cost–benefit models (Box 1) assume that plants are either carnivorous or not, and that the leaves both photosynthesize and capture prey. Model predictions, therefore, are based on an evolutionary switch from noncarnivory to carnivory in habitats with few nutrients and abundant light. However, many carnivorous plants, including pitcher plants and bladderworts, produce leaves that photosynthesize but do not capture prey, or produce traps that photosynthesize little or not at all. Plants with nonphotosynthetic carnivorous structures should have different cost–benefit functions and be under different selective pressures from those with photosynthetic carnivorous structures only[27].

For example, butterworts have leaves that both photosynthesize and capture prey. Plants that are supplemented by hand-feeding produce more mucilage and digestive glands, and consequently retain more prey on their sticky leaves, than do unfed controls[29]. In line with predictions, this response is strongly correlated with irradiance[29], in spite of the greater abundance of prey in shaded habitats. However, the response to prey does not diminish in either *Pinguicula* or *Drosera* spp. as soil nutrients increase[25,30].

Bladderworts (*Polypompholyx* and *Utricularia* spp.) are aquatic carnivorous plants, but unlike the related butterworts, they have bladder traps interspersed among photosynthetic leaves. Bladders contain some chlorophyll, but in *U. macrorhiza*, they photosynthesize at half the rate of the leaves[31]. Cost–benefit models predict an inverse correlation between bladder production and leaf production, a prediction that is supported by observations on *U. gibba*[32] and *U. foliosa*[33] but not by observations on *U. macrorhiza*[34]. Overall, cost–benefit models for the evolution of carnivory have provided a firm foundation for guiding research and interpreting results until now, but these models need some expansion to account for the diversity and plasticity of carnivorous organs.

Ecological conflicts with prey capture
There should be strong selection for carnivorous plants to evolve effective mechanisms of attracting prey, given their dependence on animal-derived nutrients (Table 1). Many plants attract insects to flowers to effect pollination, and early work on prey attraction in carnivorous plants emphasized the potential for carnivorous structures to mimic insect-pollinated flowers[35]. Flowers of all carnivorous plants are pollinated by insects, resulting in possible conflicts between pollination and prey capture. However, the majority of carnivorous plants are long-lived perennials that also reproduce vegetatively, so predation that contributes nutrients to future growth might offset reductions in seed set caused by prey–pollinator conflicts. For annuals (some *Drosera* and *Utricularia* spp. and all *Byblis* spp.), resolution of these conflicts is more crucial.

In many carnivorous plants, spatial or temporal separation between flowers and traps[36] promotes segregation of prey and pollinators. A notable exception is *Pinguicula vallisneriifolia*, in which

Box 1. Two models for the evolution of carnivory

There is a tradeoff between photosynthetic costs and benefits that could lead to the evolution of carnivory in nutrient-poor habitats (Fig. I; reproduced, with permission, from Ref. a)[a]. Givnish *et al.* hypothesize that enhancement of photosynthetic rates (P_1 and P_2) resulting from the addition of nutrients as a result of carnivory should be more rapid, and have less of a tendency to plateau in high-light and moist environments (P_1) than in dry or shady ones (P_2). Carnivory should evolve when the marginal benefits of an investment in carnivory exceed its own cost (C) – that is, when the net profit curve (Fig. I dotted lines) slopes upward near $C = 0$.
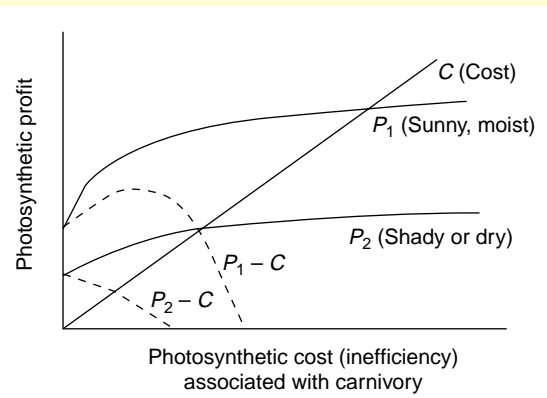
variety of light regimes, because of tradeoffs associated with two other niche axes. Carnivory is extremely rare among bromeliads (two out of approximately 3000 species), which were the inspiration for Benzing's model. There are many other mechanisms for nutrient acquisition among bromeliads[b], which might explain why pitfall traps and associated carnivory are rarely employed among this large family of monocots. Bromeliads also are much more water-stressed than are carnivorous plants, which might generally place them on the lower curve of the cost-benefit curve proposed by Givnish *et al.*[a]
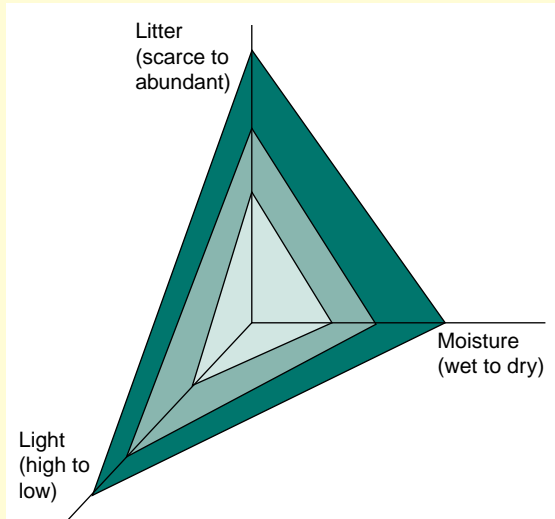

