

The Evolutionary Ecology of Carnivorous Plants

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I. Summary	2
II. Introduction	2
A. Evolution and Distribution of Carnivorous Plants	3
B. Cost-Benefit Models for the Evolution of Botanical Carnivory	4
C. Carnivorous Plants as Phytotelmata	4
D. Scope of this Review	5
III. Population Biology of Carnivorous Plants	6
A. Demography of Pitcher Plants	6
B. Nitrogen Deposition and the Demography of Pitcher Plants	10
C. Demographic Consequences of Preformation and Delayed Reproduction	16
D. Directions for Future Research	23
IV. Coexistence of Carnivorous and Noncarnivorous Plants	26
A. Disturbance-Mediated Colonization	27
B. Disturbance-Regulated Prey Capture	28
C. Disturbance-Regulated Storage	29
D. Directions for Future Research	30
V. Plant-Insect Interactions	33
A. Large-Scale Phenology and Pollination Ecology of <i>Pinguicula vallisneriifolia</i>	34
B. Small-Scale Differences in Phenology and Pollination Ecology	35
C. Scale-Independent Patterns in Phenology and Pollination	38
D. Gene Flow Within and Between Populations	38
E. Directions for Future Research	40
VI. Phytotelmata	41
A. The Inquiline Community of <i>Sarracenia purpurea</i>	42
B. Trophic Interactions in <i>Sarracenia purpurea</i> -Inquiline Communities	44
C. Metapopulation and Metacommunity Dynamics in <i>Sarracenia purpurea</i> -Inquiline Communities	48

D. Assembly of <i>Sarracenia purpurea</i> -Inquiline Communities	53
E. Short-Term Evolutionary Change in <i>Sarracenia purpurea</i> -Inquiline Communities.....	57
F. Directions for Future Research	63
VII. Conclusions: Are Carnivorous Plants Model Systems for Ecological Research?	63
Acknowledgments	64
References	64

I. SUMMARY

This review synthesizes published data and new results concerning the evolutionary ecology of carnivorous plants. These diverse taxa occur in many angiosperm clades, but are united by a common ecological “niche” – botanical carnivory. Aspects of their life-history, including developmental preformation and rapid responses to nutrient additions, make some carnivorous plants well-suited for addressing basic questions in population biology, including cost-benefit analysis of resource use and allocation, demographic trends, and population forecasting. These cost-benefit analyses also suggest ways to test hypotheses regarding coexistence of plant species in resource-limited environments. Most carnivorous plants are pollinated by insects, and the conflict between using insects as pollination vectors and as prey provides new insights into ecological and evolutionary dynamics of plant–pollinator assemblages. A subset of the carnivorous plants, the pitcher plants, host distinctive communities of invertebrates in their modified leaves. These “inquiline” communities have been developed as model systems for experimental studies of interspecific competition, food web dynamics, metapopulations and metacommunities, and species co-occurrence patterns and assembly rules. The rapid generation times of the inquilines allows for the explicit incorporation of evolutionary dynamics into experimental studies of ecological communities. These research foci suggest that carnivorous plants are model systems for a broad range of basic questions in evolutionary ecology. Aspects of their autecology and synecology permit investigations of fundamental ecological processes across the full range of spatial, temporal, and biological organization.

II. INTRODUCTION

Carnivorous plants have fascinated evolutionary ecologists, botanists, and horticulturists for centuries. Darwin (1875) provided the first detailed

experimental evidence for carnivory in several plant genera, and established once and for all that true heterotrophy existed in an autotrophic kingdom. For most of the 20th century, botanists focused on describing the anatomical specializations and physiological mechanisms required for botanical carnivory (Lloyd, 1942; Juniper *et al.*, 1989). More recently, ecologists have used cost-benefit models to explain the rarity of carnivory among plants and their restriction to well-lit, nutrient-poor, and water-logged habitats (Givnish *et al.*, 1984; Benzing, 1987, 2000). Simultaneously, detailed natural history observations on invertebrate associates of these plants were made throughout the world (reviewed in Fish, 1983; Kitching, 2000). We begin this chapter with a brief overview of the evolution and distribution of carnivorous plants, the cost-benefit models to explain their rarity, and the use of carnivorous plants as “phytotelmata” by invertebrates. We then review in detail a number of recent studies that are using carnivorous plants to explore fundamental questions in evolutionary ecology. These studies illustrate the potential for carnivorous plants to be used as model ecological systems for experimental research in a wide range of ecological subdisciplines.

A. Evolution and Distribution of Carnivorous Plants

Approximately 600 species of carnivorous plants have evolved independently within at least six different angiosperm subclasses, including both monocotyledons and eudicotyledons (Albert *et al.*, 1992; Ellison and Gotelli, 2001). Their evolutionary history provides an exceptional opportunity for conducting ecologically based studies of convergent evolution that require phylogenetically independent contrasts (Ellison and Gotelli, 2001). Carnivorous plants occur worldwide, but species richness and abundance are highest in wet, open, nutrient-poor habitats – Guyana Highlands, the southeastern United States, and Western Australia (Givnish *et al.*, 1984). Recently, substantial carnivorous plant diversity has been discovered in wet, treeless, ephemeral-flush vegetation on granitic and gneissic outcrops in parts of West Africa (Dörrstock *et al.*, 1996; Seine *et al.*, 1996).

Many carnivorous plant species have striking adaptations for prey capture, and much early ecological research on these unique plants focused on the selective benefits of carnivory. Darwin (1875) proposed that carnivory in plants represented an adaptation to nutrient-poor soils. His elegant and simple experiments were the first to illustrate the importance of captured prey as a source of nitrogen for carnivorous plants. These experiments set the stage for more rigorous and precise studies by others in the 20th century, on the mechanisms of prey capture and nutrient uptake (e.g. Chandler and Anderson, 1976; Christensen, 1976; Heslop-Harrison,

1976; Juniper and Buras, 1962; see review in Juniper *et al.*, 1989). Because carnivory is rare among plants, it is apparent that the benefits to carnivory often are outweighed by their costs, and subsequent experiments and models have emphasized the potential costs of carnivory (Givnish *et al.*, 1984).

B. Cost-Benefit Models for the Evolution of Botanical Carnivory

To address the observed botanical rarity of carnivory (<0.2% of angiosperm taxa), several studies have examined the costs associated with being a carnivorous plant (Thompson, 1981; Lüttge, 1983; Givnish *et al.*, 1984; Benzing, 2000). Most terrestrial carnivorous plants are restricted to open, wet, nutrient-poor habitats (Givnish *et al.*, 1984; Seine *et al.*, 1996), an ecological pattern that suggests that carnivory is largely incompatible with drought and shade tolerance (Givnish *et al.*, 1984; Benzing, 2000; see review of the cost-benefit models in Ellison and Gotelli, 2001). In many carnivorous plants, at least part of the function of nutrient uptake has been taken from the roots and placed with the leaves, which in most plants function primarily as photosynthetic and thermoregulatory organs. Using a cost-benefit model, Givnish *et al.* (1984) concluded that an allocation trade-off between carnivory on the one hand, and light and water capture on the other makes carnivorous plants poorer competitors for water and light than noncarnivorous plants.

However, just because photosynthetic yields of carnivorous plants are less efficient under dry and shady conditions does not mean that such plants cannot occur in habitats that experience drought or shade (e.g. Dixon and Pate, 1978; Zamora *et al.*, 1998; Zamora, 1999). There is substantial evidence to show that plastic or seasonal patterns of investment in carnivory are common in carnivorous plants (Chandler and Anderson, 1976; Dixon and Pate, 1978; Weiss, 1980; Aldenius *et al.*, 1983; Zamora *et al.*, 1998; Brewer, 1999a; Ellison and Gotelli, 2001, 2002), suggesting that alternating good and bad conditions for carnivory are typical. Under such circumstances, the ability to “turn off” carnivorous adaptations may be as or more important to a carnivorous plant’s fitness than its ability to capture prey efficiently. Such phenotypic plasticity lends itself to studies of resource allocation, demography, and insect–plant interactions, which we review below.

C. Carnivorous Plants as Phytotelmata

Approximately 25% of the carnivorous plant species occur in two unrelated plant families, Nepenthaceae and Sarraceniaceae, collectively referred to as pitcher-plants because their leaves are modified into pitcher-shaped pitfall

traps (Arber, 1941). These pitchers fill with rainwater (*Heliophora* spp. and *Sarracenia purpurea*) or digestive fluid (all other Sarraceniaceae and all *Nepenthes* spp.). In most species of *Nepenthes*, as well as in the Sarraceniaceae *Sarracenia purpurea*, *Darlingtonia californica*, and *Heliophora* spp., the fluid-filled pitchers (“phytotelmata”) are inhabited by a suite of insect (principally Diptera) larvae, mites, rotifers, protozoa, and bacteria (e.g. Fish, 1983; Nielsen, 1990; Kitching, 2000). These aquatic microecosystems long have been appreciated as model systems for food web studies because they are relatively simple (5–25 species in 3–4 trophic levels), have discrete boundaries (confined within pitchers), are easily manipulated, and can be replicated in large numbers in the field. Until recently, studies of these phytotelmata communities of pitcher plants have emphasized the macroinvertebrates (e.g. Addicott, 1974; Fish and Hall, 1978; Naeem, 1988; Heard, 1994a; Clarke, 1998; Kitching, 2000); the bacteria, protozoa, and rotifers that form the intermediate trophic level have been ignored or pooled (but see Bledzki and Ellison, 1998; Cochran-Stafira and von Ende, 1998; Kneitel and Miller, 2002; Miller *et al.*, 2002.). In this review, we highlight new results involving the macrofauna, but emphasize the dynamics of the “microfauna”; see Kitching (2000) for a comprehensive review of phytotelmata macrofauna.

D. Scope of this Review

This chapter evolved out of a symposium held at the annual meeting of the Ecological Society of America in August, 2000. All the participants – the co-authors of this paper – were asked to discuss a particular ecological question that was especially amenable to testing using carnivorous plants. The presentations ranged broadly, from basic questions in population biology, including resource use and allocation, demography, and population forecasting, through plant–plant and nonconsumer plant–animal interactions, to community-level studies of competitive dynamics, assembly rules, metapopulations, and metacommunities. Here, we synthesize these presentations through a combination of a literature review and presentation of newly published and previously unpublished data. This synthesis illustrates how a concerted focus on a group of organisms defined by their ecological “niche” – botanical carnivory – can address fundamental questions in population and community ecology. We suggest that carnivorous plants should be viewed as model systems for ecological research because these fundamental questions can be addressed at a number of levels of space, time, and biological (ecological) organization. We hope that this synthetic presentation of on-going research on this group of plants encourages others to use carnivorous plants to investigate ecological phenomena.

III. POPULATION BIOLOGY OF CARNIVOROUS PLANTS

The combinations of life history traits, habitat associations, and plant morphology possessed by carnivorous plants make them model experimental systems for addressing general questions in plant population biology, yet there are few studies of demography and population-level responses of carnivorous plants to fluctuating environments or directional environmental change (Zamora *et al.* 1998; Brewer, 2001). Most carnivorous plants are long-lived perennials, which are useful for understanding long-term environmental change (Lewis-Smith, 1994). Hence, a study of the current structure of a population represents a demographic snapshot of conditions that were present several decades ago, opening a window onto how environments for population growth have changed (Doak and Morris, 1999). Many carnivorous plants live in habitats with short growing seasons – arctic, alpine, and exposed bogs – and developmental preformation – the initiation and differentiation of flowers or leaves one or more seasons before they mature (Geber *et al.*, 1997) – is common among mid-to-high latitude species of *Pinguicula* (Worley and Harder, 1999) and *Sarracenia* (Shreve, 1906).

Two research questions are especially amenable to investigations using carnivorous plants: (1) what are the consequences of directional changes in nutrient supply (e.g. chronic nitrogen deposition or saturation) for population growth and risks of extinction? (2) What are demographic consequences of developmental preformation in fluctuating environments? Both questions require basic information on stage-specific growth, survivorship, and reproduction (Caswell, 2001), data that are sparse in the carnivorous plant literature. We first discuss the application of basic demographic models to carnivorous plants, using the northern pitcher-plant *Sarracenia purpurea* as an example, and model the population-level responses of *S. purpurea* to chronic nitrogen deposition. Second, we examine the demographic consequences of developmental preformation, using *Pinguicula vulgaris* as an example. The analyses and models, however, are applicable generally to both carnivorous and noncarnivorous plants.

A. Demography of Pitcher Plants

1. Deterministic Models

Ellison and Gotelli have collected demographic data on the northern pitcher-plant, *S. purpurea*, growing in ombrotrophic bogs of Massachusetts

(Hawley Bog) and Vermont (Molly Bog). At each site, 100 juvenile (rosette diameter < 10 cm) and 100 adult (rosette diameter ≥ 10 cm) plants were randomly selected and tagged in April 1998. We censused each plant, measured its rosette diameter, and recorded its flowering and fruiting status annually in 1998, 1999, and 2000. These data allowed us to estimate annual transition probabilities of growth, stasis, reproduction, and mortality that form the inputs for a stage-classified population projection matrix. We calculated the mean and variance of transition probabilities for 1998–1999 and 1999–2000; results for only Hawley Bog are presented here. We classified individuals into 4 discrete stages: recruits, juveniles, nonflowering adults, and flowering adults (10 cm defines the boundary between juvenile and adult size classes, because this is the minimum rosette diameter for which flowering has been observed). The time-step of the model was one year, so that the transition from flowering adult to recruit incorporated fruiting, seed set, recruitment, and early seedling mortality. The model is:

$$\mathbf{n}_{t+1} = \mathbf{A}\mathbf{n}_t \quad (1)$$

Where \mathbf{n}_t is the vector of the number of plants in each stage at time t , and \mathbf{A} is the $s \times s$ projection matrix (Caswell, 2001). We wrote a computer program in Delphi 5.0 to directly iterate Equation (1) and the more complex models that we developed. The initial stage vector (\mathbf{n}_1) was 100 plants in each of the 4 stages. After an initial transient series of 1000 time-steps, we estimated the intrinsic rate of increase (r) as $\ln(N_{t+1}/N_t)$, where $N_t = \sum_i n_{i,t}$, which matched the calculation of the logarithm of the dominant eigenvalue of the transition matrix \mathbf{A} .

The projection model from the average demographic rates (Table 1) indicates an extremely close balance between fecundity and mortality schedules. The measured intrinsic rate of increase was $r = 0.00456$ individuals individual⁻¹ year⁻¹ with a corresponding doubling time of 152 years. The elasticity of λ (where $\lambda = e^r$) to a matrix entry a_{ij} measures the proportional sensitivity of λ to a change in that entry (de Kroon *et al.*, 1986):

$$e_{i,j} = \frac{a_{i,j}}{\lambda} \frac{\partial \lambda}{\partial a_{i,j}} \quad (2)$$

Eigenvalues and eigenvectors were determined by iteration and then used to solve for elasticities. Persistence transitions (a_{ii}) specify the probabilities that individuals remain in the same stage from one time-step to the next. For the Hawley Bog transition matrix, persistence transitions for juvenile and nonflowering adults had the greatest elasticities (Table 2).

Table 1 Stage transition matrix for *S. purpurea* population at Hawley Bog, Massachusetts. Juvenile–adult transitions derived from data collected by A. M. Ellison and N. J. Gotelli from permanently marked cohorts of 100 juvenile (rosette diameter <10 cm) and 100 adult plants (rosette diameter \geq 10 cm) that were censused annually from 1998 to 2000. Recruitment rates derived from plantings of 500 seeds in 1999

	Stage at Year t			
	Recruit	Juvenile	Nonflowering Adult	Flowering Adult
Stage at year $t + 1$				
Recruit	0.00	0.00	0.00	4.00
Juvenile	0.10	0.95	0.09	0.00
Non-flowering adult	0.00	0.04	0.70	0.83
Flowering adult	0.00	0.00	0.18	0.17

Table 2 Elasticity analysis for stage transition model of Table 1. Each entry is the elasticity, which measures the relative change in population growth rate due to a small change in the stage transition (de Kroon *et al.*, 1986)

	Stage at Year t			
	Recruit	Juvenile	Nonflowering Adult	Flowering Adult
Stage at year $t + 1$				
Recruit	0.00	0.00	0.00	0.02
Juvenile	0.02	0.61	0.02	0.00
Non-flowering adult	0.00	0.03	0.18	0.05
Flowering adult	0.00	0.00	0.06	0.01

2. Stochastic Models

We used annual variability in transition rates that we measured in the field over 2–3 years to explore stochastic models of population growth (Tuljapurkar, 1990). We assumed that each transition was randomly sampled from a standard normal distribution, with no covariance among different rates (cf. Benton and Grant, 1996). Simulated transitions > 1.0 were set to 1.0, and simulated transitions < 0.0 were set to 0.0. For the recruitment rate, we set only the lower bound at 0.0 for simulated values. Consequently, the mean and variance of the simulated matrix entries in the model were not identical to the mean and variance that we measured in the field, although the actual differences may be small.

We considered two extreme scenarios: one in which all of the annual variation in measured rates was simply measurement error, and one in which

all of the annual variation in measured rates represented changing environmental conditions (environmental stochasticity). For the measurement error model, we created a matrix of random elements by sampling from the observed mean and variance for each transition. We then calculated r for this matrix. We repeated this sampling 1000 times, generating a histogram of 1000 simulated values of r , from which we determined the median and true 95% confidence interval. For the environmental stochasticity model, we created a different random transition matrix for each time-step. We iterated population growth for 1000 time-steps, and then estimated r as $\ln(N_{1000}/N_{999})$, where, as before, $N_t = \sum_i n_{i,t}$. We used these calculations to generate a histogram of 1000 simulated values of r .

For both models – measurement error and environmental stochasticity – r was slightly less than 0.0, but the confidence intervals of each model included 0 (Figure 1). The confidence interval for the model of measurement error was smaller than that for the model of environmental stochasticity. Because observed annual variability in transitions includes elements of both measurement error and environmental variability, the confidence interval for the actual value of r would be expected to be intermediate in size between the intervals generated for models that include measurement error or environmental stochasticity. Both the simple deterministic and more complex stochastic models suggest that mortality and birth schedules of

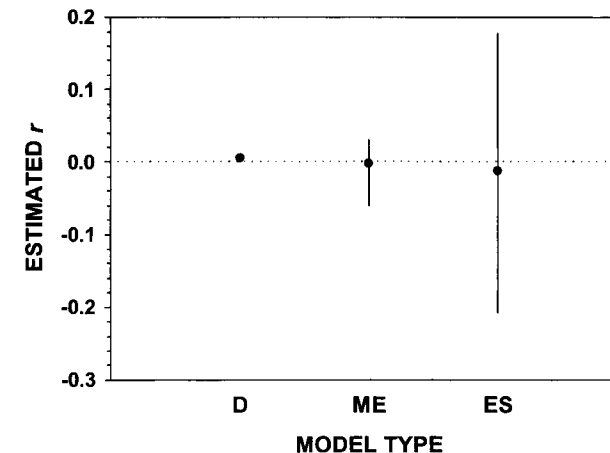


Figure 1 Estimated r for the *S. purpurea* population at Hawley Bog, Massachusetts. Each point is the mean of 1000 replications, and the vertical bars indicate the upper and lower exact 95% confidence intervals. D: deterministic model (transition probabilities given in Table 1); ME: measurement error model; ES: environmental stochasticity model.

S. purpurea at Hawley Bog are in fairly close balance, in accord with other observations for perennial plants (Caswell, 1986; Silvertown *et al.*, 1993).

B. Nitrogen Deposition and the Demography of Pitcher Plants

All carnivorous plants are nitrogen (N) limited (Adamec, 1997), but the northern pitcher-plant *S. purpurea* is an especially good subject for understanding effects of N deposition because these plants collect rainwater in their pitchers (Juniper *et al.*, 1989) and biological uptake of N occurs directly from pitchers (Adamec, 1997; Bledzki and Ellison, 1998). Therefore, these pitcher-plants should be good indicators for nitrogen deposition resulting from acidic precipitation. Additionally, pitcher-plants are typically found in nitrogen-poor ombrotrophic bogs, which receive nitrogen inputs primarily from atmospheric deposition (Hemond, 1983; Urban and Eisenreich, 1988). Although most research on nitrogen deposition has been carried out in lake, stream, and forest ecosystems (e.g. Schindler, 1988; Aber *et al.*, 1988; Finn *et al.*, 1998), in these habitats, nitrogen deposition is complicated by nutrient accumulation in soils, mycorrhizal activity, groundwater flows, and weathering of parent material (Aber *et al.*, 1988). In contrast, the simple inputs of nitrogen into ombrotrophic bogs through precipitation means it is more likely that we will be able to detect the signature of chronic N deposition.

Long-term N deposition can lead to nitrogen saturation, wherein ecosystems have decreased retention efficiency of added nitrogen. Small increases in nitrogen deposition may enhance plant growth and productivity, but chronic long-term increases have many detrimental effects, including plant nutritional deficiencies (Van Dijk and Roeloffs, 1988), decreased growth (Spink and Parsons, 1995), and decreased cold tolerance (DeHayes *et al.*, 1999). These effects at the individual-plant level may translate into an increased risk of extinction at the population level that may ultimately lead to changes in species composition of the local plant community (Heil and Diemont, 1983; Woodin and Farmer, 1993). Increased nitrogen deposition has been implicated in the extinction of several *Sphagnum* species in upland areas of northern England (Press *et al.*, 1986), and in a shift from *Calluna*-dominated heathland to grassland in the Netherlands (Heil and Diemont, 1983). Studies of nitrogen saturation have mostly emphasized ecosystem function and individual plant responses, yet these responses are intimately linked to the demographic integrity and persistence of populations. A detrimental feedback loop may emerge, in which increases in nitrogen deposition causes the extinction of species, and this attendant loss of biodiversity further degrades ecosystem function (Naeem *et al.*, 1994; Schwartz *et al.*, 2000) and system-wide capacity to absorb excess nitrogen.