Fig. I

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In a subsequent model, Benzing[b] hypothesizes that there should be a switch from carnivorous, to tubular litter-based, to ant-plant bromeliads along three niche axes: moisture, light and litter (from which bromeliads derive nutrients) (Fig. II; reproduced, with permission, from Ref. b). The surfaces in Fig. II represent the point at which the costs of specialized leaf construction exceed their marginal benefits. In contrast to Givnish *et al.*'s model, Benzing's allows for carnivory to occur in a

Fig. II

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References
a Givnish, T.J. *et al.* (1984) Carnivory in the bromeliad *Brocchinia reducta*, with a cost/benefit model for the general restriction of carnivorous plants to sunny, moist nutrient-poor habitats. *Am. Nat.* 124, 479–497
b Benzing, D.H. (2000) *Bromeliaceae: Profile of an Adaptive Radiation*, Cambridge University Press

flowers and the first functionally carnivorous leaves of the season are produced close together in both space and time[37]. Thrips and beetles are both the most common prey and the most abundant flower visitors to *P. vallisneriifolia*, and experiments demonstrate that seed set in *P. vallisneriifolia* is pollinator limited. Among individuals of *P. vallisneriifolia*, there are strong correlations between the abundance of thrips or beetles present in flowers and traps ($r = 0.98$ and 0.74, respectively)[37]. Thus, there is a clear conflict in this species between attracting pollinators and prey, which recent research has shown is partially alleviated by habitat heterogeneity[37]. In sunny habitats, larger pollinators (bees and butterflies) also visit flowers but do not get trapped. These visitors cross-pollinate plants more

effectively than do thrips, which primarily effect self pollination. In shady habitats, only the small pollinators visit flowers, and the prey–pollinator conflict is more intense.

Two studies of the details of ultraviolet (UV) reflection patterns in pitcher plant traps[38,39] have also led to new conclusions about the relationship between trap and flower attractiveness. Gloßner[38] illustrates UV reflectance patterns of both traps and flowers of the winged pitcher-plant *Nepenthes alata,* the butterworts *Pinguicula gypsicola* and *P. zecheri*, and the bladderwort *Utricularia sandersonii*. She shows that, within these phylogenetically disparate groups, flowers and traps differ in size, shape and contrast, and concludes that these species have evolved to prevent pollinators from becoming prey.

Table 1. Relative contribution of insect nitrogen to total nitrogen content for carnivorous plants