I. Nutrient Manipulation Experiment

We combined the results of long-term field censuses and manipulative experiments to develop a forecasting model of *Sarracenia* population dynamics under different nitrogen deposition regimes (Gotelli and Ellison, 2002). The effects of nutrient inputs on the population dynamics of *S. purpurea* were determined using a form of life-table response experiment (LTRE; Caswell, 2001) at Hawley Bog, Massachusetts, in which nutrient regimes in the water of juvenile and adult plants' pitchers were experimentally manipulated (Figure 2), and the growth, mortality, and reproductive rates of the plants were measured. We randomly selected 90 adult and 90 juvenile plants and assigned them to one of nine different

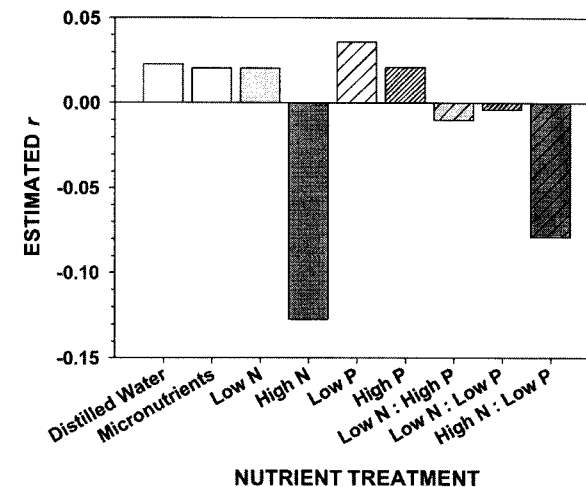


Figure 2 Estimated r for *S. purpurea* populations at Hawley Bog, Massachusetts for which we altered the nutrient concentration within pitchers through bi-monthly additions of 5 ml nutrient solutions. Ninety adult and 90 juvenile plants were randomly selected in April 1998 and assigned to one of nine different nutrient regimes: two control treatments (distilled water; micronutrients as 10% Hoagland's solution); two nitrogen (NH_4Cl) treatments (0.1; 1.0 mg/L); two phosphorous (NaH_2PO_4) treatments (0.025; 0.25 mg/L) and three treatments in which we altered the N:P ratio (0.1:0.25; 0.1:0.025; 1.0:0.025). Nutrient concentrations were chosen to bracket measured rates of annual nitrogen deposition in the field. Prey capture and inquiline colonization was prevented with glass wool plugs in the pitcher openings. Treatments were maintained during the 1998 and 1999 growing seasons. At the end of each summer, the size, survivorship, and reproductive status of all plants was recorded. In the figure, the height of each bar represents the population growth rate estimated from the deterministic population growth model; the amount of grey shading is proportional to the N concentration, and the density of hatching is proportional to P concentration.

nutrient treatments: two control treatments (distilled water or 10% concentration of micronutrients from Hoagland's Solution); two N treatments (0.1 mg or 1.0 mg NH₄-N/L as NH₄Cl); two P treatments (0.025 mg or 0.25 mg PO₄-P/L as NaH₂PO₄); and three treatments in which we altered the N:P ratio (low – 1:2.5, medium – 4:1, and high – 40:1). N concentrations were chosen to bracket measured rates of annual deposition (NADP, 2000). P concentrations were also varied to determine whether plants responded to N limitation directly or to P limitation caused by increased N availability (Bedford *et al.*, 1999; Ellison and Gotelli, 2002). We used the estimated transitions from two consecutive years (1998, 1999) of the nutrient addition experiment to construct an average stage-classified population projection matrix for each experimental nutrient regime. These experiments did not generate data on flowering or fruiting, so we assumed in all analyses that the recruitment rates were equivalent to those measured among unmanipulated controls. We analyzed the data using both a deterministic model, and a model in which the annual variation in rates represented measurement error. Measurement error is an appropriate scenario because of the small sample sizes ($N = 10$ per treatment) and the fact that the nutrient regime was being maintained for each plant in an ecological “press” experiment (Bender *et al.*, 1984). To assess variation in r among treatments, we used parametric bootstrap analysis and created a set of 1000 transition matrices for each experimental treatment. The elements in each transition matrix were chosen from a truncated normal distribution (as described above) with means and variances estimated from the annual variation in vital rates measured in the field experiment. We measured r for each randomly constructed matrix.

The measured rates of population increase varied among the nine experimental treatments (Figure 2). The highest population growth rates were measured for the controls and the P-addition treatments, and the lowest rates were measured for the high-N treatment and the high N:P ratio treatment. A model of measurement error generated similar patterns, with segregation of the 95% confidence intervals for r in each of the nine treatments. This manipulative field experiment established that population growth rates of *S. purpurea* are sensitive to nutrient levels, and that population declines can be expected with increases in either N or N:P (see Gotelli and Ellison, 2002, for additional details).

2. Forecasting *Sarracenia* Population Dynamics Under Changing Conditions of Nitrogen Deposition

Although the estimation of r in different nitrogen regimes provided insight into the equilibrium dynamics for *S. purpurea* populations, this analysis is

not realistic for forecasting purposes. In many field situations, N deposition rates can fluctuate substantially over short periods of time and change gradually over longer timescales. We extended our models to determine how population growth of *S. purpurea* would be affected under changing conditions of N deposition (Gotelli and Ellison, 2002). We used the experimental data from the control, low-N and high-N treatments to create an N function for each transition in the model. This function takes the N deposition rate as input and generates the transition probability for output. Ideally, this function could be estimated by setting up an experiment with many different N concentrations. However, with the available data, we were forced to estimate this function from only three available data points.

To estimate the N function, we made the following assumptions: (1) at concentrations $< 0.01 \text{ mg l}^{-1} \text{ yr}^{-1}$, the transition function is that observed for the control data; (2) at concentrations $\geq 10 \text{ mg l}^{-1} \text{ yr}^{-1}$ (10 times our high-N treatment) all plants are killed (transition probability = 0.0); (3) at concentrations between 0.01 and $10 \text{ mg l}^{-1} \text{ yr}^{-1}$, transition functions are determined by a simple linear extrapolation between our experimental data points plotted on a logarithmic scale of N concentration. We used long-term data from the National Atmospheric Deposition Program (NADP, 2000) to forecast trends in annual N deposition rates. Time series for NH₄ and NO₃ were available from 1984 to 1996. We used data from the monitoring station at Quabbin, Massachusetts, which is the closest station to Hawley Bog. We fit a first-order autoregressive model with correlated errors (AR-1) to forecast long-term N deposition (using Systat 6.0, SPSS Inc., Chicago). We combined concentration data ($\text{mg l}^{-1} \text{ yr}^{-1}$) for NH₄ and NO₃ to generate a single time-series of annual N deposition. Next, we fit a first-order autoregressive model with correlated errors (AR-1) to forecast long-term N deposition:

$$[N]_t = a + b[N]_{t-1} + e \quad (3)$$

where $[N]_t$ is the N deposition rate in year t , e is a Gaussian random error term, and a and b are fitted constants. In our models, we set $a = 0$, to describe a constant percentage increase or decrease in the annual deposition rates. The best-fit coefficients were $b = 0.953$ and $e \sim N(0, 0.00176)$. The initial deposition rate of N was set at $0.391 \text{ mg l}^{-1} \text{ yr}^{-1}$, the measured rate in 1998 (NADP, 2000). This autoregressive model described a decrease in N concentration over the 14 year time-series from 1984 to 1998, with an estimated decrease of 4.7% annually.

We predicted trends in N deposition rates by using the forecasting equations that were fit to the nitrogen time-series, and extrapolating them from present conditions for 1000 consecutive time-steps. We linked these predictions to the N function (effect of N on transition probabilities) by

establishing 1000 sequential transition matrices, each determined by the N concentrations in a particular year. We used the model to forecast N deposition under four scenarios: (1) best fit (continuing the current downward trend in the fitted model); (2) no change ($b = 1.0$, assuming current N levels measured in 1998, and then using the error structure of the model to forecast in the future); (3) small increase in N ($b = 1.01$, a 1% annual increase in deposition rate); (4) large increase in N ($b = 1.047$, a 4.7% annual increase in deposition rate, which is the magnitude of the measured annual decrease over the 12-year time-series). Finally, we applied these sequential matrices to an initial population vector to forecast changes in *S. purpurea* population. Complete details of these models are presented in Gotelli and Ellison (2002).

In the simple deterministic and stochastic models described previously (Figure 1), the initial population vector \mathbf{n}_1 was not important and could be arbitrarily chosen because these models settle into equilibrium behavior after a number of transient time-steps, and thence population growth rates could be estimated (Tuljapurkar, 1990). However, the more complex model that incorporates changes in N deposition cannot be analyzed this way. Because the transition matrices are changing systematically at each time-step, the system is nonhomogenous and never settles into an equilibrium state (Caswell 2001). Thus, the measured population growth rate is not really a meaningful statistic. However, it is appropriate to estimate the probability of extinction and the estimated time to extinction for such models. We used 1000 different trials of the model to estimate the probability of extinction after 100 years, which we defined as the fraction of simulated populations that declined below 1.0 individual after one century. We defined the time to extinction as the number of time-steps for which 95% of the populations had declined below 1.0 individual. This is a low and conservative extinction threshold (Ginzburg *et al.* 1982), but it may be a realistic one for long-lived perennial plants, which can persist at very small population sizes for long times. Our extinction estimates are contingent on the starting population size (estimated as 26,900 individuals at Hawley Bog) and the initial distribution of individuals among stages.

A population forecasting model of continued decrease in average N concentrations predicted virtually no extinction risk for the *S. purpurea* population at Hawley bog during the next 100 years. A more realistic model of no change in current N deposition rates predicted only a small extinction risk ($P = 0.038$), whereas even a 1% increase in the annual deposition rate generated a substantial extinction risk ($P = 0.378$). The expected time to extinction ranged from 70 to 650 years (Table 3). However, regardless of the expected extinction time, all forecasting scenarios except for the optimistic best-fit model predicted steady decreases in the size of the *Sarracenia* population (Figure 3). However, extinction times are on the order of

Table 3 Extinction risks and time to extinction of the *S. purpurea* population at Hawley Bog, Massachusetts for four different scenarios of changes in annual N deposition rates

Scenario	% Annual Change in N Deposition	Extinction Probability ¹	Time to Extinction (year) ²
Best-fit ³	-4.7	0.000	> 10,000
No change	0.0	0.038	650
Small increase	1.0	0.378	290
Worst case	4.7	0.996	70

¹ Probability of extinction is defined as the fraction of 1000 random population tracks that had gone extinct ($N < 1.0$) after 100 years.

² Time to extinction is the length of the time-series required for 950 out of 1000 random population tracks to fall below the extinction threshold.

³ The best-fit model is the forecast if annual N deposition decreases by 4.7% per year, as measured from the empirical time-series (data from National Atmospheric Deposition Program [NADP, 2000], Quabbin Massachusetts monitoring station). In all models, the initial N deposition rate was taken as $0.391 \text{ mg l}^{-1} \text{ yr}^{-1}$, the level measured at Quabbin in 1998. In the autoregressive model, the Gaussian random error term had mean = 0 and standard deviation = 0.042.

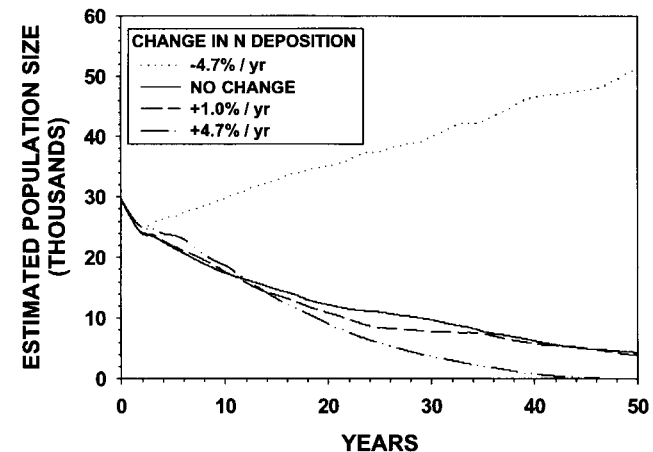


Figure 3 Population forecasts for *S. purpurea* under four N deposition forecast scenarios (Table 3). Each curve represents the results for different annual % change in N deposition rate. All models begin with an initial population size of $N = 26,900$, which is the current estimate for the population at Hawley Bog, Massachusetts. All models begin with an initial N deposition rate of $0.391 \text{ mg l}^{-1} \text{ yr}^{-1}$, the rate measured in 1998 at the NADP Quabbin, Massachusetts monitoring station. The solid line is the forecast for a model of no change in the average annual deposition rate.

decades and centuries. Without a long-term forecasting model and a prospective analysis (Caswell, 2001), it may be difficult to recognize the potential risk of extinction for slow-growing populations of perennial plants such as *S. purpurea*.

C. Demographic Consequences of Preformation and Delayed Reproduction

Our second question concerns the evolution of developmental preformation, the initiation and differentiation of flowers and/or leaves one or more years before they mature. Many carnivorous plants occupy habitats in which preformation is very common, such as arctic and alpine regions, and exposed bogs (Sørensen, 1941; Diggle, 1997; Geber *et al.*, 1997). Plants with developmental preformation seem more likely to mature seeds before the end of short growing seasons, but their responses to surplus resources or unusually long seasons may be delayed relative to plants without preformation. Indeed, delayed responses to environmental variation are characteristic of arctic communities (Billings and Mooney, 1968; Shaver and Kummerow, 1992) and plants with preformation (Mark, 1968, 1970; Boeken, 1989; Svensson *et al.*, 1993; Worley and Harder, 1999). The costs and benefits of preformation have never been assessed, either theoretically or empirically. Here, we provide a framework with which to investigate the evolution of preformation by placing responses to fluctuating environments in a demographic context. Carnivorous plants are well-suited to testing these ideas because one aspect of environmental quality – nutrient availability – is easily manipulated. The genus *Pinguicula* holds great potential as the incidence of preformation varies among species, allowing for comparisons between species that are otherwise similar in life history, habitat requirements, and morphology.

1. Preformation in *Pinguicula*

The evolution of preformation may be best assessed by considering demographic responses to environmental variation because its advantages are likely to reflect the frequency of good and poor growing seasons. For example, the benefits of preformation for seed maturation will be greatest when growing seasons are short. However, the delayed responses associated with preformation may carry a demographic cost under unusually long growing seasons or increased resource availability. Here, we use a simple demographic model to consider the probable consequences of the above responses, and the environmental conditions likely to favor the evolution of preformation.

Approximately 50 species of butterworts (*Pinguicula* spp.) occur worldwide in habitats ranging from damp microsites in arctic and alpine tundra, through lowland swamps in the southeastern USA, to seasonally moist areas in Central and South America and the Caribbean (Casper, 1966; Legendre, 2000). All are rosette-forming perennials, but the wide range of habitats they occupy correspond to a broad range in the extent and timing of preformation observed in each species. Most temperate species overwinter as a subterranean winter bud that develops from the apical meristem during the growing season and which produces the leaves and flowers in the next season (Casper, 1966; Legendre, 2000). Species growing in the more moderate climates of the southeastern USA, Central America, and parts of Europe remain green year-round, and preliminary investigation suggests that preformation does not occur in these species (T. E. Miller, personal observation). Several mountainous species from Central America and in Mediterranean climates form succulent and noncarnivorous winter rosettes during the dry season instead of winter buds. Preformation has not been investigated in these species, but some produce flowers both in winter and summer (Casper, 1966; Legendre, 2000), suggesting that preformation is unlikely. The broad range of variation in the occurrence of preformation allows for a thorough investigation of its functional significance within a single clade. The occurrence of preformation in other carnivorous taxa (e.g. *Sarracenia*) could allow for investigations of its ecological significance independent of evolutionary history.

2. Demographic Transitions in Fluctuating Environments

Expected responses to environmental variation by plants with and without preformation were incorporated into a stage-based matrix model. A base transition matrix was assumed to represent an average year for both populations with and without preformation (Table 4). This matrix was typical of long-lived perennials in that adult survival was high (90%) and seedling survival was low (25%), and transitions between adult stages had the greatest influence on population growth rates (Silvertown, 1993; Table 5). The population growth rate predicted by this matrix was $\lambda = 1.087$. Because delaying reproduction is likely to be most costly when survival is low, transition matrices were also calculated for adult survivals of 70 and 50%, and seedling survivals of 19.4 and 13.4% respectively. These matrices were constructed by multiplying all transitions in the base matrix by 0.7/0.9 or 0.5/0.9.

We focused on how preformation influences the reproductive responses to environmental fluctuations for two reasons. First, qualitative effects of reproductive changes on transition matrices are easy to predict. Second,

Table 4 Transition matrix used for populations with 90% survival of adults. The values in this matrix represent an average year, which was assumed to be equivalent for populations with and without preformation. Transitions were altered to represent seasons responses to good (long, high resource) and poor (short) growing seasons as illustrated in Figure 4

	Stage at Year t		
	Seedling	Nonfruiting Adult	Fruiting Adult
Stage at year $t + 1$			
Seedling	0.00	0.00	3.00
Nonfruiting adult	0.22	0.60	0.70
Fruiting adult	0.03	0.30	0.22

Table 5 Elasticity analysis for stage transition model of Table 4. Each entry is the elasticity, which measures the relative change in population growth rate due to a small change in the stage transition (de Kroon *et al.*, 1986)

	Stage at Year t		
	Seedling	Nonfruiting Adult	Fruiting Adult
Stage at year $t + 1$			
Seedling	0.000	0.000	0.136
Nonfruiting Adult	0.112	0.297	0.192
Fruiting Adult	0.025	0.241	0.060

empirical observations exist to support our assumptions. In good conditions (long seasons) populations lacking preformation were assumed to increase reproductive output in the current year, t (Figure 4). In contrast, populations with preformation did not increase seedling output until the following year, $t+1$, because commitment of meristems to current reproduction already was complete when they experienced good conditions in year t (Figure 4). Both demographic studies and experiments involving resource enhancement support the idea that reproductive responses are delayed in *Pinguicula* (Karlsson *et al.*, 1991; Svensson *et al.*, 1993; Thorén and Karlsson, 1998; Worley and Harder, 1999) and in other species with preformation (Geber *et al.*, 1997). In our model, good years increased the probability that seedlings of both life history types reached adult classes and the probability that adults moved to, or remained in, the reproductive class (Figure 4). Overall survival was not affected by environmental conditions. For 90% adult survival, all changes in transitions among adult plants were 0.05, whereas changes involving seedlings were 0.01. Transitions for 70 and 50% survival were multiplied by 0.7/0.9 or 0.5/0.9, respectively.

		ENVIRONMENT	
		GOOD	POOR
NO PREFORMATION	t	$\begin{bmatrix} 0 & 0 & \uparrow \\ \uparrow & \downarrow & \downarrow \\ \uparrow & \uparrow & \uparrow \end{bmatrix}$	$\begin{bmatrix} 0 & 0 & \downarrow \\ \downarrow & \uparrow & \uparrow \\ \downarrow & \downarrow & \downarrow \end{bmatrix}$
		$\begin{bmatrix} 0 & 0 & \text{---} \\ \text{---} & \text{---} & \text{---} \\ \text{---} & \text{---} & \text{---} \end{bmatrix}$	$\begin{bmatrix} 0 & 0 & \text{---} \\ \text{---} & \text{---} & \text{---} \\ \text{---} & \text{---} & \text{---} \end{bmatrix}$
	$t+1$	$\begin{bmatrix} 0 & 0 & \text{---} \\ \text{---} & \text{---} & \text{---} \\ \text{---} & \text{---} & \text{---} \end{bmatrix}$	$\begin{bmatrix} 0 & 0 & \text{---} \\ \text{---} & \text{---} & \text{---} \\ \text{---} & \text{---} & \text{---} \end{bmatrix}$
		$\begin{bmatrix} 0 & 0 & \text{---} \\ \text{---} & \text{---} & \text{---} \\ \text{---} & \text{---} & \text{---} \end{bmatrix}$	$\begin{bmatrix} 0 & 0 & \text{---} \\ \text{---} & \text{---} & \text{---} \\ \text{---} & \text{---} & \text{---} \end{bmatrix}$
PREFORMATION	t	$\begin{bmatrix} 0 & 0 & \text{---} \\ \uparrow & \downarrow & \downarrow \\ \uparrow & \uparrow & \uparrow \end{bmatrix}$	$\begin{bmatrix} 0 & 0 & \text{---} \\ \downarrow & \uparrow & \uparrow \\ \downarrow & \downarrow & \downarrow \end{bmatrix}$
		$\begin{bmatrix} 0 & 0 & \text{---} \\ \text{---} & \text{---} & \text{---} \\ \text{---} & \text{---} & \text{---} \end{bmatrix}$	$\begin{bmatrix} 0 & 0 & \text{---} \\ \text{---} & \text{---} & \text{---} \\ \text{---} & \text{---} & \text{---} \end{bmatrix}$
	$t+1$	$\begin{bmatrix} 0 & 0 & \uparrow \\ \text{---} & \text{---} & \text{---} \\ \text{---} & \text{---} & \text{---} \end{bmatrix}$	$\begin{bmatrix} 0 & 0 & \text{---} \\ \text{---} & \text{---} & \text{---} \\ \text{---} & \text{---} & \text{---} \end{bmatrix}$
		$\begin{bmatrix} 0 & 0 & \text{---} \\ \text{---} & \text{---} & \text{---} \\ \text{---} & \text{---} & \text{---} \end{bmatrix}$	$\begin{bmatrix} 0 & 0 & \text{---} \\ \text{---} & \text{---} & \text{---} \\ \text{---} & \text{---} & \text{---} \end{bmatrix}$

Figure 4 Expected responses by populations with and without preformation to good (long) and poor (short) years. Dashes indicate no change in a transition. The three stages in each matrix are (top to bottom and left to right): seedlings, nonfruiting adults, and fruiting adults (as in Table 4). Good years increase seedling survival, and the proportion of adults reaching, or remaining in the reproductive classes. Good years also increase reproduction, but the increase is delayed in populations with preformation. Poor years have the opposite effects of good years, but populations with preformation flower early enough to complete seed maturation and therefore do not decrease reproductive output.

Responses to poor conditions (short seasons) also differed between plants with and without preformation. In populations without preformation, poor seasons reduced seedling production in t whereas reproduction was not affected in populations with preformation. This effect may be important even for species that differ only in the extent of preformation, rather than in its occurrence. For example, *P. alpina* produces its flowers much earlier in the year than *P. vulgaris*, perhaps because the preformed flowers of *P. alpina* are further differentiated (Molau, 1993). *P. alpina* also completes seed maturation in years that *P. vulgaris* populations at comparable elevations lose their seed crops to low temperatures at the end of the growing season (Thorén and Karlsson, 1998). We assumed that seedlings of both population types were less likely to move to adult classes, and adults were less likely to move to, or remain in, the reproductive class (Figure 4), but overall survival was not altered by poor seasons. In both life history types, transitions in year $t + 1$ were not affected by poor conditions in year t (Figure 4).

3. Estimating Population Growth in Variable Environments

We compared rates of population growth between populations with and without preformation in the presence of stochastic variation in environmental conditions. All simulations were conducted with MATLAB, version 5.3, and were based on programs written by C. Horvitz and S. Tuljapurkar (unpublished manuscript). First, we constructed vectors that represented environmental rates over a 2000 year period, in which good years occurred with probability 0.3, poor years with probabilities ranging from 0 to 0.3 depending on the analysis, and the remaining years were average. Each environmental state corresponded to the transition matrices for populations with or without preformation described above. In effect, populations without preformation experienced a maximum of three environmental states, average, good, and poor. Populations with preformation experienced six states because years following a good year differed from those following poor or average years, as is illustrated in Figure 4. For each combination of good and poor years, the same sequence of environmental states was used to estimate growth by populations with and without preformation.

Transition matrices over the 2000 year period were used to estimate rates of stochastic population growth as follows. For each time-step we multiplied the population vector, \mathbf{n} , by the appropriate transition matrix, \mathbf{A} , according to the demographic equation:

$$\mathbf{n}_{t+1} = \mathbf{A}_t \mathbf{n}_t \quad (4)$$

After 1000 years, the populations had reached a stable stage distribution, and we used the subsequent 1000 years for the remaining calculations. For each time-step, population growth was calculated as

$$\text{growth}_{t+1} = N_{t+1}/N_t \quad (5)$$

where $N_t = \sum_i n_{i,t}$ as before. Mean growth rate $\bar{r}_s = (1/t) \sum_t \text{growth}_t$, this 1000 year period was used to estimate the stochastic rate of population growth,

$$\lambda_s = \exp(\bar{r}_s) \quad (6)$$

4. Demographic Costs of Delaying Reproduction

Our first analysis considered how the magnitude of delayed responses to good years affected λ_s in populations with preformation relative to populations with immediate responses to good years, i.e. populations lacking preformation. These comparisons were made for populations with adult survival of 90, 70, and 50% because we expected the costs of delaying reproduction to be more severe as survival between years decreased. For all

estimates we assumed a 30% probability of good years, and that populations without preformation responded to good years with a 33% increase in current reproduction (seedling production). In populations with preformation, good years caused delayed increases in reproduction ranging from 0 to 33%. Good years affected transitions other than reproduction as described above (see Section III.C.2) and illustrated in Figure 4.

Both the magnitude of delayed reproductive responses and adult survival influenced relative growth by populations with and without preformation. Differences between the two life history types are represented by the ratio $\lambda_{s, \text{preformation}} : \lambda_{s, \text{no-preformation}}$. A ratio of 1.0 indicates that population growth was identical for populations with and without preformation, whereas ratios < 1.0 indicates lower growth by populations with preformation. All estimates of this ratio were close to 1.0 (Figure 5A), reflecting the small elasticity for seedling output (Table 5). As expected, increases in the magnitude of delayed reproduction resulted in higher growth rates by populations with preformation relative to populations without preformation, and the effects of delaying reproduction were more severe for lower rates of adult survival (Figure 5A).

One counter-intuitive result from this analysis was that populations with preformation achieved the same λ_s with lower reproductive responses to good years than occurred in populations without preformation. Population growth rates between the two developmental types were equivalent when delayed increases in reproduction were 30% in populations with preformation, even though populations without preformation increased current reproduction by 33% (Figure 5A). Furthermore, delayed increases in seedling output above 30% resulted in higher growth rates in populations with preformation than in populations without preformation (Figure 5a). The mathematical explanation for this result is that more plants reached the fruiting class in a good season, so that delayed increases in reproduction applied to a higher proportion of the population. In reality, plants that fruit in year $t + 1$ only because of enhanced resources in year t are unlikely also to have enhanced reproductive output in year $t + 1$. Thus identical increases in current and delayed seedling output seem improbable, even if surplus resources could be converted to current and future reproduction with equal efficiency. Unfortunately, no empirical data exist to indicate whether delayed reproductive responses by plants with preformation are comparable to immediate responses by plants without preformation.

5. Benefits of Early Seed Set

Our second analysis explored how poor (short) seasons affect population growth in populations with and without preformation. As above, we

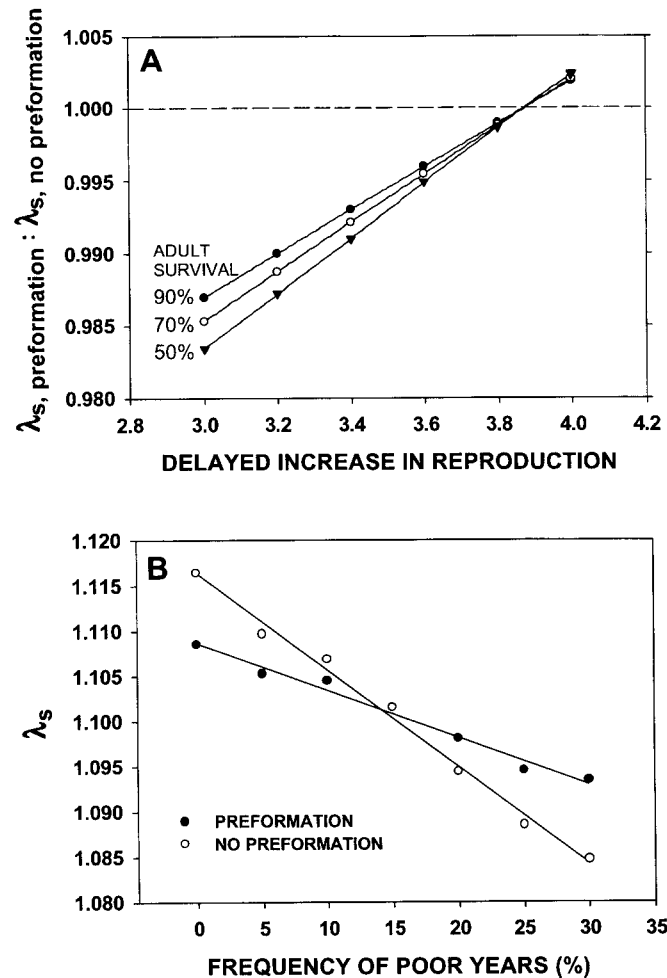


Figure 5 A. Growth rates in populations with preformation relative to populations without preformation as a function of delayed increases in reproduction by plants with preformation. Increased reproduction was in response to good (long) seasons, which occurred at a frequency of 30%. A 33% increase in seedling production during t was assumed for populations without preformation. B. Changes in rates of population growth (λ) as the frequency of poor (short) seasons increased from 0–30%. The frequency of good years was held constant at 30%. Populations without preformation increased seedling output in t by 33% in response to good years, and decreased seedling output by 33% in poor years. Good years caused populations with preformation to increase seedling output by 13% in $t+1$, whereas seedling output was not affected by poor years.

assumed a 30% probability of good years, and that populations without preformation responded to good years with a 33% increase in current reproduction. We further assumed that the surplus resources in good years were not converted to future reproduction with 100% efficiency, so delayed increases in reproduction in populations with preformation were only 13%. The incidence of poor years varied from 0 to 30%. Poor years reduced reproduction by populations without preformation by 33%, but did not affect seedling output by plants with preformation. We assumed 90% adult survival and remaining transitions were affected as described above (see Section III.C.2) and illustrated in Figure 4.

The frequency of short seasons determined whether populations with preformation grew more rapidly than populations without preformation, and seems likely to influence whether selection favors preformation. Growth rates of populations both with and without preformation declined as the frequency of short years increased (Figure 5B). This decrease occurred because seedlings were less likely to reach adult stages, and adult plants were less likely to reach or remain in the reproductive class than in good or average years (Figure 4). The effect of poor years was most severe for populations without preformation (Figure 5B) because these years also reduced seed production. In this example, population growth rates were equivalent in plants with and without preformation when poor years occurred at a rate of 15%, half the frequency of good years (Figure 5B). These results indicate that the ranges of species or populations without preformation may, in part, be restricted by the length of the growing season. The ideal test of this interpretation would be to compare related species differing in the occurrence of preformation over a latitudinal or elevational gradient.

D. Directions for Future Research

These preliminary analyses demonstrate the utility of two unrelated carnivorous plant species for examining questions of how plants respond to directional and fluctuating changes in nutrient availability, and how these responses may be mediated by developmental preformation. The combination of demographic censuses, life-table response experiments, and long-term feeding experiments have allowed us to construct realistic forecasting models for both *S. purpurea* and *P. vulgaris*. This approach could be used effectively with other plant populations, both carnivorous and noncarnivorous, to address basic issues in demography and population growth. We close this section by discussing both limitations of these models and prospects for their future development and use.

1. Limitations of the Models

The matrix models that we used have some obvious limitations. First, they do not include any density dependence – transition probabilities are not affected by current population size (cf. Grant and Benton, 2000). However, carnivorous plant population densities are typically low, and there is little evidence of simple density-dependence from experimental field manipulations of *S. purpurea* (A.M. Ellison and N.J. Gotelli, unpublished data). These models also do not include any spatial dynamics. There is a good deal of microtopography in habitats such as ombrotrophic bogs where carnivorous plants are common. Small-scale spatial variation has been documented in rates of nitrogen deposition (Ohlson and Økland, 1998) and prey capture (Zamora *et al.*, 1998). Similarly, we have not considered spatial variability in prey capture associated with microclimatic heterogeneity as described for *P. vulgaris* (Karlsson *et al.*, 1987; Thorén and Karlsson, 1998), or the variation in allocation of prey-derived nutrients when soil nutrients are also variable (Karlsson *et al.*, 1991).

We also need to consider interactions among nutrient sources for these plants. For *S. purpurea*, we have not modeled interactions of prey capture and pitcher-plant inquilines, the bacteria, protozoa, and invertebrates that inhabit its pitchers (see Section VI). Ants are the most common prey of *S. purpurea* (Cresswell, 1991; Newell and Nastase, 1998), and ant abundance is sensitive to gradients in productivity and nutrient availability (Andersen, 1992; Bestelmeyer and Wiens, 1996). Ants even may affect mineralization of nitrogen and carbon in bogs (Petal, 1998). Consequently, prey inputs to pitcher-plants are likely to change with altered nitrogen deposition regimes. Similarly, nitrogen concentrations in pitcher water may affect the diversity and abundance of the inquiline community, and hence the breakdown of prey and release of nutrients (Cochran-Stafira, 1993; Kneitel and Miller, 2002).

It is unclear whether these indirect effects of habitat quality will magnify or dampen the direct effects of nutrients on modeled demographic transitions. In *S. purpurea*, the net effects of inquiline activity may be small compared to other pathways of nitrogen. For example, Chapin and Pastor (1995) found that insect prey contributed only 10% of the nitrogen required by *S. purpurea* in a Minnesota bog. Preliminary measurements at Hawley Bog also suggest that little plant nitrogen is contributed by inquiline activity and prey breakdown. However, phosphorous production by rotifers may be very important (Bledzki and Ellison 1998), especially in light of the finding that population growth rate is sensitive to the N:P ratio (Figure 2).

Both *S. purpurea* and *P. vulgaris* exhibit developmental preformation (Shreve, 1906; Worley and Harder, 1999). Our model based on *P. vulgaris* quantifies the intuitive argument that preformation is advantageous when growing seasons are short, but not when growing seasons are long or unusually rich in resources. The responses to environmental variation that we assumed are supported by empirical evidence and our model thus captures some important consequences of preformation. However, preformation may have advantages and demographic consequences in addition to those considered here. For example, preformation decouples organ development from organ function so that plants could time developmental events to take advantage of temperatures, light levels, or specific nutrients that are not available throughout the growing season. In addition, plants with and without preformation may differ in their vegetative responses to variation in resource availability, especially when leaves also are preformed. Finally, we assumed that plants with preformation allocate surplus resources directly to future reproduction. In reality, delayed reproductive responses may be mediated through changes in plant size (Worley and Harder, 1999). Both of the above two circumstances may cause transitions involving adult plants to differ between plants with and without preformation. These possibilities may alter the relative advantages of preformation, and they highlight the need for empirical investigations comparing related species possessing and lacking preformation.

2. Prospects for Future Research

The diversity of growth forms in *Pinguicula* as well as variation among habitats in the length of growing seasons indicate that this genus may contain other species with which to conduct comparative studies of preformation. The occurrence of preformation in *S. purpurea* may provide an opportunity to compare its consequences in unrelated taxa. Although the timing of floral initiation is currently unknown in most *Pinguicula* species, it seems likely to vary widely. Indeed, Molau (1993) suggests that the extent of preformation may differ even between two temperate species, *P. vulgaris* and *P. alpina*. The variation among *Pinguicula* species may provide a unique opportunity to investigate preformation. Mexico and the milder areas of Europe hold the most potential areas for comparative studies of *Pinguicula*, because both regions include species with and without winter dormancy (Casper 1966, Legendre, 2000). Ideally, these studies would monitor natural variation in demography, as well as responses to experimental manipulations of resource levels. Such studies will identify the demographic consequences of preformation, and clarify the selective pressures leading to its evolution.

IV. COEXISTENCE OF CARNIVOROUS AND NONCARNIVOROUS PLANTS

Most terrestrial plant communities that contain carnivorous plants also contain a large number of noncarnivorous plants, and they are among the richest herb-dominated plant communities in the world (Peet and Allard, 1993; Dörrstock *et al.*, 1996; Seine *et al.*, 1996). Cost-benefit analyses (Givnish *et al.*, 1984; Benzing, 1987, 2000) suggest that carnivorous plants are poor competitors that occupy very restricted sets of "niche-space" within their habitats, although these niches have not been defined explicitly. In addition, it is necessary to define differences in niche-space between co-occurring carnivorous and noncarnivorous plants and to test for competitive interactions between carnivorous and noncarnivorous plants (Svensson, 1995). Beyond simply estimating competition coefficients, a full understanding of the adaptive significance of carnivory must include broader studies of resource competition and species coexistence.

One general hypothesis to explain species coexistence is that regular disturbances prevent competitive displacement or exclusion of poor competitors (Platt, 1975; Connell, 1978). Disturbance-mediated coexistence of carnivorous plants and noncarnivorous plants may occur in at least three different ways. First, intense disturbances (e.g. small-patch openings, alternating droughts and wet periods) may permit the establishment of fugitive carnivorous species (the *colonization hypothesis*). Second, recurring low-intensity disturbances may be associated with increases in the availability of light and prey-capture efficiency in carnivorous plants. As a result, carnivorous plants may optimize resource capture by increasing investment in carnivory with increasing light levels (the *prey-capture hypothesis*). Third, disturbance-related increases in limiting resources may be exploited efficiently by carnivorous plants and subsequently stored during years of lower resource availability (the *storage hypothesis*). These three hypotheses are not mutually exclusive and the relative importance of disturbance-mediated colonization, prey capture, and storage in maintaining the coexistence of carnivorous and noncarnivorous plants may depend on the life history of the carnivorous plant species.

Brewer examined the relative importance of these three disturbance-mediated processes using a set of field experiments with three unrelated carnivorous plant species, *Sarracenia alata*, *Drosera capillaris*, and *Utricularia juncea*, in a southern Mississippi seepage bog (described in Brewer, 1999a,c). A comparison of their relevant life history and biomass allocation traits is presented in Table 6. *S. alata* is the largest and longest-lived of the three species and has the lowest reproductive allocation.

Table 6 Summary of life span and average biomass allocation of 20 individuals of each of three carnivorous plant species. Reproductive allocation includes the mass of the scape, a leafless, flower-bearing stalk (data of J. S. Brewer 1999b,c, and unpublished)

Species	Life Span	Dry Mass	% Reproductive Allocation
<i>Sarracenia alata</i>	> 50 yr/genet	14.3 g/ramet	0.9
<i>Drosera capillaris</i>	< 10 yr	0.06 g	5.0
<i>Utricularia juncea</i>	1 yr (annual)	0.01 g	91.0

Both *D. capillaris* and *U. juncea* are much smaller and much shorter-lived. Both have higher reproductive allocation than does *S. alata*.

A. Disturbance-Mediated Colonization

The two small, short-lived species, *D. capillaris* and *U. juncea*, responded rapidly to artificial disturbance to groundcover vegetation with dramatic increases in seedling density (Figure 6). In contrast, the long-lived species, *S. alata*, did not colonize small patches in 1997, nor was colonization observed in the subsequent two years. Thus, *D. capillaris* and *U. juncea* may be regarded as fugitives or efficient colonizers that escape competition from neighboring plants by dispersing through time or space (Brewer, 1999b, c). The ability of short-lived species such as *D. capillaris* and *U. juncea* to escape competition by producing persistent seed banks that respond rapidly to small disturbances may be critical to their persistence.

In addition to being fugitives, short-lived carnivorous species with high reproductive effort also may be effective ruderal strategists (*sensu* Grime, 1979) in nutrient-poor and ephemeral habitats (Brewer, 1999b), habitats for which Grime (1979) argued that there was no viable terrestrial-plant strategy for persistence. Specifically, Grime (1979) argued that the rapid maturation needed to produce numerous offspring in ephemeral habitats was not possible when nutrient levels remained chronically low during otherwise favorable windows for growth. However, wet and nutrient-poor ephemeral habitats in West Africa ("Inselbergs": Dörrstock *et al.*, 1996) frequently are dominated (in terms of species number) by carnivorous plants, particularly short-lived species in the genera *Utricularia* and *Genlisea*. Favorable conditions for growth of Inselberg vegetation are determined by the abundance of water (Dörrstock *et al.*, 1996) and nutrient levels remain low during the brief wet periods. The dominance of Inselberg vegetation or disturbed microsites by ruderal species that obtain nutrients from some source other than the soil (e.g. carnivorous plants,

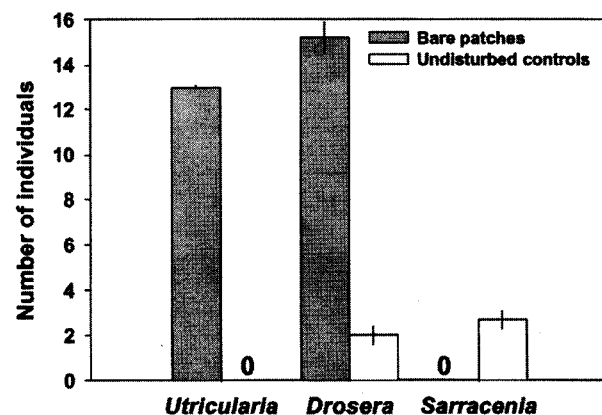


Figure 6 Responses of three carnivorous plant species to artificial disturbances at Wolf Branch Bog and Little Red Creek Bog, Mississippi, USA (Brewer 1999a-c). Sixteen pairs of 0.5×0.5 patches were created; each pair consisted of one control patch and one cleared with application of a short-lived herbicide in May 1996. Two weeks later, all standing dead and litter were clipped and removed from the disturbed plot. were 0.5×0.5 m. Plant densities were determined 1 year after creation of the bare patches. Error bars are ± 1 standard error.

hemi-parasites, epiphytes) would seem to provide an exception that proves Grime's rule (Brewer 1999b).

B. Disturbance-Regulated Prey Capture

Because of its long life span and the lack of a persistent seed-bank, *S. alata* in these Mississippi seepage bogs did not respond to disturbance through increased colonization (Figure 6). It did, however, respond to a reduction in aboveground competition caused by disturbance (fire) by increasing its efficiency of prey capture. Pitcher-plants in unburned sites produced significantly taller pitchers with greater mass allocated to support tissue at the expense of the volume of the capture chamber than did pitchers at burned sites. Consequently, the amount of prey captured per unit mass of pitcher produced was significantly lower at the unburned site (Figure 7).

Disturbance-regulated allocation to carnivory appears to be an important means by which perennial sit-and-wait foraging plants such as *S. alata* optimally allocate resources to light or prey capture (Brewer, 1999a). Similar patterns of flexible allocation to carnivorous structures in contrasting habitats have been demonstrated using *Pinguicula vallisnerifolia* (Zamora et al., 1998). The notion that plants either invest in the capture of one

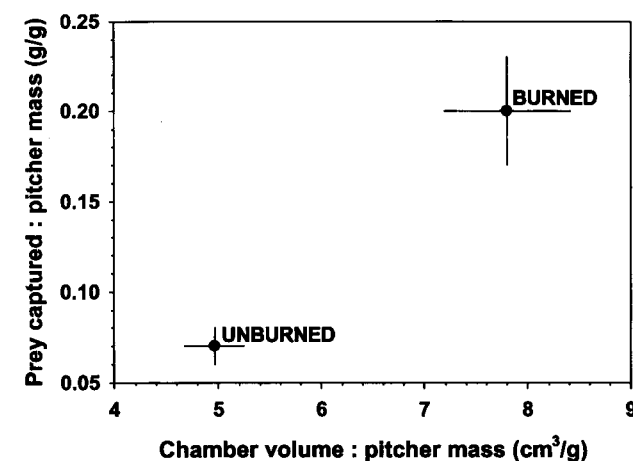


Figure 7 Changes in pitcher morphology and prey-capture efficiency of *S. alata* in response to fire. Four populations of pitcher plants in Stone and Harrison Counties in southern Mississippi were studied in August 1999. Two of the sites (DeSoto South and DeSoto North) had been burned earlier that year, while the other two (Wolf Branch and Sandy Creek) had not. All four sites had been burned regularly (once every 3–5 years) in the past 20 years and were similar in species composition, shrub density, and pitcher-plant density. Twenty live, undamaged *S. alata* pitchers with similar diameters were collected at each site. Pitcher volume was estimated by calculating the volume of a cone with length equal to that measured for the pitcher chamber and basal diameter equal to the measured internal diameter at the lip. Pitchers were dissected and all prey mass was removed. Pitchers and prey were dried for 72 h at 40°C, then weighed. Nested ANOVA (variation among pitchers was nested within site, and site variation was nested within burn treatment) was used to analyze the data. The nonsignificant site(burn treatment) term was pooled with the pitcher(site) term, and this pooled error term was used to test the effect of burn treatment on pitcher volume : pitcher mass ($P < 0.0001$) and prey mass : pitcher mass ($P < 0.0001$).

resource at the expense of another or optimally forage for both appears to be a false dichotomy; carnivorous plants can do both. This observation has important implications for resolving a long-standing, contentious debate on the nature of resource competition (Grime, 1979; Tilman, 1982, 1988, 1990; Keddy, 1989; see Section IV.D).