Trap type	Growth habit	Species	Mean % insect nitrogen	Refs
Bladder	Aquatic	*Utricularia vulgaris*	51.8	22
	Terrestrial	*Polypompholyx multifida*	21.0	55
Sticky leaf	Rosette	*Drosera rotundifolia*	26.5	56
	Rosette	*Drosera erythrorhiza*	19.6	55
	Vine	*Drosera macrantha*	54.2	55
	Vine	*Drosera modesta*	34.5	55
	Vine	*Drosera pallida*	87.1	55
	Vine	*Drosera subhirtella*	35.6	55
	Erect, low growing	*Drosera huegelli*	57.3	55
	Erect, low growing	*Drosera menziesii*	36.7	55
	Erect, low growing	*Drosera stolonifera*	51.4	55
	Erect, tall	*Drosera gigantea*	49.1	55
	Erect, tall	*Drosera heterophylla*	47.2	55
	Erect, tall	*Drosera marchantii*	64.7	55
Pitcher	Rosette	*Cephalotus follicularis*	26.1	18
(pitfall)	Vine	*Nepenthes mirabilis*	61.5	18
	Rosette	*Darlingtonia californica*	76.4	18
	Rosette	*Heliamphora* sp.	79.3	18
	Rosette	*Brocchinia reducta*	59.8	18
	Rosette	*Sarracenia purpurea*	10.0	20

Moran *et al.*[39] describe UV spectra and pitcher morphology for six species of *Nepenthes*, a dioecious, pitcher-forming genus, with approximately 80 palaeotropical species. In the lowlands of northwest Borneo, *N. rafflesiana* and *N. gracilis* often grow together and potentially compete for the same prey resources. Of the two, there is a significantly greater contrast in *N. rafflesiana* between the peristome (the attractive lip of the pitcher that is well endowed with extra-floral nectaries) and the pitcher body in spectral reflectance wavelengths (UV, blue and green) that are most attractive to insects. *Nepenthes rafflesiana* also has larger pitchers than does *N. gracilis*, produces a sweet, attractive fragrance[40] and is more successful at catching flower-visiting insects: bees, moths, flies and thrips. By contrast, *N. gracilis* capture more beetles, hemipteran bugs, ants and total flightless prey. Moran *et al.* further conclude that these two sympatric species are partitioning prey, a phenomenon observed in other mixed assemblages of carnivorous plants[41,42].

Demographic models of carnivorous plants
Following on from the extensive studies of the effects of carnivory on the survivorship, growth and reproduction of carnivorous plants, formal demographic analyses of these plants have recently been developed[4,43,44]. Such analyses integrate growth, survivorship and reproduction responses to estimate the finite rate of population increase (λ) and other measures of equilibrium population structure. λ can be used to forecast future population size[45] and has been interpreted as an important measure of individual fitness that could be maximized by natural selection[46]. Models for the evolution of carnivory require fitness estimates for carnivorous plants growing under a range of environmental conditions. Such tests are still a long way off, but the output from demographic models of population growth of carnivorous plants could be used as input for testing such models.

Long-term field studies of individual leaf (ramet) and entire plant (genet) demography are possible because the persistent leaves and rosettes of many carnivorous plants are easy to mark permanently. Most carnivorous plants have poorly developed roots and predicting their population dynamics should not be complicated by temporal variation in root:shoot ratios. They also rarely develop persistent seed banks[47] so oscillations and time lags are not induced by delayed germination. Many carnivorous plant populations are endangered or threatened[48,49], and quantitative demographic analyses are needed to forecast their risk of extinction[50]. Because of their rapid responsiveness to variation in air-, water- and soil-borne nutrient levels[4,51], carnivorous plants might be especially useful for understanding extinction risks in the face of long-term environmental change[52], including chronic N deposition[4] and global climate change.

A recent study by Brewer[44] demonstrates the power of a demographic analysis of population growth of carnivorous plants. The yellow pitcher plant *Sarracenia alata* is common in wet pine savannas of the southeastern USA (Ref. 53). Its rosettes grow vegetatively and flower in multiple years beginning in year three, and can persist for several decades. In these habitats, recurrent fires (with an average period of three years) enhance the fecundity of *S. alata* and are thought to be necessary for maintaining active population growth[54]. Brewer[44] constructed a stage-based matrix model of population growth and examined the consequences of altered fire frequency on population growth rate. His analysis suggests that the finite rate of increase (λ), was higher for annually burned populations ($\lambda = 1.104$) than for populations

Table 2. Average mass-based maximum photosynthetic rates (P_{max}) and photosynthetic nitrogen use efficiencies (PNUE) for carnivorous plants[a]