C. Disturbance-Regulated Storage

Although *S. alata* was capable of changing pitcher morphology in response to fire (Figure 7), such changes might still be insufficient to prevent their

competitive displacement by noncarnivorous plants. Fire-regulated storage may provide an additional mechanism by which *S. alata* effectively competes with noncarnivorous plants. Following fire, *S. alata* increased investment in pitchers at the expense of rhizomes and roots (Brewer, 1999a). Starved pitcher-plants did not exhibit reduced growth rates when growing alongside noncarnivorous plants (J.S. Brewer, unpublished data). However, denying prey to pitcher-plants did reduce their growth rates when neighbors were reduced and investment in pitchers was at its peak (J.S. Brewer, unpublished data). Hence, the long-lived *S. alata* competed successfully with surrounding groundcover vegetation via fire-regulated plasticity in carnivory and belowground storage of biomass assimilated from resources captured at higher rates following fire (Brewer, 1999a). In this way, *S. alata* stored resources gained in good years for resource capture. Such a strategy may allow for coexistence of *S. alata* with noncarnivorous plants that are more efficient competitors for light and nutrients but do not exhibit a comparable level of adaptive fire-regulated plasticity.

D. Directions for Future Research

Because of their unique adaptations to a specific environmental template, carnivorous plants can be used as a model system to study the more fundamental and general problem of species coexistence in changing environments. Carnivorous plants have the ability to escape or tolerate competition from noncarnivorous plants, and the adaptations they employ to reduce the impact of competition vary according to their life history. Trade-offs between colonizing ability and longevity play an important role in the coexistence of short-lived carnivorous plants and longer-lived noncarnivorous plants. In contrast, adaptive plasticity may be important in permitting perennial carnivorous species to compete effectively with perennial noncarnivorous species. Future observations and experiments using carnivorous plants to study these trade-offs could provide a means of testing hypotheses associated with a long-standing debate on plant competition (Grime, 1979; Tilman, 1982).

1. Two "Alternative" Hypotheses

Grime (1977, 1979) proposed a mechanism by which competition occurs in plant communities (the *C-S-R strategy hypothesis*). Specifically, he argued that in productive and relatively undisturbed habitats, long-lived plants with relatively high growth rates and extensive morphological plasticity (strong *competitors*) should displace rapidly growing but short-lived plants with high investment in reproduction (*ruderals*). The strong competitors

should also displace long-lived but slowly growing plants with high investment in storage and defense (*stress-tolerators*). Thus, Grime predicted that competition reduces species diversity in productive habitats because of the displacement of ruderal and stress-tolerant species.

Tilman (1982) proposed a different mechanism by which competition occurs in plant communities (the *resource-ratio hypothesis*). In a system in which two species compete for the same limiting resource, competitive exclusion occurs as a result of one species having a lower requirement for that limiting resource at equilibrium (Tilman, 1982). As soil fertility increases, the resource most limiting to growth shifts from soil nutrients to some other resource or resources (e.g. Tilman, 1988). As a result, a species that is a better competitor for light but a poor competitor for nutrients displaces a species that is a better competitor for nutrients but a poor competitor for light. A good competitor for light is assumed to be a species that invests a significant fraction of biomass into stems and leaves (Tilman, 1988). Competition is predicted to reduce species' diversity in productive habitats by reducing spatial heterogeneity in the supply of limiting soil resources (Tilman and Pacala, 1993).

2. What is Competitive Ability?

The mechanisms of competition differ between the C-S-R and resource ratio hypotheses (Goldberg, 1990; Grace, 1991). Although both hypotheses describe competitive ability as a plant's ability to deplete resources and avoid areas of resource depletion created by other plants, they disagree over how competition operates in habitats in which soil resources are chronically in short supply. According to the C-S-R hypothesis, species adapted to nutrient-poor soils (i.e. stress-tolerators) escape competition *in time*, by storing resources, using them conservatively, and taking advantage of periodic reductions in competition or increases in resource supply. In contrast, the resource-ratio hypothesis predicts that species adapted to nutrient-poor soils (i.e. belowground competitors) escape competition *in space* by maintaining high allocation to roots, thereby providing them access to soil resources that are not available to species with smaller root systems. Because both storage and soil-resource uptake are accomplished by roots and other belowground parts in many plants, both hypotheses predict that allocation to belowground parts likely would be greater in plants adapted to nutrient-poor soils. Hence, neither hypothesis can be refuted by measuring root-shoot ratios along productivity gradients.

Some researchers have attempted to examine the mechanisms of competition by separating competitive effects into aboveground and

belowground components (e.g. Wilson and Tilman, 1995; Twolan-Strutt and Keddy, 1996). The rationale behind these experiments was that, if belowground competition were intense in nutrient-poor soils, then its intensity would decline with increasing soil fertility (as predicted by the resource-ratio hypothesis). Experiments of this type have yielded conflicting results. One explanation is that separating competitive effects into aboveground and belowground components did not allow investigators to assess the relative importance of competition for nutrients and competition for water. Wilson and Tilman (1995) found significant belowground competition in a dry to mesic habitat with infertile soils, whereas Twolan-Strutt and Keddy (1996) found that belowground competition was not particularly intense in infertile soils of the wetlands they studied. Perhaps much of what these investigators measured when they examined belowground competition was competition for water, not nutrients, and that this form of competition was more intense in drier habitats. Measuring belowground competition is no substitute for directly measuring competition for nutrients and water.

3. *Competition for Water between Carnivorous and Noncarnivorous Plants*

Plant communities containing carnivorous plants represent an ideal system in which to examine separately belowground competition for nutrients and water. Terrestrial carnivorous plants are unique in that many species invest a significant fraction of biomass into the attraction and capture of nutrients aboveground (e.g. pitchers, attractive pigments, trapping hairs, mucilage). In contrast, uptake of water is accomplished primarily by belowground organs (roots). Such spatial separation of water uptake and nutrient uptake in carnivorous plants results in relatively low allocation to roots compared to noncarnivorous plants of the same size (J. S. Brewer, unpublished data). Comparisons of competitive responses of carnivorous plants and noncarnivorous plants along fertility gradients thus provide a way to measure the intensity of belowground competition for water as a function of soil fertility.

The resource-ratio hypothesis predicts that if competitive ability is determined by allocation to a particular type of uptake organ (i.e. roots vs prey traps), then as soil fertility increases, carnivorous plants will be at a competitive disadvantage relative to noncarnivorous plants of similar size. This is because as soil fertility increases, growth becomes limited more by light and water than by nutrients. The larger root systems of noncarnivorous plants should confer a competitive advantage in habitats in which competition for water is intense. In contrast, the C-S-R hypothesis predicts

that if competitive ability of adults is determined by high relative growth rate and vegetative mobility, then as soil fertility increases, slower-growing plants with a reduced capacity for clonal growth will be at a competitive disadvantage relative to faster-growing plants with well-developed vegetative mobility.

These two hypotheses are not mutually exclusive. For example, rhizomatous carnivorous plants may be favored over nonrhizomatous carnivorous rosettes in fertile soils (predicted by the C-S-R hypothesis), and both growth forms may incur a competitive disadvantage to comparable noncarnivorous plants (predicted by the resource-ratio hypothesis). However, by examining functional responses of *entire communities* to soil fertility gradients, one could evaluate the relative importance of these different mechanisms of competition in terms of their impact on species diversity. In this way, new insights could be gained into the role that interspecific competition plays in determining community structure and species diversity.

V. PLANT-INSECT INTERACTIONS

The physical environment also can strongly affect the outcome of ecological interactions other than competition (e.g. Dunson and Travis, 1991; Bronstein, 1994; Thompson, 1994; Travis, 1996). Site-specific effects in plant-insect relationships may be particularly important, because the physical environment governs the ecophysiology both of plants, given their sessile lifestyle, and of insects, due to their small size. Ecological and evolutionary consequences of plant-insect interactions can vary among contrasting environments, even at very small spatial scales (Herrera, 1995b, 1997; Zamora, 1995). When insects are pollinators, the consequences of the spatial structuring of plant-animal interactions can directly determine the direction and magnitude of gene flow and the potential for evolutionary differentiation.

Environmental gradients, such as gradients in elevation, and differences in exposure or moisture availability, quite often generate significant barriers to gene flow via effects on plant phenology and pollinators, enhancing genetic differentiation among semi-isolated populations (Linhart and Grant, 1996). For this reason, estimation of the spatial and temporal dynamics of gene flow via pollen or seeds must consider ecological factors that can determine gene flow in a landscape context (Sork *et al.*, 1999). Furthermore, different agents of selection in space may generate different selection pressures on a microscale. Barriers to gene flow and differential selection pressures can act synergistically, producing and maintaining heterogeneity in natural populations.

Carnivorous plants are ideal organisms with which to study the ecology and evolution of plant–animal interactions in heterogeneous environments, because these plants depend upon animals in several different ways (Givnish, 1989; Juniper *et al.*, 1989). Like most angiosperms, carnivorous plants can be eaten by herbivorous animals and pollinated by insects. Nevertheless, they differ from the other plant species in having the capacity to catch animal prey and assimilate captured nutrients. As discussed above, most carnivorous plants are restricted to nutrient-poor habitats that present relatively homogeneous conditions of insolation and substrate moisture, at least during the growing season. In Mediterranean habitats, however, most carnivorous plants in the genus *Pinguicula* grow in scattered rocky and wet sites in primarily limestone mountains. The complex orography of Mediterranean mountains provides contrasting sunny (hot and dry) and shady (cool and wet) exposures. Unlike ephemeral sunny and shady patches in a forest, the contrasting exposures in the rocky relief of mountains are persistent in time and offer relatively constant radiation, temperature and moisture conditions over thousands of years. These environments are hypothesized to condition plant reproductive ecology and gene flow via pollinators, even at a very limited spatial scales, producing temporal (phenological) barriers and spatial barriers in the distribution and abundance of plants and their interacting animals.

This hypothesis has been tested with the endemic carnivorous plant *P. vallisneriifolia*, which inhabits crevices in wet, rocky habitats that span a broad range of irradiance and temperature regimes (Zamora *et al.*, 1996, 1998; Zamora, 1999). Here, we describe how environmental heterogeneity determines the flowering phenology of *P. vallisneriifolia* and its plant–pollinator interactions, and explore the consequences of this heterogeneity for gene flow via pollen transfer. These studies illustrate how these plants can be used as model systems to study the effects of spatial and temporal heterogeneity on ecological and evolutionary dynamics of plant populations.

A. Large-Scale Phenology and Pollination Ecology of *Pinguicula vallisneriifolia*

P. vallisneriifolia has a scattered geographic distribution, with populations of variable sizes (normally 100–10,000 reproductive plants per population). This species shows remarkable spatial variation (within and between populations) in floral traits such as size, shape, color patterns of the corolla, and presence of floral guides (R. Zamora, *unpublished data*). *P. vallisneriifolia* is self-compatible, but spontaneous autogamy does not occur due to herkogamy. Experimental hand-crosses resulted in nearly

100% fruit set. Hand-pollinated flowers produced twice as many fruits, and larger seeds per capsule than naturally pollinated flowers. Thus, Zamora (1999) concluded that seed production by *P. vallisneriifolia* is pollen-limited and pollen transfer is limited by the availability of insect pollinators. Because of their small size, seeds of *P. vallisneriifolia* likely are wind-dispersed, but gene flow via seeds appears to be limited because the capsule opens towards the rock wall (geoautochory). This directional dispersal results in most seeds settling very near to the parent plant.

Flowering phenology of *P. vallisneriifolia* was studied in 11 populations distributed broadly throughout its range in the Sierras de Cazorla, Segura y Las Villas, an orographically complex area of Spain with mountainous escarpments and narrow valleys (Zamora, 1999). All populations grew on cliffs that vary in their exposure to direct sunlight. At these sites, flowering phenology depended principally on the orientation of the cliff where the plants grow, and secondarily on altitude (Figure 8). Populations situated at lower altitudes started to flower in April, well before the populations situated at higher altitudes. However, populations situated at similar altitudes can still differ markedly in flowering phenology, depending on the exposure of the cliff – populations growing in southern exposures flower before the populations growing in northern ones (Figure 8). For example, the Agracea population fruits while the Covacho population is still flowering, despite the fact that both populations are at the same altitude, and are only 1 km apart (Figure 8).

Thirty-six flying insects visited flowers of *P. vallisneriifolia* in these populations during a total of 88 observation hours (mainly *Bombylius* sp., *Lassioglossum* sp., and *Bombus terrestris*). The presence of these floral visitors appeared to be associated with irradiance, as they were almost absent from the shadiest populations (Table 7). Even in the sunniest populations, however, the presence of flower visitors was restricted to the period of sunlight on the plants: 90% of floral visitors were observed during 17% of the total observation time. In contrast to the rarity of these medium-to-large pollinators, in all populations but one, thrips (*Taeniothrips meridionalis*) and beetles (*Eusphalerum scribae*) visited the flowers. In the sunniest populations, thrips were frequent floral visitors, whereas in the shadiest populations, thrips were rare (Table 7). The shadiest populations had the lowest fruiting success, probably because of the scarcity of pollinators (Table 7).

B. Small-Scale Differences in Phenology and Pollination Ecology

Zamora (1999) also studied flowering phenology and pollinators of *P. vallisneriifolia* in three populations in the center of its geographical range

SITE (ELEVATION IN m)

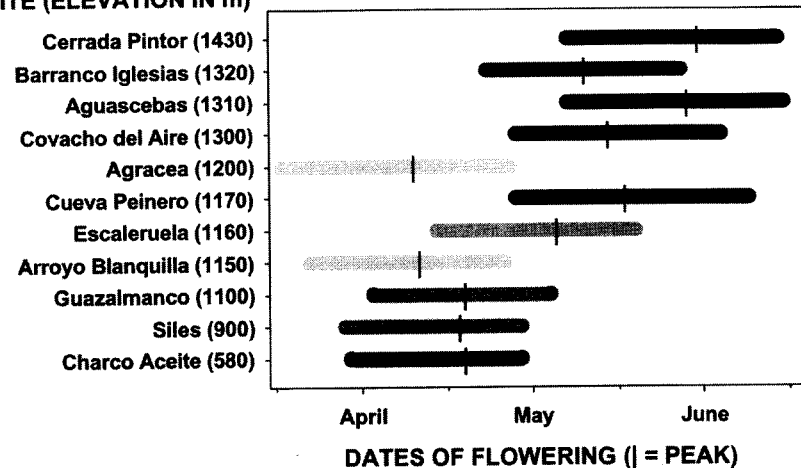


Figure 8 Flowering phenology of populations of *P. vallisneriifolia*. The percentage of plant populations in flower was estimated by weekly visits between April and July 1992 in 11 populations. Population phenological stage was determined by creating a scale using the proportion of reproductive plants in flower with three levels: start of flowering (<25% of reproductive plants in bloom), peak flowering (>75% of reproductive plants in bloom), and end of flowering (<25% of plants in bloom). Bar shading is proportional to insolation at each site, which ranged from 0 (black bars) to 300 (lightest bars) minutes per day.

Table 7 Results of pollination censuses conducted during 1992 in 11 populations of *P. vallisneriifolia* broadly distributed throughout its geographical range (Zamora, 1999). Values are means \pm 1 standard error

	Sunny ¹	Shady ²
Large pollinators (number observed/10 h)	4.5 \pm 1.5	0.2 \pm 0.3
Thrips (% of flowers occupied)	35.6 \pm 12.5	9.0 \pm 8.1
Beetles (% of flowers occupied)	7.0 \pm 1.6	7.0 \pm 0.1
Reproductive success (# Fruit : # Flower)	67.7 \pm 7.5	32.7 \pm 7.2

¹ Populations were classified as "Sunny" ($N = 8$) when plants received direct sunlight for 1–5 h/day.

² Populations were classified as "Shady" ($N = 3$) when plants received no direct sunlight during blooming.

that, although within 10 m of each other, had statistically different ($P < 0.05$, all variables) levels of insolation, temperature, and relative humidity (Table 8). The flowering period for the sunlit population was from May 5 to June 8 (peak flowering on May 22) and for the shade and deep shade population from May 12 to June 15 (peak flowering on June 2). Although

Table 8 Abiotic conditions, pollinator abundance, and reproductive success in three portions of a single population of *P. vallisneriifolia* (Zamora, 1999). Each portion was separated by 10 m. Values for irradiance, air temperature, and relative humidity are means \pm 1 standard error for hourly measurements taken on 8 June 1994. Pollinator censuses were performed in 1994 and 1995, as described in Table 7

	Sunlit ¹	Shade	Deep Shade
Abiotic conditions			
Irradiance (W/m ²)	128.2 \pm 25.5	29.2 \pm 4.8	6.5 \pm 0.6
Air Temperature (°C)	19.8 \pm 1.6	18.4 \pm 0.7	17.1 \pm 0.5
Relative Humidity (%)	50.0 \pm 4.4	56.3 \pm 3.7	63.6 \pm 3.4
Pollinators			
Large (number observed/10 h)	33.7 \pm 11.2	1.7 \pm 1.9	0
Thrips (% of flowers occupied)	95.0 \pm 1.4	43.5 \pm 2.4	2.5 \pm 0.3
Thrips (number/flower)	5.0 \pm 0.28	1.1 \pm 0.14	0.02 \pm 0.01
Beetles (% of flowers occupied)	4.5 \pm 0.3	13.0 \pm 2.8	14.0 \pm 0.36
Beetles (number/flower)	0.03 \pm 0.01	0.15 \pm 0.03	0.17 \pm 0.14
Reproductive success			
Number of Fruits : Number of Flowers	75 \pm 5.7	40 \pm 2.3	60 \pm 0.0
Number of seeds/capsule	107.2 \pm 21.1	67.1 \pm 16.0	96.0 \pm 21.4

¹Sunlit: 2 h/day of direct morning sun; Shade: north-facing cliff with no direct sunlight; Deep Shade: small cave at the bottom of the north-facing cliff.

flowering time of plants within the same population growing in different exposures overlapped for most of the blooming period, plants in the sunny exposures began flowering before plants in the shaded ones. For example, a plant in a sector of the cliff facing west and receiving approximately 6 h of direct afternoon and evening sunlight started flowering 20 days before the rest of the plants of the same population. Thus, even within the same population, plants in microhabitats differing in exposure also differed in onset and timing of flowering.

In the shade and deep shade populations, pollinators were uncommon (Table 8). Significantly more large pollinators ($P < 0.0001$) visited flowers in the sunlit population (Table 8). Even in this habitat, however, 87% of the floral visitors were observed when sunlight fell directly on the flowers, during <50% of the total observation time. Thrips were very common at flowers in the sunlit population, less abundant in the shade population, and virtually absent from the deep shade population (Table 8). In contrast, beetles were less abundant in the sunlit population than in the shade and deep shade ones. Results of pollinator censuses in these three geographically proximate habitats were qualitatively similar to those obtained in the large-scale survey: medium-to-large pollinators and thrips were almost absent from the shadiest habitats. Thus, microgeographic variation in the

abiotic environment leads to the potential for within-population isolation of patches exposed to different environmental regimes, despite their small separation.

C. Scale-Independent Patterns in Phenology and Pollination

The cliffs where *P. vallisneriifolia* grows cast shadows where sunlight barely reaches. In these shady places where temperatures remain low during blooming, occupancy by many ectothermal insect species is limited because they cannot remain active below certain temperatures (Corbet, 1990; Herrera, 1995a). Even in the sunniest exposures, both large- and small-scale studies showed that most medium-sized pollinators foraged at flowers only during the short period when sunlight fell directly on the flowers, presumably relying on solar radiation for suitable flight temperatures (Kingsolver, 1985; Pivnick and McNeil, 1986; Herrera, 1997). Small pollinators visited flowers in all habitats, however. Thrips primarily visited flowers in the sunlight, and beetles visited those in the shade. There was site-specific predictability in the interaction between *P. vallisneriifolia* and its pollinators, because the same species of pollinators invariably appeared in the same microclimatic setting, regardless of spatial scale.

D. Gene Flow Within and Between Populations

Within populations, spatial proximity may permit pollen flow. However, the highly patchy and heterogeneous environment of *P. vallisneriifolia* populations can impose strong limitations to gene flow: realized pollen dispersal depends both on the movements of pollen by vectors and on post-pollination events that determine the mating system (Levin and Kerster, 1974; Loveless and Hamrick, 1984; Krauss, 1994). In *P. vallisneriifolia*, outcrossing results in fruiting success that is statistically similar to selfing, whether measured in terms of fruit-set, seed set, or seed mass (Zamora, 1999). Observed seed set is likely to represent a mixture of outcrossed and self-fertilization, with a bias towards selfing because of environmental limitations to pollinator movements. The resulting low outcrossing rate favors paternity pools of limited spatial size that can severely restrict gene flow among plants, even within the same population.

Pollen dispersal appears to be concentrated within habitats, and is confined within patches by steep gradients in irradiance and thermal regimes and associated pollinator assemblages (see also Herrera, 1995b). Spatial variability in the abundance and species composition of the pollinator assemblage translates into differential reproductive success for

P. vallisneriifolia (Tables 7, 8) because plants are pollen limited. Pollen flow engendered by small pollinators – thrips and beetles – is even more restricted. These pollinators spend most of their time foraging on the same flower, resulting in autogamy. In addition, the carnivorous *P. vallisneriifolia* very frequently captures small flower visitors (Zamora, 1999). The capture of thrips and beetles by the plant depletes an already limiting resource for plant reproduction, the number of free (untrapped) pollen vectors. The value of such insects as pollinators may decrease, since trapped insects cannot transfer pollen loads. Taken together, these data raise the prospect of sympatric evolutionary diversification among proximate populations in contrasting exposures.

Similarly, gene flow via pollen between populations may be strongly constrained, and the intensity of divergent selection may be fueled, because of asynchronous flowering phenology resulting from differences in exposure or altitude and differential distribution of pollinators among sunny and shade habitats, as well as geographical distance and complex landscape orography. Table 9 illustrates the range of possible results, considering population-level variation in distance and microclimate. The combination of close and similar microclimates produces no differences in flowering phenology and pollinator assemblages. Large spatial separation and contrasting microclimates lead to the largest differences in both flowering phenology and pollinator assemblages. In this case, gene flow is limited temporally by phenology and spatially by microclimate, and geographic differentiation is promoted. The other two combinations can also bring about microevolutionary variability, but less than that resulting from the interaction of distance and microclimate. Interestingly, these patterns also can lead to evolutionary convergence, a common feature among carnivorous plants (Ellison and Gotelli, 2001). If plant phenology and the structure of pollinator assemblages are as strongly constrained by microclimate as described here, then we predict that the plant–pollinator interactions will

Table 9 Degrees of diversification resulting from the two main sources of variability, microclimate and distance, between populations of *P. vallisneriifolia*

	Microclimate	
	Similar	Different
Spatial separation		
Small	None	Low
Large	Low	High

converge, and there will be repeatable, directional selective pressures on plants and pollinators under similar abiotic scenarios, regardless of the spatial distance separating populations.

E. Directions for Future Research

Microclimatic differences increase variation in flowering phenology among nearby populations, while reducing variation among distant populations growing at similar elevations and exposures. Microclimate also affects directly the distribution and abundance of pollinators. The ecological mechanisms generating and maintaining variability in *P. vallisneriifolia* can be generalized to other plant–animal systems that occur in patchy environments. When the main source of spatial variability for plant–animal interactions is microclimate, not geographical distance, as it is for *P. vallisneriifolia* and its pollinators, one can ask whether this source of microclimatic variability favors selective mosaics within populations. Further, the same pollinators of *P. vallisneriifolia* occur throughout its geographical range, but different subsets of this pollinator assemblage appear in different abiotic settings, irrespective of distance. Plant–pollinator assemblages such as these that occur over large geographic scales are ideal model systems with which to test whether there is spatial variation in the outcomes of interactions, as proposed by Thompson’s (1994, 1999a, b) theory of geographic mosaics of interactions. Alternatively, do repeatable spatial or temporal patterns of interactive outcomes resulting from similar abiotic conditions give rise to similar plant phenological responses and similar pollinator species?

Classical theoretical models that analyze gene flow stem from concepts based on an isolation-by-distance approach. Isolated populations become differentiated through mutations and genetic drift. Reductions or changes of pollinator species have been proposed to accompany variations in the size of fragmented populations, and these reductions affect seed production and outcrossing rate (Aizen and Feinsinger, 1994; Kearns *et al.*, 1998). The observations of *P. vallisneriifolia* and its pollinators clearly show the need to consider other factors affecting gene movement in addition to distance and fragment size, such as the degree of synchrony in flowering phenology, and the behavioral responses of pollinators to contrasting microclimates. These ecological factors also can determine strongly and limit the spatial and temporal dynamics of pollen flow within the context of complex landscapes (Sork *et al.*, 1999).

Studies combining these two approaches – geographic mosaics of interactions and analysis of ecological impacts on gene flow – can be used to ask whether there is a correspondence between microclimatically driven

heterogeneity and genetic variability within populations and whether reproductive isolation by microclimatic barriers can lead to speciation. In past studies, changes in the ploidy level have been viewed as the basic mechanism for evolutionary diversification in *Pinguicula* (Casper, 1972; Zamora *et al.*, 1996). Ecological isolation and adaptation to different environments represent a different, ecologically driven mechanism for evolutionary diversification. At a minimum, the results to date lead to exciting questions connecting plant reproductive ecology with evolutionary aspects of plant populations and plant–animal interactions. A relevant question is whether, within populations, gene flow via pollen or seeds is too low, and the intensity of divergent selection in contrasting exposures too high, to favor morphological or reproductive divergence with consequences for speciation.

How important are these ecological mechanisms relative to random drift in the evolution of differences between populations? Because of genetic drift, isolated populations of *P. vallisneriifolia* may be prone to loss of genetic variability within populations and genetic divergence among populations (Barret and Kohn, 1991; Coyne, 1992; Schemske *et al.*, 1994). Ecological isolation by microclimate represents a premating barrier to gene flow. The mosaic of flowering asynchrony, differential animal assemblages and resulting gene-flow barriers invariably spurs additional variability, both within populations and between populations. These mechanisms can act synergetically, and can amplify ecologically driven speciation of flowering plants in habitats where spatial distance, complex orography, and microclimatic barriers limit gene flow, and prompt local differentiation. The result is an increasing likelihood of speciation (Rice and Hostert, 1993; Orr and Smith, 1998).

VI. PHYTOTELMATA

Many of the carnivorous plants with leaves modified into pitfall traps – the pitcher-plants in the genera *Sarracenia*, *Darlingtonia*, *Heliophora*, *Cephalotus* and *Nepenthes* – host low-to-moderate-diversity communities of “inquilines” – bacteria, protozoa, rotifers, and invertebrates (mostly mites and dipteran larvae). These “phytotelmata” communities have been studied for decades, and the natural history and food web structure of their invertebrate communities have been sufficiently well-documented (reviewed in Cochran-Stafira, 1993; Kitching, 2000) that they can now be used as model experimental systems for a wide variety of studies examining trophic interactions, food web dynamics, and metapopulation structure across a range of timescales. We focus on these topics using the *S. purpurea* inquiline communities as our exemplar.

A. The Inquiline Community of *Sarracenia purpurea*

S. purpurea ranges throughout Canada and the eastern USA where it grows in bogs, nutrient-poor fens, and seepage swamps (Folkerts, 1999). Among the 11 species of *Sarracenia*, *S. purpurea* is the only one that hold pools of water in the tubular leaves for an extensive period of time (Folkerts, 1999). The leaves are produced approximately every 20 days (Fish and Hall, 1978) and can hold up to 50 ml of water. A high diversity of arthropods, including collembola, ants, spiders, millipedes, and grasshoppers, are attracted to the leaves where they drown in the standing water. The decomposition of these prey provides the energy to support the inquiline community that consists of bacteria, fungi, protozoans, algae, rotifers, flatworms, nematodes, mites, and fly larvae. Throughout its range, the inquiline community of *S. purpurea* is quite similar, and is organized into a three-level food web (Fish, 1983; see Figure 9). Detritivores – the slime mite *Sarraceniopus gibsonii*, and larvae of the midge *Metriocnemus knabi* and the sarcophagid fly *Fletcherimyia fletcheri* – consume prey items that are further decomposed by bacteria. Bacteria serve as the primary source of food for the rest of the community. Protozoans and rotifers (usually *Habrotrocha rosa*) make up the second trophic level and consume bacteria as well as detritus. The top trophic level is occupied by the omnivorous mosquito larvae *Wyeomyia smithii*, which consumes protozoa, rotifers, and bacteria. *F. fletcheri* also consumes rotifers and small *W. smithii* larvae (Bledzki and Ellison, 1998).

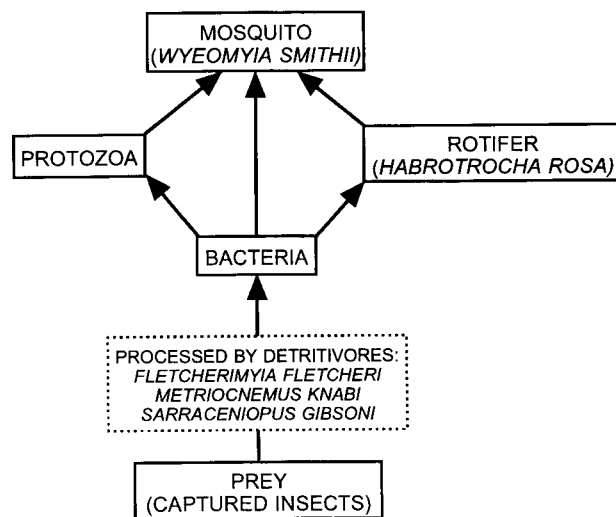


Figure 9 Simplified food web structure of *Sarracenia purpurea*-inquiline communities.

Table 10 Approximate generation times for inquilines of *S. purpurea*

Taxon	Generation time (days)
Bacteria	0.014
Protozoa	0.1–0.5
Rotifers	2
Mosquito larvae (in pitcher)	21

Data from Istock *et al.* (1975); Bledzki and Ellison (1998); Pianka (2000).

Experimental studies using the *S. purpurea* inquiline system began with Addicott's (1974) work of the effects of *W. smithii* predation on protozoan species diversity. Heard (1994a) investigated the processing chain mutualism between *W. smithii* and *M. knabi* larvae, and Cochran-Stafira and von Ende (1998) studied multi-trophic-level interactions among mosquito larvae, protozoa and bacteria. More recent work has expanded the focus of these studies to include the rotifer (Petersen *et al.*, 1997; Bledzki and Ellison, 1998) and bacterial (Miller *et al.*, 2002; N. Ward, A. M. Ellison, and N. J. Gotelli, unpublished data) assemblages within the pitchers.

The inquiline community is an excellent system to use for testing predictions of food web theory. The inquilines have short generation times (Table 10) and relatively short experiments can capture the dynamics of the system (Addicott, 1974; Cochran-Stafira and von Ende, 1998). The food web can be manipulated and replicated easily, in both the laboratory and the field. The discrete nature of the community (bordered by the walls of the pitcher-plant leaf) defines the scale at which local dynamics occur. Within pitchers, the spatial scale of the community is relatively consistent and so whole-system experiments can be conducted with the pitcher inquilines with less concern for within-pitcher spatial variability.

Observed variation in species abundances that occur among pitcher-plant communities (Harvey and Miller, 1996) also can be used to study the dynamics of metapopulations and metacommunities. Harrison and Taylor (1997) criticized earlier laboratory and greenhouse tests of multi-species metapopulation models because of low replication or insufficient numbers of generations. They also argued that the few field tests of metapopulation models were flawed because the organisms studied either had dormant life stages that might mask extinction and colonization processes, or had differential susceptibility to abiotic causes of extinction. *S. purpurea* inquilines solve these problems: pitchers themselves are relatively short-lived habitats that vary in productivity with age and

season (Cochran-Stafira, 1993), and inquilines that inhabit a given pitcher must therefore colonize new pitchers before the demise of the current one. (2) the abundance of pitchers in any one bog permits high levels of replication; (3) these communities can be studied for multiple generations because of the rapid population turnover of many of the species; (4) although some species do have dormant life history stages (e.g. protozoan cysts), the ephemeral nature of the habitat itself requires that dispersal occur if the population of that species is to persist; (5) the most likely causes for extinction due to abiotic factors would be drought (pitchers fail to fill with water) or destruction of the pitcher. In both cases, all the inquilines would be at the relatively the same risk for extinction since all are aquatic.

Properties of the *S. purpurea* inquiline system also can generate new perspectives on community assembly rules (*sensu* Diamond, 1975; Weiher and Keddy, 1999). Most research to date on community assembly has not been experimental: notable exceptions are the laboratory microcosm studies by Drake and coworkers (1991, 1993), Sommer (1991), and Lawler (1993a), and the field studies of Weiher and Keddy (1995). In these studies, as in more traditional statistical analyses of patterns of species co-occurrences, interactions between the assembling communities and their habitats have been neglected (Gotelli and Graves, 1996). However, biogenic habitats, such as the growing and developing leaves of *S. purpurea*, can create considerable habitat complexity (Jones *et al.*, 1997) that can modify subsequent colonization and potential for coexistence. Inquilines are known to respond to pitcher properties, such as leaf age (Fish and Hall, 1978; Heard, 1994b), and so the inquiline community of *S. purpurea* can be used as a model system to test, in the field, whether assembling communities respond to changes in plant (habitat) characteristics.

B. Trophic Interactions in *Sarracenia purpurea*-Inquiline Communities

1. Experimental Studies

Pitcher-plant inquilines have been used for two studies of top-down effects on food webs (Addicott, 1974; Cochran-Stafira and von Ende, 1998) and one study that examined top-down and bottom-up effects simultaneously (Kneitel and Miller, 2002). These studies all have used similar species, but differed in their questions, approaches, and conclusions (Table 11). To test predictions of Paine (1966) regarding keystone predators, Addicott (1974) conducted a field survey and experiment in Michigan on the relationship between predator (*Wyeomyia smithii*) densities and abundance, evenness,

Table 11 Comparison of three food-web studies conducted with inquiline communities of *S. purpurea*

	Addicott (1974)	Cochran-Stafira and von Ende (1998)	Kneitel and Miller (2002)
Experimental location	Field	Lab	Field
Natural species richness	High	Low	High
Nutrient levels	High	Low	None, Low, High
Predator densities (mosquito larvae/ml)	0–1.6	0, 0.2	0, 0.3, 2.7
Experimental duration	1 month in each of 3 months	4 days	23 days
Sampling intensity (days between samples)	14	1	2–3
Predation effect on protozoa diversity	Decrease	Increase	Increase and decrease (interaction with resources)
Trophic cascade?	–	Yes (abundance)	Yes (abundance and richness)
Omnivory important	–	No	No

and species richness of protozoa and rotifers. The study was conducted in 3 different months (May, August, and October) and sampling was done approximately every 2 weeks. Little information was provided on prey levels in the communities during the experiments (Table 11). Increasing densities of *W. smithii* generally produced a monotonically decreasing level of protozoan abundance and species richness, but did increase evenness (Addicott, 1974). Protozoan species varied in abundance as the result of both community (leaf) age and *W. smithii* density. However, competitive interactions among protozoans and rotifers were not quantified and it was not clear how the relative importance of competition and predation affected Addicott's results.

Cochran-Stafira and von Ende (1998) created highly controlled mixtures in the laboratory of every possible combination of *W. smithii*, three species of protozoans, and four species of bacteria, all derived from natural inquiline communities. This experimental design allowed for explicit examination of direct and indirect effects of competition and predation in this three trophic level food web. Cochran-Stafira and von Ende (1998) also tested for effects of predation by *W. smithii* larvae on protozoa and bacteria. They considered short-term effects and presented data from a 72-hour sample that used low productivity and mosquito larvae density levels relative to field conditions. In this experiment, *W. smithii* acted as a keystone predator by facilitating the coexistence of protozoan competitors (Cochran-Stafira and von Ende, 1998). Predation also had positive indirect effects on the bacterial community: bacterial abundance increased slightly in

the presence of *W. smithii*, decreased in the presence of both *W. smithii* and protozoa, and was suppressed even further when only protozoa were present. Interestingly, this trophic cascade did not occur through a reduction of the abundance in the intermediate trophic level as predicted by Hairston *et al.* (1960), but by changes in relative abundance patterns of a species in a given trophic level. These results suggested that omnivory probably plays a minor role in the dynamics of this system.

Kneitel and Miller (2002) used natural densities of predator and prey treatments in a “press” (*sensu* Bender *et al.*, 1984) field experiment in which they measured the effect of predation on bacteria abundance and richness, mite abundance, rotifer abundance, and protozoan abundance. Since resources and predators are known to vary among pitchers, three levels of each were used as treatments. Sampling was conducted every 2 to 3 days for 23 days. Resource addition (prey carcasses) resulted in an increase of all abundance variables measured (Table 12). The size of resource effects (Rosenthal and Rosnow, 1985; Redmond *et al.*, 1989) was greater for rotifers and protozoa in the middle trophic level than it was for bacteria in the basal trophic level, a pattern seen in other systems (Osenberg and Mittlebach, 1996). Protozoan and bacterial species richness also increased with added resources (Table 12). Following addition of top-predators, abundance of rotifers decreased greatly, abundance of protozoa at the same trophic level were unaffected, and abundance of bacteria increased (Table 13). Bacterial richness also increased with increasing predation levels (Table 13). A predator \times resource interaction was exhibited by protozoan species richness, which decreased at low resource levels, but increased slightly at higher resource levels (Kneitel and Miller, 2002).

The results of these studies led to three conclusions. First, heterogeneity in predator resistance occurred at the intermediate trophic level. Second, a trophic cascade (affecting both abundance and richness) occurred through the *W. smithii*–rotifer–bacteria pathway. Third, omnivory was probably not important to the dynamics of this system. Variation in resource and predator densities is important to understanding food web dynamics (Hunter and Price, 1992), and other laboratory experiments support

Table 12 Prey-addition effects on abundance and species richness of inquiline species inhabiting *S. purpurea* pitchers (data from Kneitel and Miller, 2002). See Figure 9 for an illustration of the food web of this community

Taxon	Change in Abundance (%)	Change in Richness (%)
Protozoa	50	111
Rotifers	66	0
Bacteria	7.4	19
Mites	76	0

Table 13 Predator-addition effects on abundance and species richness of inquiline species inhabiting *S. purpurea* pitchers (data from Kneitel and Miller, 2002). See Figure 9 for an illustration of the food web of this community

Taxon	Change in Abundance (%)	Change in Richness (%)
Protozoa	0	0
Rotifers	–53	0
Bacteria	0.5	1.5
Mites	0	0

the importance of variation of resources in this system (J. M. Kneitel, unpublished data). Competitive interactions between protozoans and rotifers decreased with increasing resources. In addition, predation effects by *W. smithii* on protozoa and rotifers differed with increasing productivity levels and differed if they were alone or in competition.

2. Similarities and Differences Among These Studies

Food web studies of the inquiline community of *S. purpurea* (Table 11) have provided valuable insights into this system, as well as experimental tests of predictions from food web theory. *W. smithii*, the keystone predator in this system, facilitates coexistence of protozoa on short timescales (Cochran-Stafira and von Ende, 1998), but also can decrease or not affect protozoan diversity on longer timescales (Addicott, 1974; Kneitel and Miller, 2002). In addition, predation effects can vary among the species within a trophic level (Cochran-Stafira and von Ende, 1998; Kneitel and Miller, 2002). These predator effects also cascade to the basal trophic level (Cochran-Stafira and von Ende, 1998; Kneitel and Miller, 2002) and affect bacterial abundance and species richness. These studies differed in their approaches and conclusions despite using the same experimental community (Table 11). Possible sources of variation were: differences in experimental setting, length of experiments, sampling regime, natural protozoan species richness, resource levels, and predator densities (Table 11). These differences are a strength of the *S. purpurea*-inquiline system: investigations of observed variation in this system could provide insights into mechanisms and consequences of food web heterogeneity.

3. Prospects for Future Research

Future research on trophic dynamics of the *S. purpurea*-inquiline system must standardize techniques in experimental approaches across the

geographic range of the community. Measurement of nutrient flow through the web should be addressed directly to identify which nutrients are important, and how the rates of nutrient input and decay vary spatially and temporally. Combining this information with knowledge of food web structure, we can address the degree of species redundancy within trophic levels or guilds, relationships between community diversity and stability, and the importance of indirect effects. These topics have been addressed most frequently using very simple communities of microorganisms, such as bacteria and protozoans, mostly in laboratory settings (Lawler, 1993b; Lawler and Morin, 1993; Balciunas and Lawler, 1995; Morin, 1999; Bohannan and Lenski, 2000). Natural microcosms, such as the phytotelmata communities of carnivorous plants (Fish, 1983; Kitching, 2000), provide a more realistic and complex system with which to explore food web dynamics. The past success of experiments with these model systems highlights their utility in addressing central questions in community ecology.

C. Metapopulation and Metacommunity Dynamics in *Sarracenia purpurea*-Inquiline Communities

Metapopulation theory (Hanski and Simberloff, 1997; Hanski, 1999) has provided us with a starting point for understanding and modeling the spatial dynamics of one or a few species in patchy habitats. But species do not typically exist on their own as isolated entities dependent on some limiting resource or habitat type for their continued existence; rather, they exist as links in complex webs of interactions within ecological communities. It is not, therefore, much of a conceptual stretch to extend the metapopulation concept to the community level. If a metapopulation is defined as a set of local populations linked by dispersal, the extension can be made that a metacommunity is a set of local communities in different locations, coupled by dispersal of one or more of their constituent members (Hanski and Gilpin, 1991; Holt, 1997). Although there is considerable laboratory and field evidence to support single or two species metapopulation models, initial efforts to provide empirical support for multispecies community models have been less successful (but see Holyoak and Lawler, 1996a,b). Kareiva (1990) argued that while there is much theoretical support for spatially distributed dynamics in ecological communities, experimental design and logistical problems have prevented us from making full use of the data sets that have been generated. For example, he criticized the failure of many papers to report the number and size of patches and the distance between patches. He also decried the absence of data on between-patch dispersal rates without which it is impossible to determine whether patches reflect truly spatially subdivided populations (although he did acknowledge

that this is logistically challenging). Harrison and Taylor (1997) also contended that conclusive tests of classical (*sensu* Levins, 1970) multispecies metapopulation dynamics are logistically very difficult and therefore rare. However, their argument was based on the observation that of the many well-studied systems that have been labeled *metapopulations*, very few actually conform to the narrow definition of a classical metapopulation. They cautioned that metapopulations have a variety of structures, and this variation has significant implications for the coexistence and persistence of species and the relative importance of regional versus local processes.

1. Establishing the *S. purpurea*-Inquiline System as a Model for Metacommunity Studies

Field studies of metacommunity dynamics have not yet been attempted because of the logistical problems of finding suitable model systems from which it is possible to collect reliable data. We combined published data with additional field data collected by Cochran-Stafira to determine whether the inquiline communities of *S. purpurea* satisfy five requirements (based on the definition of a metacommunity) for metacommunity studies:

1. The community is distributed among individual habitat patches surrounded by areas of unsuitable habitat.
2. Habitat patches are heterogeneous in nature.
3. Species within local habitat patches (pitchers) are at risk for extinction and persist at the regional (bog) level through colonization of new habitat patches.
4. Species interactions contribute to extinction risk at the local scale.
5. Not all habitat patches contain the same species assemblage. This criterion assumes that there is a regional species pool, and each patch contains some subset of this pool. This has implications for determining the appropriate structural model for the pitcher-plant metacommunity (*sensu* Harrison and Taylor 1997).

The first criterion is clearly satisfied because pitchers provide the only phytotelmata habitat within the larger bog landscape (Fish and Hall, 1978). Water-filled pitchers of *S. purpurea* are the only suitable oviposition sites for the obligate dipteran commensals and may serve as the exclusive habitat for the mite *S. gibsoni*. The surrounding bog mat is inhospitable to most of the inquilines, since in typical northeastern and midwestern United States bogs there is little or no surface water during the growing season (D. L. Cochran-Stafira, personal observations).