Species	Structure	P_{max} (nmol CO_2 g^{-1} s^{-1})	PNUE (μmol CO_2 mol N^{-1} s^{-1})	Refs
Pinguicula alpina	Leaves	69.30	45.4	27
Pinguicula villosa	Leaves	41.80	29.4	27
Pinguicula vulgaris	Leaves	56.70	37.7	27
Drosera rotundifolia	Leaves	45.60	33.6	27
Sarracenia purpurea	Leaves	29.70	N.D.	26
Aldrovanda vesiculosa	Leaves	76.50	N.D	57
Utricularia macrorhiza	Bladders	23.62	N.D	31
Utricularia macrorhiza	Leaves	53.23	N.D	31

[a]Abbreviations: N, nitrogen, N.D., no data.

burned at three-year intervals ($\lambda = 1.044$) or for unburned populations ($\lambda = 1.028$). Enhanced recruitment in regularly burned populations shifts the stable stage distribution towards smaller plants. Distributions of reproductive value (the expected number of offspring that will be produced by an individual of age *x*) are similar for annually burned populations and those burned at longer intervals. In both scenarios, transition probabilities for the persistence of juveniles and adults are the most important contributors to λ. Infrequent fires might still be important because they suppress the development of woody vegetation that can eventually shadow and outcompete *S. alata*. Such demographic analyses could be applied profitably to other populations and species of carnivorous plants, especially those that are rare and in need of intensive management.

Conclusions and directions for future research

Comparative and experimental studies at a wide range of scales using unrelated organisms that share similar strong selective pressures can provide new insights into ecological processes and evolutionary dynamics. Carnivorous plants are exemplars for such studies, which have ranged from ecophysiology to adaptive evolution. Cost–benefit models have provided a central focus for research for nearly two

decades, and accumulating data have exposed the strengths and weaknesses of these models and highlighted additional research needs. The primary data needed for refining these models are measurements across carnivorous taxa of photosynthetic rates as a function of nutrient availability; and photosynthetic capacity of noncarnivorous organs of carnivorous plants. Developmental variability in investment in carnivorous structures and sequestration of nutrients for future growth or reproduction should be accounted for in calculations of the efficiency of photosynthetic N use. These models do not account for ecological conflicts between prey capture and pollination, yet this conflict can affect not only evolutionary trends in allocation to carnivorous organs, but also individual fitness and population dynamics.

A research approach that incorporates reproductive effort and success, consequent population dynamics and clear measures of fitness will illuminate the interplay of phylogenetic constraints and evolutionary convergence in the evolutionary ecology of carnivorous plants. Because carnivorous plants are threatened by overcollecting, habitat destruction and environmental change, the results of such studies should guide conservation and management strategies for these unique plants.

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Conservation genetics: where are we now?

Philip W. Hedrick

Genetic studies in endangered species have become widespread in the past decade, and with new information from various genome projects, new applications and insights are forthcoming. Generally, neutral variants are used for conservation applications, and when combined with highly variable loci and/or many more markers, these approaches should become much more informative. Conservation genetics is also concerned with detrimental and adaptive variation, which are more difficult to identify and characterize; however, the ability to predict the extent of such variation might become more successful and applied in future conservation efforts. Neutral variants might be used to identify adaptive variants, but the overlay of different mutational processes and selective regimes suggests that extreme caution should be used in making such identifications.

The recent extinction of many species, and continuing threats to many more has made conservation biology crucial in the 21st century. Although ecological, political, economic, and other forces might be of primary concern for avoiding the extinction of most endangered species, for long-term persistence, genetics and related considerations has also been a focus of conservation effort. In particular, the application of new molecular techniques[1] has made examination of genetics in endangered species feasible and genetic analysis has become widely used in conservation research.

Here, as an organizational theme for examining the status and possible future of conservation genetics, I consider the three major types of genetic variation – NEUTRAL, DETRIMENTAL and ADAPTIVE (see Glossary) – and discuss how each is used in the conservation of endangered species. Of course, whether a particular variant is neutral, detrimental or adaptive depends on the environment, population size, genetic background and so on. For example, a particular allele that is adaptive, such as providing resistance to an infectious disease in one environment, could be detrimental when the pathogen is absent because of a pleiotropic cost associated with that allele. Alternatively, genetic variants that are neutral in one situation could be adaptive in another.

I also consider one of the great promises of neutral molecular variation, that of the use of the extent and pattern of neutral variation to predict the amount and significance of detrimental and adaptive variation. Although it has not proven compelling in some cases, with more informative loci and more genes, we might be able to utilize such observed associations better in the future.

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