The second criterion is also met because pitchers represent dynamic but ephemeral habitat patches. Physically, pitchers vary in size, volume, and

age. The pitchers last 1–3 seasons before degenerating (Fish and Hall, 1978). Prey capture rates vary over time (Wolfe, 1981; Cochran-Stafira, 1993) and with pitcher size (Cresswell, 1991). Fluid pH is highest in young pitchers and becomes increasingly acidic over time, reaching a minimum after 6 weeks (Figure 10). This variability, along with other age-related changes in pitcher characteristics (Fish and Hall, 1978) is associated with temporal trends in bacterial densities and abundances of mosquito and midge larvae (Figure 10). Although it is not clear whether the numbers of mosquitoes and midges within individual pitcher change over time as a result of additional oviposition, there is a marked increase in larval biomass as they grow. This may well lead to increased predation pressure on protozoa and rotifers.

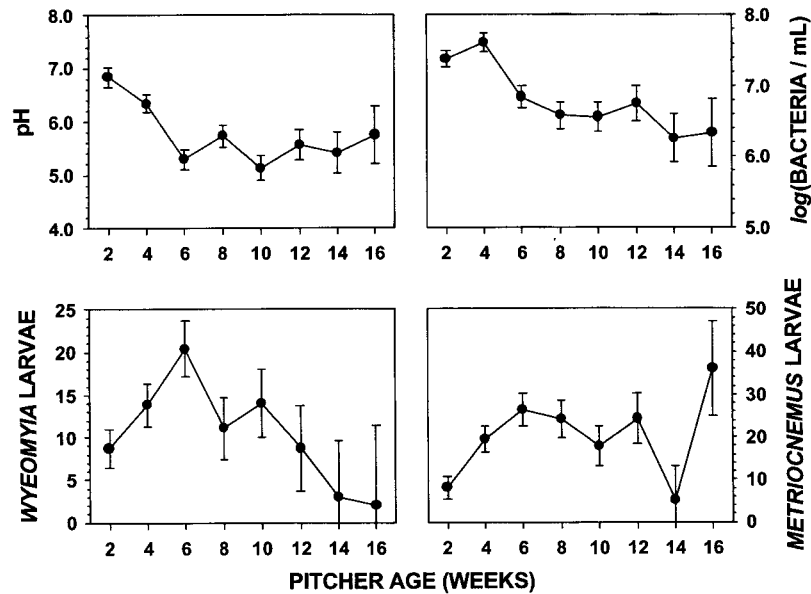


Figure 10 Temporal trends in pH, bacterial density, and abundance of *W. smithii* and *M. knabi* in *S. purpurea* pitchers. Data collected from June to September 1993 by D. L. Cochran-Stafira from 100 randomly selected plants. Because a complete census of inquilines requires destructive sampling of pitchers (Nastase *et al.*, 1991), it was not possible to follow community dynamics over time within individual pitchers. Similarly aged replicate pitchers were identified by marking newly opened pitchers with a date code. This sampling allowed for sampling of leaves of different age classes over the entire collection season, and replication of samples from each age class by date and across all sampling dates. pH was measured in the field. Bacterial population density was determined using plate counts, and no attempt was made to identify the bacteria to species. Larvae of *W. smithii* and *M. knabi* in each leaf were counted.

Because of the ephemeral nature of the pitcher habitat, mites, rotifers, and microorganisms must colonize new pitchers before the degeneration of their natal habitat patch results in a local extinction. Thus the third criterion, that species within local habitat patches are at risk for extinction and persist at the regional (bog) level through colonization of new habitat patches is also met. Long-term census data at Cedarburg Bog, a large string-bog in southeastern Wisconsin, USA, shows the same groups of protist, small metazoan, and dipteran species persisting throughout the bog landscape for more than 10 years despite deaths of individual pitchers as well as entire plants (D. L. Cochran-Stafira, unpublished data). Mosquitoes, midges, and sarcophagid flies readily colonize new pitchers as females choose them for oviposition sites; however, the triggers and mechanisms for the migrations of these and other pitcher commensals are unknown. The histiostomatid mite *S. gibsonii* has a migratory stage, the deutonymph, in its life cycle. Deutonymphs have been observed leaving older pitchers and congregating around the tips of unopened pitchers, which the mites enter immediately after it opens (O'Connor, 1994). Nonphoretic dispersal to nearby pitchers may be the norm, but *S. gibsonii* retains vestigial morphological adaptations for phoresy and may use this for long-distance dispersal. The mechanism by which the rotifer *Habrotrocha rosa* reaches new pitchers is also unknown, but it is common in interstitial water in *Spagnum* bogs as well as in pitchers (Bledzki and Ellison, 2002). Dispersal of microbes and protists is presumed to occur via rain-splash, air-borne propagules, phoresy by prey insects or commensals, or from debris falling from the surrounding vegetation. Depending on the species, colonization may be a strictly stochastic phenomenon, or may involve habitat-choice decisions (Heard, 1994b).

The fourth criterion, that species interactions contribute to extinction risk, has been demonstrated for the dipterans, rotifers and protozoa. Mosquito larvae function as keystone predators (Addicott, 1974; Cochran-Stafira and von Ende, 1998; Table 11). Larvae of *F. fletcheri* not only alter the nutritional base of the food web by processing prey carcasses, but also feed on mosquito larvae and rotifers (Bledzki and Ellison, 1998). Midge larvae may be able to escape predation by fly larvae and locate younger, more productive pitchers by migrating to other pitchers (D. L. Cochran-Stafira, personal observation). Competitive exclusion has been demonstrated for some inquiline protozoa (Cochran-Stafira and von Ende, 1998), and *Habrotrocha rosa* has been observed to exclude two other rotifer species occasionally collected from pitchers, *Philodina* sp. and *Lecane* sp. (D. L. Cochran-Stafira, unpublished data).

Finally, not all habitat patches contained the same species assemblage. At Cedarburg Bog, larvae of *W. smithii* larvae were found in >80% of all pitchers sampled, whereas *M. knabi* larvae were found in >90% of the

pitchers. In contrast, *F. fletcheri* was relatively rare, occurring in < 5% of the pitchers. *H. rosa* was found in over 50% of pitchers, and other species of rotifers were very rare and usually only appear in pitchers where *H. rosa* was absent or at very low population densities (see also Bledzki and Ellison, 2002). Protozoan and bacterial species richness and composition was highly variable among pitchers (Addicott, 1974; Cochran-Stafira, 1993), as well as bogs (D. L. Cochran-Stafira, unpublished data). Analysis of species association patterns for all consumer taxa offers support for the hypothesis that certain species are positively associated with each other while others are negatively associated or have no interaction pattern. As described in the next section, these patterns can be used to predict how each local pitcher community assembles from regional species pools. Some combinations are favored while others are prohibited by strong species interactions. The presence of some species may be determined by stochastic colonization events rather than species interactions. Mites were positively associated with rotifers, and mosquito and midge larvae were positively associated, a pattern that would be expected since the species are involved in a processing chain commensalism (Heard, 1994a). The bacterivorous ciliates *Colpoda* and *Cyclidium*, while shown to be competitors in laboratory microcosm experiments, were positively associated in field samples at Cedarburg Bog. This may stem from the sensitivity of ciliates to predation by *Wyeomyia* larvae, and the subsequent occurrence of ciliates only in pitchers where mosquitoes are absent or at very low densities. Heterotrophic microflagellates did not show any association patterns with any of the other inquilines.

2. Prospects for Future Research

Based on literature data and new field observations, it is clear that the *S. purpurea*-inquiline community is an exemplary metacommunity. It fulfills all the criteria of current models (Hanski and Gilpin, 1991) and corrects faults that have been identified (Kareiva, 1990; Harrison and Taylor, 1997). It affords a relatively simple but natural metacommunity with multiple trophic levels and a web of direct and indirect food web interactions. The development of the community is rapid and communities in multiple stages of development can be studied within a short amount of time. Manipulations are relatively easy to carry out and large numbers of replicates are possible because of the high numbers of pitchers at any given site.

Additional data are required on dispersal rates and distances, and extinction rates for each of the inquilines. It is also necessary to evaluate the importance of patch numbers and dynamics as well as spatial arrangements,

since these have been shown to affect the persistence time of predator-prey metapopulations in simulations and laboratory microcosm experiments (Holyoak, 2000; Keymer *et al.*, 2000). It seems to be appropriate to consider the populations of *W. smithii*, *F. fletcheri*, and *M. knabi* as metapopulations because of their obligate association with *S. purpurea* for oviposition sites. However, the degree of migration between plant populations is unknown. It has been suggested that *W. smithii* has limited colonization abilities due to the inability of the adults to survive for extended periods of time once outside the bog's microclimate (S. M. Scheiner, personal communication; D. L. Cochran-Stafira, personal observation). Indeed, bogs with healthy *S. purpurea* populations but entirely lacking *W. smithii* have been reported (Addicott, 1974). Colonization abilities and the distribution patterns for *F. fletcheri* and *M. knabi* are similarly unknown. Finally, the degree to which the other pitcher inquilines are obligately associated with *S. purpurea* remains to be discovered.

In a world of increasing habitat fragmentation, understanding the dynamics of subdivided populations and communities and incorporating variation in habitat size, edge effects, and spatial structure are crucial to the development of effective conservation strategies (Hanski and Simberloff, 1997; Hanski, 1999). Metapopulation models of single species and multi-species assemblages have produced predictions that, if valid, may significantly alter our approach to preserving threatened communities and ecosystems. Results from modeling experiments (Tilman *et al.*, 1994) suggest that as habitats are increasingly fragmented, even dominant competitors may be lost from the remaining fragments, and persistence and extinction of metapopulations are also influenced by the rate at which the landscape changes (Keymer *et al.*, 2000). Communities may become less stable as migration increases, suggesting that in metacommunities, species interactions increase the risk of extinctions (Hanski, 1999). Experimental evidence to test these models is lacking to date, but the *S. purpurea*-inquiline system should be a valuable model with which to develop realistic, testable models of metacommunity dynamics.

D. Assembly of *Sarracenia purpurea*-Inquiline Communities

Diamond (1975) first suggested that communities on islands could be characterized by a set of "assembly rules" – deterministic patterns of distribution and abundance controlled by interspecific competition. Other investigators have extended and refined these assembly rules, hypothesizing preferred assemblages of species ("favored states" of Fox and Brown, 1993) and relatively constant proportions of species sets defined empirically or statistically (Wilson and Roxburgh, 1994; Wilson *et al.*, 1995). Supporters of

assembly rules argue that competition, in the form of resource preemption or competitive hierarchies, structures communities, whereas critics of assembly rules assert that they are tautologies lacking predictive power or that evidence for consistent patterns of community structure, much less for assembly rules, is not compelling (see review in Gotelli and Graves, 1996). Community assembly likely involves more processes than interspecific competition (Weiher and Keddy, 1999), and exploring interactions between the assembling community and its changing habitat template can provide new insights into the range of possible assembly rules.

Ellison and Gotelli have used the *S. purpurea*-inquiline community to examine experimentally interactions between habitat change and the co-occurrence patterns of five of the inquilines: the larvae of the dipterans *F. fletcheri*, *W. smithii*, and *M. knabi*; the mite *S. gibsonii*, and the rotifer *H. rosa*. They used null model analysis (Gotelli and Entsminger, 2000) to test for both temporal and spatial constancy in community structure of *S. purpurea* pitchers.

1. Temporal Changes in the Assembly of the Inquiline Community

We first tested for temporal variability in the co-occurrence patterns of these five inquilines by experimentally manipulating the availability of pitchers over time and then testing for temporal homogeneity among the experimental replicates. We examined abundance of each species every week in 60 pitchers assigned randomly to three treatment groups: pitchers available for colonization immediately upon opening; pitchers available for colonization three weeks after opening (plugged prior to that time with glass wool); and pitchers available for colonization six weeks after opening. The experiment was duplicated at two sites, Hawley Bog in northwestern Massachusetts, and Molly Bog in northwestern Vermont.

At Hawley Bog, the inquiline communities that started in older leaves had significantly more species co-occurrences than expected by chance, and among replicates, communities assembled in older leaves were more homogeneous than those assembled in younger leaves. (Figure 11). In contrast, at Molly Bog, there were no temporal patterns in assembly, and, in fact, species co-occurrence patterns were not different from a random draw from the available species pool (Figure 11). The overall ANOVA yielded a significant ($P < 0.05$) treatment effect (due to the strong pattern at Hawley Bog) and a significant site \times treatment ($P < 0.01$) interaction. A parallel set of 20 control plants, in which we monitored assembly in all leaves as they were produced and became available for colonization, showed no significant temporal pattern ($P > 0.7$). This result, along with the data shown in Figure 11 suggest that absolute leaf age (= habitat age) is a more important

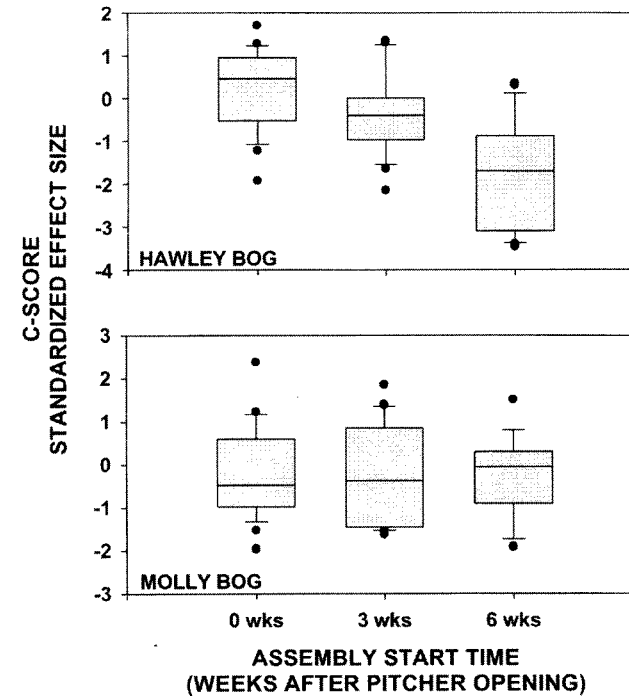


Figure 11 Effects of leaf age on co-occurrence patterns of five inquilines inhabiting leaves of *S. purpurea*. For each pitcher, we constructed an inquiline \times time matrix, where each entry was a 1 (inquiline present) or a 0 (inquiline absent). This matrix is analogous to a site \times species matrix used in null models for community assembly (Gotelli and Graves, 1996). Thus, we had 20 matrices for each of the three treatment groups (pitchers available for colonization 0, 3, and 6 weeks after opening). We then calculated a measure of co-occurrence, the C-score (Stone and Roberts, 1990), which measures the average number of checkerboard units per species pair across the entire inquiline \times time matrix. This observed C-score (C_{obs}) was compared with 1000 simulated C-scores (C_{sim}) from randomized matrices (rows fixed, columns equiprobable; see Gotelli and Graves, 1996, for additional details on randomization methods) to determine its exact P value. A large C-score suggests significantly less co-occurrence (strong effects of interspecific competition) than expected by chance alone, whereas a small C-score suggests significantly more co-occurrence than expected. For comparative purposes, C-scores for each matrix are converted to standardized effect sizes ($SES = [C_{obs} - \text{mean } C_{sim}] / SD_{sim}$). The null hypothesis (no temporal segregation in species) is that $SES = 0$; species segregation is suggested by $SES > 0$ and species aggregation is suggested by $SES < 0$. If $|SES| > 1.96 (= t_{0.05(4)})$, it is considered significant at the 0.05 level. Box-and-whisker plots illustrate distributions of SESs for the 20 leaves in each treatment group. Central line in each box is the median, box boundaries are upper and lower quartiles, “whiskers” extend to upper and lower deciles, and all outliers (beyond upper and lower deciles) are illustrated by solid circles.

determinant of assembly for the inquiline communities than the age of the communities themselves. This result is supported by extensive field observations at Cedarburg Bog (Cochran-Stafira, 1993).

2. Spatial Variation in the Assembly of the Inquiline Community

We used the same data set to test for spatial variation in assembly of the inquiline community at each sample date (Figure 12). At Hawley Bog, there was no trend in spatial pattern of inquiline co-occurrences, either within treatment groups or as the summer progressed, although the variability in our measure of co-occurrence (the standardized effect size of the C-score of Stone and Roberts, 1990) appears to increase over time. In contrast, at Molly Bog, all treatments showed significant aggregation in inquilines by the end of the summer (Figure 12), and there were no significant differences among the treatments in this effect.

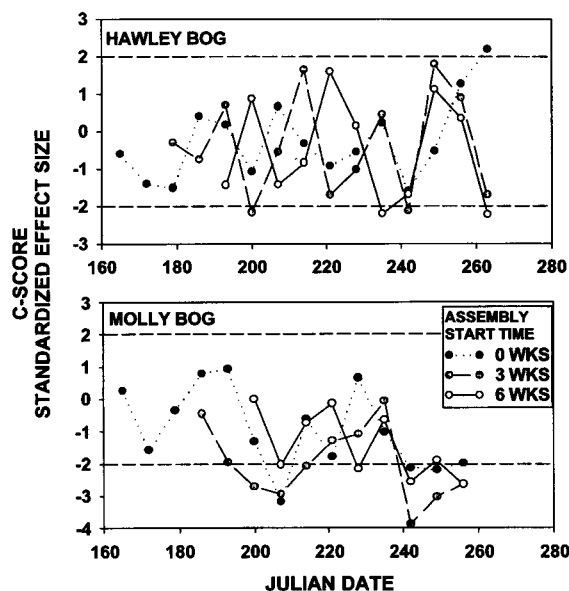


Figure 12 Effects of leaf age on spatial variability in inquiline co-occurrences. The data used in Figure 11 were re-structured into inquiline \times pitcher matrices, and a single matrix was constructed for each sampling time. We then examined the time course in standardized effect size of the C-score (as in Figure 11) for each treatment. Note the reference lines at $SES = \pm 1.96$. When the SES crosses this line, it indicates significant segregation (if $SES > 1.96$) or aggregation ($SES < -1.96$) of inquilines among pitchers.

3. Prospects for Future Research

Taken together, the results presented (Figures 11–12) suggest that single “snapshots” of community structure are insufficient to determine co-occurrence patterns or assembly rules for the *S. purpurea*-inquiline communities. They also demonstrate that the *S. purpurea*-inquiline community is amenable to field experiments examining patterns of co-occurrence from which we can eventually derive assembly rules for these groups of species.

Our experimental manipulations of pitcher availability over time illustrated that at one site (Hawley Bog), physical changes in habitat (i.e. leaf age) were more important determinants of temporal patterns of co-occurrence than was community age. Our analyses of replicate communities also illustrated that community structure varies spatially, especially at Molly Bog. Both sets of analyses suggested that inquiline communities tended towards species aggregations, not segregation, a conclusion in line with described facilitations between *M. knabi* and *W. smithii* (Heard, 1994a). Because we did not measure abundances of protozoa, which may compete with rotifers for food, we were unable to assess segregation between these taxa that occur at the same trophic level (Figure 9). Incorporation of protozoa into studies of community assembly of the inquiline food web, as begun by Cochran-Stafira and von Ende (1998), is a high priority for further research in this area.

We have only begun to examine characteristics of the pitchers that change during the time when inquiline communities are assembling. Other key characteristics include: pitcher volume and the actual volume and chemical characteristics (cf. Figure 9) of liquid in the pitchers; spatial position and orientation of the pitcher (cf. Kingsolver, 1979, 1981), and pitcher turnover rates and senescence. All of these “habitat” characteristics will interact with life history traits of the inquilines, including their body size, dispersal and oviposition behavior (e.g. Heard, 1994b), and may vary among instars. Both *S. purpurea* and its inquilines will be affected by climate, especially rainfall (that fills the pitchers), which was unusually low in 1999 when these experiments were conducted. Given that we have developed a model experimental system for studying species co-occurrence in the field, we expect to use it to generate a new suite of assembly rules appropriate for dynamic habitats that are not in equilibrium.

E. Short-Term Evolutionary Change in *Sarracenia purpurea*-Inquiline Communities

Historically, community ecology has taken a strong evolutionary view when addressing broad community patterns, and there should be no exception made for the *S. purpurea*-inquiline community.

Whenever the rates of ecological processes overlap with the rates of potential evolutionary change, evolutionary dynamics should be incorporated into ecological studies, but predicting when these rates will overlap is difficult. The rate of evolution of a trait is dependent on its heritability (e.g. Mousseau and Roff., 1987) and the intensity of selection, which itself can be controlled by experimental treatments (e.g. Endler, 1986). Both field and laboratory experiments have demonstrated significant evolutionary change over a small number (<3) of generations, but studies of ecological processes that simultaneously attempt to quantify evolutionary changes are lacking.

The evolutionary responses of the pitcher-plant mosquito, *W. smithii*, have been studied for several decades (Istock *et al.*, 1975, 1976a,b; Bradshaw and Lounibos, 1977; Bradshaw and Holzapfel 1986; Bradshaw *et al.*, 1997, 1998), but these studies have not examined directly the impact of these evolutionary dynamics on ecological interactions within the inquiline community. Miller and Kneitel have taken advantage of the *S. purpurea*-inquiline community to examine the evolutionary change in an ecological process – the competitive ability of bacterial species. They compared the performance of bacteria from bacterial communities of different ages, and the time-course of competitive interactions among bacteria that occur naturally in *S. purpurea* pitchers in the Apalachicola National Forest, Sumatra, Florida, USA (site described in Harvey and Miller, 1996).¹

1. Competitive Interactions Among Bacterial Communities of Different Ages

Competitive performance of bacteria from communities of different ages was tested with bacteria grown alone and in competition. A 0.5 ml sample of pitcher fluid was removed from 12 newly opened *S. purpurea* pitchers on 11 May 1999. This sample was serially diluted and plated out on Luria agar. After 48 hours growth, different strains of bacteria were identified by colony growth, color, and texture on the agar plates. Another sample was collected from 12 newly opened leaves in the same area on 8 June 1999, and similarly plated and scored. On 15 June, the communities from the first (“6-week”) and second (“1-week”) set of leaves were resampled and scored in the same manner. Bacterial strains were selected for further study if they were found in (1) at least two of the 6-week communities and in both their 1-week and 6-week censuses and (2) at least two of the 1-week communities.

¹This population of *S. purpurea* has recently been described as a new species, *Sarracenia rosea* (Naczi *et al.*, 1999).

This allowed for comparisons of relatively older strains (found in pitchers for a minimum of 35 days) with younger strains (maximum of 7 days). Selected strains were transferred to Luria broth and incubated for 12 hours.

A significant number of the 6-week communities failed to persist for the entire six weeks. Three leaves were damaged and failed to hold water, while two leaves died due to unknown causes. All 1-week communities survived the one week in which they were used. Surviving 6-week communities produced significantly more ($P = 0.03$) bacterial types on Luria agar than 1-week communities (4.3 in 6-week vs 3.0 in 1-week). Four different species were found in two or more 6-week and 1-week communities. These species were not identified, but were distinguished by colony growth traits: slimy, yellow, white, and pink. After isolation as pure cultures, each species was grown for 24 hours in monoculture and in competition with a common competitor, the beta-proteobacterium *Chromobacterium violaceum*, previously isolated from this population of *S. purpurea* (R. Reeves, personal communication). We estimate that these cultures achieve a stable number of cells within 8 hours – the final density of cells in most cultures was between 10^7 and 10^9 cells per ml.

In all cases, the competitive responses of bacteria from the 1-week communities were near 0 (Figure 13), indicating that the growth in competition with *Chromobacterium* was similar to growth in monoculture. However, for slimy and white bacteria, growth of the 6-week strains was suppressed 10–20% in competition, when compared to growth in monoculture ($P = 0.07$ and $P = 0.003$, respectively; (Figure 13). Growth of the 6-week strains of pink and yellow bacteria was similar to that in the 1-week strains: there was no evident effect of interspecific competition (Figure 13).

2. Time-Course of Competitive Interactions Among Bacteria

To document the time-course of competitive interactions, Miller and Kneitel conducted a similar study in the summer of 2000 in which they quantified the temporal pattern of competition and monoculture growth of a single bacterial species. Ten empty newly-opened pitchers were marked on 20 June 2000 and filled with 30 ml sterile water to initiate “old” communities. Four weeks later, ten additional empty and newly-opened pitchers were marked to initiate “young” communities and filled with 30 ml sterile water. In both cases, the leaves filled rapidly with rainwater, bacteria, and various other inquilines. On July 28, the ten old communities (now 38-day-old) and the ten young communities (now 8-day-old) were sampled, and bacteria scored as described above. One colony type was chosen that was found in three communities of each age, while a second colony type was chosen for its

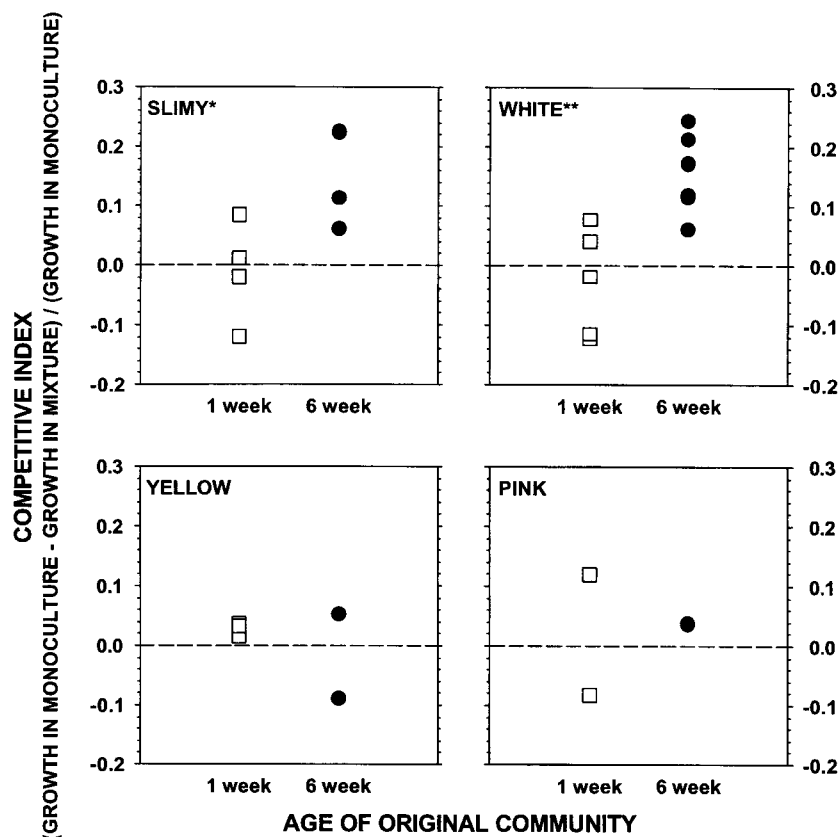


Figure 13 Competitive ability of four morphotypes of bacteria grown alone and in competition with *Chromobacterium violaceum*. For each 6-week and 1-week strain, 0.02 ml of its culture was placed in a macrocentrifuge tube with 20 ml of 10% luria, either alone or with 0.02 ml of the *C. violaceum* culture. The cultures were allowed to grow for 24 hours, then serially diluted and plated on Luria agar. Cell counts per ml were used to quantify the amount of suppression due to competition by comparing growth in two-species mixtures with that in monocultures (Miller, 1996): $C = (\text{monoculture growth} - \text{two-species growth}) / \text{monoculture growth}$. The growth of 1-week and 6-week strains for each species in monoculture and in competition were statistically compared using ANOVA on log-transformed cell counts from the agar plates. * - $P < 0.05$; ** - $P < 0.01$

distinctive color and growth form to serve as the common competitor, with methods for competition as described above. This time, however, the cultures were grown in broth created from pitcher-plant fluid collected from the field, strained of larger particles, then microfiltered to remove bacteria. All cultures were sampled every 12 hours for 60 hours, using serial dilutions and counting colony abundance on Luria agar plates as before.

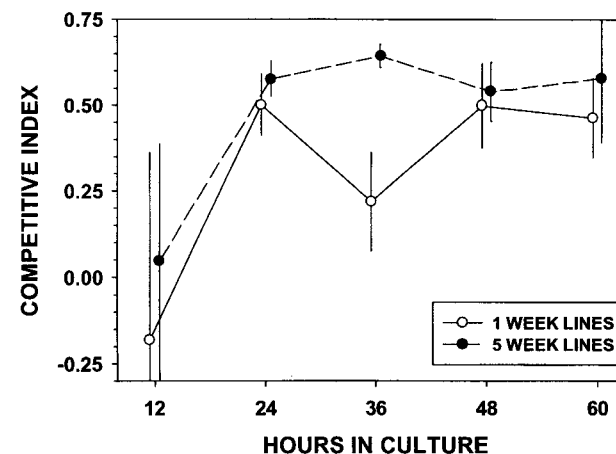


Figure 14 Effect of the presence of a competitor on bacterial growth through time for strains from communities of different ages. The competitive index expresses growth as a function of growth in monoculture (see text), with one standard error. At each census, competitive effects were quantified after standardizing by monoculture growth, as described in Figure 13. Effects of age of community on the competitive index were evaluated using repeated-measures ANOVA.

In this experiment, the competitive ability of only one species was tested against a standard, but competition was followed at 12-hour intervals. The competitive effects on both old and young strains were not apparent at 12 hours, but strains from both community types were suppressed to around 50% of their monoculture growth at all later censuses (Figure 14). At each census, growth of the old strain was more suppressed by competition than was the young strain; overall, there was a significant effect of age of community on the competitive index ($P < 0.05$).

In both experiments, it was somewhat surprising to find that bacteria from old communities were apparently poorer competitors than those from younger communities. Because inquiline communities generally have high densities of bacteria, that have had time to adapt to these conditions and ought to be better competitors than those with less time to adapt to high densities. There are several possible explanations for the observed discrepancy. First, natural conditions may not have been adequately mimicked, either in growth conditions or in time. Competitive interactions could have been affected by nutrient levels or other missing portions of the community (e.g. predators or other competitors). Second, related to this, these studies were conducted with only bacteria present – no other portions of the natural inquiline community were present. Thus, the observed response could be expected if trade-offs occurred between

traits related to competition and other factors, such as predation, and if these other factors have greater effects than competition in natural inquiline communities.

3. Prospects for Future Research

These results suggest that significant evolutionary changes occurred at ecological timescales. Innumerable studies on population genetics and evolution have quantified significant evolutionary responses to selection in a relatively short time-frame. Despite this, most studies of ecological communities have ignored possible evolutionary changes in component species. At times, these studies have been done over very short periods of time (e.g. within generations of all component species), during which it seems inappropriate to be concerned about possible evolutionary changes. However, many studies have been conducted over much long periods of time. For example, there is a tradition of ecological studies in small, controlled habitats that goes back to Gause's studies of *Paramecium* (Gause, 1934; see also Huffaker, 1958; Vandermeer, 1969). This traditional type of study, testing basic ecological hypotheses in simple controlled systems, recently has come back into favor (Daehler and Strong, 1996), with tests of concepts such as productivity–diversity relationships, dispersal effects on diversity (Warren, 1996), predator–prey dynamics and metapopulations (Holyoak and Lawler, 1996b), trophic cascades (Balciunas and Lawler, 1995), and the roles of omnivores on community stability (Morin, 1999). Most of these studies have been conducted over many generations of the component, mostly very short-lived, species and yet, to our knowledge, almost none have considered potentially evolutionary forces that may have contributed to their results. A rare exception is a recent study on the effects of productivity on the relative importance of competition and predation using bacteria and a bacteriophage predator (Bohannan and Lenski, 2000). The results of this study did not support predictions about rates of competitive exclusion, a result that may be explained by the evolution of competitive ability during the course of the experiment.

We suggest that future experimental studies in community ecology at least need to consider the potential evolutionary changes in populations during these experiments. Even better would be if future studies incorporated ways to quantify evolution as it proceeds during experiments. It is very likely that this approach may ultimately lead to a further understanding of the role of evolution in structuring communities. As with the other community-level studies discussed above, the *S. purpurea*-inquiline community could be used as a model system for

such experiments. Comparative work using inquilines of *Nepenthes* spp. and *Darlingtonia californica* could add to the generality of the results obtained from such studies.

F. Directions for Future Research

The inquiline communities of pitcher-plants around the world have been used to study food web structure, principally through description and statistical inference (Fish, 1983; Kitching, 2000). More recently, these food webs have been experimentally manipulated to examine predictions of general models of food web structure and dynamics (Cochran-Stafira and von Ende, 1998; Kneitel and Miller, 2002; Miller *et al.*, 2002; and data presented above). These experimental manipulations to date have relied on the inquiline communities of *S. purpurea*. Comparable experimental studies using the inquilines of other pitcher-plants, especially the unrelated *Nepenthes* and *Cephalotus*, would be especially useful for generalizing these results and making significant contributions to theories of food web structure and community assembly. It is also clear that the understudied components of these food webs – bacteria and protozoa – must be included in such studies, both because of their key positions in the donor-controlled food webs (Figure 9) and because they have sufficiently rapid generation times that evolutionary change can occur easily and predictably during the time course of the average experiment.

VII. CONCLUSIONS: ARE CARNIVOROUS PLANTS MODEL SYSTEMS FOR ECOLOGICAL RESEARCH?

In this overview, we have illustrated that the mixture of autotrophy and heterotrophy characteristic of carnivorous plants provides ample opportunities to address general and open questions of resource allocation, life history strategies and demography, plant–plant interactions and species coexistence, and plant–insect interactions. The unique pitfall trap structures of the pitcher-plants provide habitats for tightly knit assemblages of bacteria, protozoa, rotifers and invertebrates, and these communities provide easily manipulated replicates for studies of food webs and community assembly at scales ranging from individual communities through metapopulations to metacommunities. The dynamic nature of the pitchers, and the rapid lifecycle of the inquilines allows for integration of evolutionary change into models of ecological dynamics.

We suggest that a concerted focus by ecologists and evolutionary biologists on this group of plants, some of which are phylogenetically

related and others of which exhibit remarkable convergence in a set of unique ecological traits will lead to a richer understanding of ecological phenomena. Furthermore, such a concerted effort could lead to real replication of ecological studies, a rarity in our discipline. Carnivorous plants are cultivated readily, so a mixture of greenhouse and field experiments are possible. All in all, this group of plants, once viewed as little more than botanical curiosities, have the potential to become the *Drosophila* of ecology.

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REFERENCES

- Aber, J., McDowell, W., Nadelhoffer, K., Magill, A., Berntson, G., Kamakea, M., McNulty, S., Currie, W., Rustad, L. and Fernandez, I. (1988) Nitrogen saturation in temperate forest ecosystems. *BioScience* **48**, 921–934.
- Adamec, L. (1997) Mineral nutrition of carnivorous plants: a review. *Bot. Rev.* **63**, 273–299.
- Addicott, J.F. (1974) Predation and prey community structure, an experimental study of the effect of mosquito larvae on the protozoan communities of pitcher plants. *Ecology* **55**, 475–492.
- Aizen, M.A. and Feinsinger, P. (1994) Forest fragmentation, pollination, and plant reproduction in a Chaco dry forest, Argentina. *Ecology* **75**, 330–351.
- Albert, V.A., Williams, S.E. and Chase, M.W. (1992) Carnivorous plants: phylogeny and structural evolution. *Science* **257**, 1491–1495.
- Aldenius, J., Carlsson, B. and Karlsson, S. (1983) Effects of insect trapping on growth and nutrient content of *Pinguicula vulgaris* L. in relation to the nutrient content of the substrate. *New Phytol.* **93**, 53–59.
- Andersen, A.N. (1992) Regulation of “momentary” diversity by dominant species in exceptionally rich ant communities of the seasonal tropics. *Am. Nat.* **140**, 401–420.
- Arber, A. (1941) On the morphology of the pitcher-leaves in *Heliophora*, *Sarracenia*, *Darlingtonia*, *Cephalotus*, and *Nepenthes*. *Ann. Bot.* **5**, 563–578.

- Balcianas, D. and Lawler, S.P. (1995) Effects of basal resources, predation, and alternative prey in microcosm food chains. *Ecology* **76**, 1327–1336.
- Barrett, S.C.H. and Kohn, J.R. (1991) Genetic and evolutionary consequences of small population size in plants: implications for conservation. In: *Genetics and Conservation of Rare Plants* (Ed. by D.A. Falk and K.E. Holsinger), pp. 3–30. Oxford University Press, New York.
- Bedford, B.L., Walbridge, M.R. and Aldous, A. (1999) Patterns of nutrient availability and plant diversity of temperate North American wetlands. *Ecology* **80**, 2151–2169.
- Bender, E.A., Case, T.J. and Gilpin, M.E. (1984) Perturbation experiments in community ecology: theory and practice. *Ecology* **65**, 1–13.
- Benton, T.G. and Grant, A. (1996) How to keep fit in the real world: elasticity analyses and selection pressures on life-histories in a variable environment. *Am. Nat.* **147**, 115–139.
- Benzing, D.H. (1987) The origin and rarity of botanical carnivory. *Trends in Ecology and Evolution* **2**, 364–369.
- Benzing, D.H. (2000) *Bromeliaceae: Profile of an Adaptive Radiation*. Cambridge University Press, Cambridge.
- Bestelmeyer, B.T. and Wiens, J.A. (1996) The effects of land use on the structure of ground-foraging ant communities in the Argentine chaco. *Ecol. Appl.* **6**, 1225–1240.
- Billings, W.D. and Mooney, H.A. (1968) The ecology of arctic and alpine plants. *Biol. Rev.* **43**, 481–530.
- Blanca, G., Cueto, M., Martinez-Lirola, M.J. and Molero Mesa, J. (1998) Threatened vascular flora of Sierra Nevada (southern Spain). *Biol. Cons.* **85**, 269–285.
- Bledzki, L.A. and Ellison, A.M. (1998) Population growth and production of *Habrotrocha rosa* Donner (Rotifera, Bdelloidea) and its contribution to the nutrient supply of its host, the northern pitcher plant *Sarracenia purpurea* L. (Sarraceniaceae). *Hydrobiologia* **385**, 193–200.
- Bledzki, L.A. and Ellison, A.M. (2002) Rotifer diversity in 32 bogs in Massachusetts and Vermont (Northeast USA) with the first record of *Cephalodella anebodica* and *Colurella obtusa clausa* from North America. *Hydrobiologia (in review)*.
- Boeken, B. (1989) Life histories of desert geophytes – the demographic consequences of reproductive biomass partitioning patterns. *Oecologia* **80**, 278–283.
- Bohannan, B.J.M. and Lenski, R.E. (2000) The relative importance of competition and predation varies with productivity in a model community. *Am. Nat.* **156**, 329–340.
- Bradshaw, W.E. and Holzapfel, C.M. (1986) Geography of density-dependent selection in pitcher-plant mosquitoes. In: *The Evolution of Insect Life-cycles* (Ed. by F. Taylor and F. Karban), pp. 48–65. Springer-Verlag, New York.
- Bradshaw, W.E. and Lounibos, L.P. (1977) Evolution of dormancy and its photoperiodic control in pitcher-plant mosquitoes. *Evolution* **21**, 546–567.
- Bradshaw, W.E., Armbruster, P.A. and Holzapfel, C.M. (1998) Fitness consequences of hibernation diapause in the pitcher-plant mosquito, *Wyeomyia smithii*. *Ecology* **79**, 1458–1462.
- Bradshaw, W.E., Holzapfel, C.M., Kleckner, C.A. and Hard, J.J. (1997) Heritability of development time and protandry in the pitcher-plant mosquito, *Wyeomyia smithii*. *Ecology* **78**, 969–976.
- Brewer, J.S. (1999a) Short-term effects of fire and competition on growth and plasticity of the yellow pitcher plant, *Sarracenia alata* (Sarraceniaceae). *Am. J. Bot.* **86**, 1264–1271.

- Brewer, J.S. (1999b) Effects of competition, litter and disturbance on an annual carnivorous plant (*Utricularia juncea*). *Plant Ecol.* **140**, 159–165.
- Brewer, J.S. (1999c) Effects of fire, competition, and soil disturbances on regeneration of a carnivorous plant (*Drosera capillaris*). *Am. Midl. Nat.* **141**, 28–42.
- Brewer, J.S. (2001) A demographic analysis of fire-stimulated seedling establishment of *Sarracenia alata* (Sarraceniaceae). *Am. J. Bot.* **88**, 1250–1257.
- Bronstein, J.L. (1994) Conditional outcomes in mutualistic interactions. *Trends Ecol. Evol.* **9**, 214–217.
- Casper, S.J. (1966) Monographie der Gattung *Pinguicula* L. *Biblio. Bot.* **127–128**, 1–209.
- Casper, S.J. (1972) *Pinguicula* L. – In: *Flora Europaea* (Ed. by T.G. Tutin, V.H. Heywood, N.A. Burges, D.M. Moore, D.H. Valentine, S.M. Walters and D.A. Webb), vol. 3, pp. 294–296. Cambridge University Press, Cambridge.
- Caswell, H. (1986) Life cycle models for plants. *Lect. Math. Life Sci.* **18**, 171–233.
- Caswell, H. (2001) *Matrix Population Models*, 2nd edition. Sinauer, Sunderland.
- Chandler, G.E. and Anderson, J.W. (1976) Studies on the nutrition and growth of *Drosera* species with reference to the carnivorous habitat. *New Phytol.* **76**, 129–141.
- Chapin, C.T. and Pastor, J. (1995) Nutrient limitations in the northern pitcher plant *Sarracenia purpurea*. *Can. J. Bot.* **73**, 728–734.
- Clarke, C. (1998) A re-examination of geographical variation in *Nepenthes* food webs. *Ecography* **21**, 430–436.
- Christensen, N.L. (1976) The role of carnivory in *Sarracenia flava* L. with regard to specific nutrient deficiencies. *J. Elisha Mitchell Sci. Soc.* **92**, 144–147.
- Cochran-Stafira, D.L. (1993) *Food Web Interactions and Bacterial Community Structure in Sarracenia purpurea Pitchers*. Ph.D. dissertation. Northern Illinois University, DeKalb, Illinois.
- Cochran-Stafira, D.L. and von Ende, C.N. (1998) Integrating bacteria into food webs: studies with *Sarracenia purpurea* inquilines. *Ecology* **79**, 880–898.
- Connell, J.H. (1978) Diversity in tropical rain forests and coral reefs. *Science* **199**, 1302–1310.
- Corbet, S.A. (1990) Pollination and the weather. *Isr. J. Bot.* **39**, 13–30.
- Coyne, J.A. (1992) Genetics and speciation. *Nature* **355**, 511–515.
- Cresswell, J. (1991) Capture rates and composition of insect prey of the pitcher plant *Sarracenia purpurea*. *Am. Midl. Nat.* **125**, 1–8.
- Daehler, C.C. and Strong, D.R. (1996) Can you bottle nature? The roles of microcosms in ecological research. *Ecology* **77**, 663–664.
- Darwin, C. (1875) *Insectivorous Plants*. Murray, London.
- de Kroon, H., Plaisier, A. van Groenendael, J. and Caswell, H. (1986) Elasticity: the relative contribution of demographic parameters to population growth rate. *Ecology* **67**, 1427–1431.
- DeHayes, D.H., Schaberg, P.G., Hawley, G.J. and Strimbeck, G.R. (1999) Acid rain impacts on calcium nutrition and forest health. *BioScience* **49**, 789–800.
- Diamond, J.M. (1975) Assembly of species communities. In: *Ecology and Evolution of Communities* (Ed. by M.L. Cody and J.M. Diamond), pp. 342–444. Harvard University Press.
- Diggle, P.K. (1997) Extreme preformation in alpine *Polygonum viviparum*: an architectural and developmental analysis. *Am. J. Bot.* **84**, 154–169.
- Dixon, K.W. and Pate, J.S. (1978) Phenology, morphology, and reproductive biology of the tuberous sundew, *Drosera erythrorhiza* Lindl. *Aust. J. Bot.* **26**, 441–454.

- Doak, D.F. and Morris, W. (1999) Detecting population-level consequences of ongoing environmental change without long-term monitoring. *Ecology* **80**, 1537–1551.
- Dörrstock, S., Porembski, S. and Barthlott, W. (1996) Ephemeral flush vegetation on inselbergs in the Ivory Coast (West Africa). *Candollea* **51**, 407–419.
- Drake, J.A. (1991) Community-assembly mechanics and the structure of an experimental species ensemble. *Am. Nat.* **137**, 1–26.
- Drake, J.A., Flum, T.E., Witteman, G.J., Voskuil, T., Hoylman, A.M., Creson, C., Kenny, D.A., Huxel, G.R., Larue, C.S. and Duncan, J.R. (1993) The construction and assembly of an ecological landscape. *J. Anim. Ecol.* **62**, 117–130.
- Dunson, W.A. and Travis, J. (1991) The role of abiotic factors in community organization. *Am. Nat.* **138**, 1067–1091.
- Ellison, A.M. and Gotelli, N.J. (2001) Evolutionary ecology of carnivorous plants. *Trends Ecol. Evol.* **16**, 623–629.
- Ellison, A.M. and Gotelli, N.J. (2002) A fine-scale indicator of nitrogen saturation in northern ecosystems. *Proc. Nat. Acad. Sci., USA* **99**, 4409–4412.
- Endler, J.A. (1986) *Natural Selection In The Wild*. Princeton University Press, Princeton.
- Finn, M.E., Poth, M.A., Aber, J.D., Baron, J.S., Bormann, B.T., Johnson, D.W., Lemly, A.D., McNulty, S.G., Ryan, D.F. and Stottlemeyer, R. (1998) Nitrogen excesses in North American ecosystems, predisposing factors, ecosystem responses, and management strategies. *Ecol. App.* **8**, 706–733.
- Fish, D. (1983) Phytotelmata, flora and fauna. In: *Phytotelmata: Terrestrial Plants as Host for Aquatic Insect Communities* (Ed. by J.H. Frank and L.P. Lounibos), pp. 1–27. Plexus Publishing, Medford.
- Fish, D. and Hall, D.W. (1978) Succession and stratification of aquatic insects inhabiting the leaves of the insectivorous pitcher plant *Sarracenia purpurea*. *Am. Midl. Nat.* **99**, 172–183.
- Folkerts, D. (1999) Pitcher plant wetlands of the southeastern United States: arthropod associates. In: *Invertebrates in Freshwater Wetlands of North America: Ecology and Management* (Ed. by D.P. Batzer, R.B. Rader and S.A. Wissinger), pp. 247–275. John Wiley and Sons, New York.
- Fox, B.J. and Brown, J.H. (1993) Assembly rules for functional groups in North American desert rodent communities. *Oikos* **67**, 358–370.
- Gause, G.F. (1934) *The Struggle for Existence*. Williams and Wilkins, Baltimore.
- Geber, M.A., Watson, M.A., and de Kroon, H. (1997) Organ preformation, development, and resource allocation in perennials. In: *Plant Resource Allocation* (Ed. by F.A. Bazzaz and J. Grace), pp. 113–141. Academic Press, London.
- Ginzburg, L.R., Slobodkin, L.B., Johnson, K. and Bindman, A.G. (1982) Quasiextinction probabilities as a measure of impact on population growth. *Risk Anal.* **2**, 171–181.
- Givnish, T.J. (1989) Ecology and evolution of carnivorous plants. In: *Plant-Animal Interactions* (Ed. by W.G. Abrahamson), pp. 242–290. McGraw-Hill, New York.
- Givnish, T.J., Burkhardt, E.L., Happel, R.E. and Weintraub, J.D. (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.
- Goldberg, D.E. (1990) Components of resource competition in plant communities. In: *Perspectives on Plant Competition* (Ed. by J. Grace and D. Tilman), pp. 27–49. Academic Press, San Diego.

- Gotelli, N.J. and Ellison, A.M. (2002) Nitrogen deposition and extinction risk in the northern pitcher plant *Sarracenia purpurea*. *Ecology* **83**, 2758–2765.
- Gotelli, N.J. and Enstminger, G. (2000). *EcoSim version 5.0*. Acquired Intelligence, Inc. and Keesey-Bear, Burlington.
< <http://www.uvm.edu/bio/faculty/~ngotelli/EcoSim> >
- Gotelli, N.J. and Graves, G.R. (1996) *Null Models in Ecology*. Smithsonian Institution Press.
- Grace, J.B. (1991) A clarification of the debate between Grime and Tilman. *Func. Ecol.* **5**, 503–507.
- Grant, A. and Benton, T.G. (2000) Elasticity analyses for density-dependent populations in stochastic environments. *Ecology* **81**, 680–693.
- Grime, J.P. (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* **111**, 1169–1194.
- Grime, J.P. (1979) *Plant Strategies and Vegetation Processes*. John Wiley and Sons, London.
- Hairston, N.G., Smith, F.E. and Slobodkin, L.B. (1960) Community structure, population control and competition. *Am. Nat.* **44**, 421–425.
- Hanski, I. (1999) *Metapopulation Ecology*. Oxford University Press, New York.
- Hanski, I. and Gilpin, M. (1991) Metapopulation dynamics: empirical and theoretical investigations. Academic Press, London.
- Hanski, I. and Simberloff, D. (1997) The metapopulation approach: its history, conceptual domain, and application to conservation. In: *Metapopulation Biology, Ecology, Genetics, and Evolution* (Ed. by I.A. Hanski and M.E. Gilpin), pp. 5–26. Academic Press, London.
- Harrison, S. and Taylor, A.D. (1997) Empirical evidence for metapopulation dynamics. In: *Metapopulation Biology, Ecology, Genetics, and Evolution* (Ed. by I.A. Hanski and M.E. Gilpin), pp. 27–42. Academic Press, London.
- Harvey, E. and Miller, T.E. (1996) Variance in composition in inquiline communities in leaves of *Sarracenia purpurea* L. on multiple spatial scales. *Oecologia* **108**, 562–566.
- Heard, S.B. (1994a) Pitcher-plant midges and mosquitoes: a processing chain commensalism. *Ecology* **75**, 1647–1660.
- Heard, S.B. (1994b) Imperfect oviposition decisions by the pitcher plant mosquito (*Wyeomyia smithii*). *Evol. Ecol.* **8**, 493–502.
- Heil, G.W. and Diemont, W.M. (1983) Raised nutrient levels change heathland into grassland. *Vegetatio* **53**, 113–120.
- Hemond, H.F. (1983) The nitrogen budget of Thoreau's Bog. *Ecology* **64**, 99–109.
- Herrera, C.M. (1995a) Floral biology, microclimate, and pollination by ectothermic bees in an early-blooming herb. *Ecology* **76**, 218–228.
- Herrera, C.M. (1995b) Microclimate and individual variation in pollinators: flowering plants are more than their flowers. *Ecology* **76**, 1516–1524.
- Herrera, C.M. (1997) Thermal biology and foraging responses of insect pollinators to the forest floor irradiance mosaic. *Oikos* **78**, 601–611.
- Heslop-Harrison, Y. (1976) Enzyme secretion and digest uptake in carnivorous plants. In: *Perspectives in Experimental Biology* (Ed. by N. Sunderland), pp. 463–476. Pergamon Press, Oxford.
- Holt, R.D. (1997) From metapopulation dynamics to community structure: some consequences of spatial heterogeneity. In: *Metapopulation Biology, Ecology, Genetics, and Evolution* (Ed. by I.A. Hanski and M.E. Gilpin), pp. 149–164. Academic Press, London.
- Holyoak, M. (2000) Habitat patch arrangement and metapopulation persistence of predators and prey. *Am. Nat.* **156**, 378–389.
- Holyoak, M. and Lawler, S.P. (1996a) Persistence of an extinction-prone predator-prey interaction through metapopulation dynamics. *Ecology* **77**, 1867–1879.
- Holyoak, M. and Lawler, S.P. (1996b) The role of dispersal in predator-prey metapopulation dynamics. *J. An. Ecol.* **65**, 640–652.
- Huffaker, C.B. (1958) Experimental studies on predation: dispersion factors and predator-prey oscillations. *Hilgardia* **27**, 343–383.
- Hunter, M.D. and Price, P.W. (1992) Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* **73**, 724–732.
- Istock, C.A., Wasserman, S.S. and Zimmer, H. (1975) Ecology and evolution of the pitcher-plant mosquito. 1. Population dynamics and laboratory responses to food and population density. *Evolution* **29**, 296–312.
- Istock, C.A., Vavra, K.J. and Zimmer, H. (1976a) Ecology and evolution of the pitcher-plant mosquito. 3. Resource tracking by a natural population. *Evolution* **29**, 548–557.
- Istock, C.A., Zisfein, J. and Vavra, K.J. (1976b) Ecology and evolution of the pitcher-plant mosquito. 2. The substructure of fitness. *Evolution* **30**, 535–557.
- Jones, C.G., Lawton, J.H. and Shachak, M. (1997) Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* **78**, 1946–1957.
- Juniper, B.E. and Buras, K. (1962) How pitcher plants trap insects. *New Sci.* **13**, 75–77.
- Juniper, B.E., Robins, R.B. and Joel, D.M. (1989) *The Carnivorous Plants*. Academic Press, London.
- Kareiva, P. (1990) Population dynamics in spatially complex environments: theory and data. *Phil. Trans. Roy. Soc., Biol. Sci.* **330**, 175–190.
- Karlsson, P.S. and Pate, J.S. (1992) Resource allocation to asexual gemma production and sexual reproduction in south-western Australia pygmy and micro stilt-form species of sundew (*Drosera* spp., Droseraceae). *Aust. J. Bot.* **40**, 353–364.
- Karlsson, P.S., Nordell, K.O., Carlsson, B.Å. and Svensson, B.M. (1991) The effect of soil nutrient status on prey utilization in four carnivorous plants. *Oecologia* **86**, 1–7.
- Karlsson, P.S., Nordell, K.O., Eirefelt, S. and Svensson, A. (1987) Trapping efficiency of three carnivorous *Pinguicula* species. *Oecologia* **73**, 518–521.
- Kearns, C.A., Inouye, D.W. and Waser, N.M. (1998) Endangered mutualism: the conservation of plant-animal interactions. *Ann. Rev. Ecol. Syst.* **29**, 83–112.
- Keddy, P.A. (1989) *Competition*. Chapman and Hall, London.
- Keymer, J., Marquet, P.A. Velasco-Hernandez, J.X. and Levin, S.A. (2000) Extinction thresholds and metapopulation persistence in dynamic landscapes. *Am. Nat.* **156**, 478–494.
- Kingsolver, J.G. (1979) Thermal and hydric aspects of environmental heterogeneity in the pitcher plant mosquito. *Ecol. Mono.* **49**, 357–376.
- Kingsolver, J.G. (1981) The effect of environmental uncertainty on morphological design and fluid balance in *Sarracenia purpurea* L. *Oecologia* **48**, 364–370.
- Kingsolver, J.G. (1985) Butterfly thermoregulation, organismic mechanisms and population consequences. *J. Res. Lepid.* **24**, 1–20.
- Kitching, R.L. (2000) *Food Webs and Container Habitats: The Natural History and Ecology of Phytotelmata*. Cambridge University Press, Cambridge.

- Kneitel, J.M. and Miller, T.E. (2002) Resource and top-predator regulation in the pitcher plant (*Sarracenia purpurea*) inquiline community. *Ecology* **83**, 680–688.
- Krauss, S. (1994) Restricted gene flow within the morphological complex species *Personia mollis* (Proteaceae): contrasting evidence from the mating system and pollen dispersal. *Heredity* **73**, 142–154.
- Lawler, S.P. (1993a) Direct and indirect effects in microcosm communities of protists. *Oecologia* **93**, 184–190.
- Lawler, S.P. (1993b) Species richness, species composition and population dynamics of protists in experimental microcosms. *J. Anim. Ecol.* **62**, 711–719.
- Lawler, S.P. and Morin, P.J. (1993) Food web architecture and population dynamics in laboratory microcosms of protists. *Am. Nat.* **141**, 675–686.
- Legendre, L. (2000) The genus *Pinguicula* L. (Lentibulariaceae): an overview. *Acta Bot. Gall.* **147**, 77–95.
- Levin, D.A. and Kerster, H.W. (1974) Gene flow in seed plants. *Evol. Biol.* **7**, 139–220.
- Levins, R. (1970) Extinction. In: *Some Mathematical Problems in Biology* (Ed. by M. Gerstenhaber), pp. 75–107. American Mathematical Society, Providence, Rhode Island.
- Lewis-Smith, R.I. (1994) Vascular plants as bioindicators of regional warming in Antarctica. *Oecologia* **99**, 322–328.
- Linhart, Y.B. and Grant, M.C. (1996) Evolutionary significance of local genetic differentiation in plants. *Ann. Rev. Ecol. Syst.* **27**, 237–277.
- Lloyd, F.E. (1942) *The Carnivorous Plants*. Ronald Press, New York.
- Loveless, M.D. and Hamrick, J.L. (1984) Ecological determinants of genetic structure in plant populations. *Ann. Rev. Ecol. Syst.* **15**, 65–95.
- Lüttge, U. (1983) Ecophysiology of carnivorous plants. In: *Encyclopedia of Plant Physiology* (Ed. by O. Lange, P. Nobel, O. Osmond and H. Ziegler), vol. 12C, pp. 489–517. Springer-Verlag, Heidelberg.
- Mark, A.F. (1968) Factors controlling irregular flowering in four alpine species of *Chionochoa*. *Proc. N. Z. Ecol. Soc.* **15**, 55–60.
- Mark, A.F. (1970) Floral initiation and development in New Zealand alpine plants. *N. Z. J. Bot.* **8**, 67–75.
- Miller, T.E. (1996) On quantifying the intensity of competition across gradients. *Ecology* **77**, 978–981.
- Miller, T.E., Kneitel, J.M. and Burns, J.H. (2002) Effect of community structure on invasion success and rate. *Ecology* **83**, 898–905.
- Molau, U. (1993) Reproductive ecology of the three Nordic *Pinguicula* species (Lentibulariaceae). *Nord. J. Bot.* **13**, 149–157.
- Morin, P. (1999) Productivity, intraguild predation, and population dynamics in experimental food webs. *Ecology* **80**, 752–760.
- Mousseau T.A. and Roff, D.A. (1987) Natural selection and the heritability of fitness components. *Heredity* **69**, 181–197.
- Naczi, R.F.C., Soper, E.M., Case, F.W., Jr., and Case, R.B. (1999) *Sarracenia roesa* (Sarraceniaceae), a new species of pitcher plant from the southeastern United States. *Sida* **18**, 1183–1206.
- NADP (2000) National Atmospheric Deposition Program
< <http://nadp.sws.uiuc.edu/default.html> >
- Naeem, S. (1988) Resource heterogeneity fosters coexistence of a mite and a midge in pitcher plants. *Ecol. Mono.* **58**, 215–227.
- Naeem, S., Thompson, L.J., Lawler, S.P., Lawton, J.H. and Woodfin, R.M. (1994) Declining biodiversity can alter the performance of ecosystems. *Nature* **368**, 734–737.

- Nastase, A.J., de la Rosa, C.L. and Newell, S.J. (1991) A comparison of three methods for collecting dipteran insect larvae which inhabit the northern pitcher plant (*Sarracenia purpurea*). *Am. Midl. Nat.* **125**, 356–359.
- Newell, S.J. and Nastase, A.J. (1998) Efficiency of insect capture by *Sarracenia purpurea* (Sarraceniaceae), the northern pitcher plant. *Am. J. Bot.* **85**, 88–91.
- Nielsen, D.W. (1990) Arthropod communities associated with *Darlingtonia californica*. *Annals of the Entomological Society of America* **83**, 189–200.
- O'Conner, B.M. (1994) Life-history modifications in astigmatid mites. In: *Mites, Ecological and Evolutionary Analyses of Life-History Patterns* (Ed. by M.A. Houck), pp. 136–159. Chapman and Hall, New York.
- Ohlson, M. and Økland, R.H. (1998) Spatial variation in rates of carbon and nitrogen accumulation in a boreal bog. *Ecology* **79**, 2745–2758.
- Orr, M.R. and Smith, T.B. (1998) Ecology and speciation. *Trends Ecol. Evol.* **13**, 502–506.
- Osenberg, C.W. and Mittlebach, G.G. (1996) The relative importance of resource limitation and predator limitation in food chains. In: *Food Webs: Integration of Patterns and Dynamics*. (Ed. by G.A. Polis and K.O. Winemiller), pp. 134–148. Chapman and Hall, New York.
- Paine, R.T. (1966) Food web complexity and species diversity. *Am. Nat.* **100**, 65–75.
- Peet, R.K. and Allard, D.J. (1993) Longleaf pine vegetation of the southern Atlantic and eastern Gulf Coast regions, a preliminary classification. In: *The Longleaf Pine Ecosystem: Ecology, Restoration and Management* (Ed. by S.H. Hermann), pp. 45–81. Tall Timbers Research Station, Tallahassee.
- Petal, J. (1998) The influence of ants on carbon and nitrogen mineralization in drained fen soils. *App. Soil Ecol.* **9**, 271–275.
- Petersen, R.L., Hanley, L. and Duffield, R.M. (1997) Occurrence of the rotifer, *Habrotrocha* cf. *rosa* Donner, in the purple pitcher plant, *Sarracenia purpurea* L. (Sarraceniaceae), along the eastern seaboard of North America. *Hydrobiologia* **354**, 63–66.
- Pianka, E.R. (2000) *Evolutionary Ecology*. Addison Wesley Longman, San Francisco.
- Pivnick, K.A. and McNeil, J.N. (1986) Sexual differences in the thermoregulation of *Thymelicus lineola* adults (Lepidoptera, Hesperidae). *Ecology* **67**, 1024–1035.
- Platt, W.J. (1975) The colonization and formation of equilibrium plant species associations on badger disturbances in tallgrass prairie. *Ecol. Mono.* **45**, 285–305.
- Press, M.C., Woodin, S.J. and Lee, J.A. (1986) The potential importance of an increased atmospheric nitrogen supply to the growth of ombrotrophic *Sphagnum* species. *New Phytol.* **103**, 45–55.
- Redmond, A.M., Robbins, L.E. and Travis, J. (1989) The effects of pollination distance on seed production in three populations of *Amianthium muscaetoxicum* (Liliaceae). *Oecologia* **79**, 260–264.
- Rice, R.R. and Hostert, E.E. (1993) Laboratory experiments on speciation: what have we learned in 40 years? *Evolution* **47**, 1637–1653.
- Rosenthal, R. and Rosnow, R.L. (1985) *Contrast Analysis: Focused Comparisons in the Analysis of Variance*. Cambridge University Press, Cambridge.
- Rosenzweig, M.L. and Abramsky, Z. (1993) How are diversity and productivity related? In: *Species Diversity in Ecological Communities: Historical and Geographical Perspectives* (Ed. by R.E. Ricklefs and D. Schluter), pp. 52–65. University of Chicago Press, Chicago.
- Schemske, D.W., Husband, B.C., Ruckelshaus, M.H., Goodwillie, C., Parker, I.M. and Bishop, J.G. (1994) Evaluating approaches to the conservation of rare and endangered plants. *Ecology* **75**, 584–606.

- Schindler, D.W. (1988) Effects of acid rain on freshwater ecosystems. *Science* **239**, 149–157.
- Schwartz, M.W., Bridgham, C.A., Hoeksema, J.D., Lyons, K.G., Mills, M.H. and van Mantgem, P.J. (2000) Linking biodiversity to ecosystem function: implications for conservation ecology. *Oecologia* **122**, 297–305.
- Seine, R., Porembski, S. and Barthlott, W. (1996) A neglected habitat of carnivorous plants: Inselbergs. *Feddes Report*. **106**, 555–562.
- Shaver, G.R. and Kummerow, J. (1992) Phenology, resource allocation and growth of arctic vascular plants. In: *Arctic Ecosystems in a Changing Climate: An Ecophysiological Perspective* (Ed. by F.S. Chapin III, R.L. Jefferies, J.F. Reynolds, G.R. Shaver, and J. Svoboda), pp. 193–211. Academic Press, San Diego.
- Shreve, F. (1906) The development and anatomy of *Sarracenia purpurea*. *Bot. Gaz. (Old Ser.)* **42**, 107–126.
- Silvertown, J., Franco, M., Pisantry, I. and Mendoza, A. (1993) Comparative plant demography: relative importance of life-cycle components to the finite rate of increase in woody and herbaceous perennials. *J. Ecol.* **81**, 465–476.
- Sommer, U. (1991) Convergent succession of phytoplankton in microcosms with different inoculum species composition. *Oecologia* **87**, 171–179.
- Sørensen, T. (1941) Temperature relations and phenology of the northeast Greenland flowering plants. *Meddelelser om Grønland* **125**, 1–305.
- Sork, V.L., Nason, J., Campbell, D.R. and Fernandez, J.F. (1999) Landscape approaches to historical and contemporary gene flow in plants. *Trends Ecol. Evol.* **14**, 219–224.
- Spink, A.J. and Parsons, A.N. (1995) An experimental investigation of the effects of nitrogen deposition on *Nartheicum ossifragum*. *Env. Poll.* **90**, 191–198.
- Stone, L. and Roberts, A. (1990) The checkerboard score and species distributions. *Oecologia* **85**, 74–79.
- Svensson, B.M. (1995) Competition between *Sphagnum fuscum* and *Drosera rotundifolia*, a case of ecosystem engineering. *Oikos* **74**, 205–212.
- Svensson, B.M., Carlsson, B.Å., Karlsson, P.S. and Nordell, K.O. (1993) Comparative long-term demography of three species of *Pinguicula*. *J. Ecol.* **81**, 635–645.
- Thompson, J.N. (1981) Reversed animal-plant interactions: the evolution of insectivorous and ant-fed plants. *Biol. J. Linn. Soc.* **16**, 147–155.
- Thompson, J.N. (1994) *The Coevolutionary Process*. University of Chicago Press, Chicago.
- Thompson, J.N. (1999a) The raw material for coevolution. *Oikos* **84**, 5–16.
- Thompson, J.N. (1999b) Specific hypothesis on the geographic mosaic of coevolution. *Am. Nat.* **153**, S1–S14.
- Thorén, L.M. and Karlsson, P.S. (1998) Effects of supplementary feeding on growth and reproduction of three carnivorous plant species in a subarctic environment. *J. Ecol.* **86**, 501–510.
- Thorén, L.M., Karlsson, P.S. and Tuomi, J. (1996) Somatic cost of reproduction in three carnivorous *Pinguicula* species. *Oikos* **76**, 427–434.
- Tilman, D. (1982) *Resource Competition and Community Structure*. Princeton University Press, Princeton.
- Tilman, D. (1988) *Plant Strategies and the Dynamics and Structure of Plant Communities*. Princeton University Press, Princeton.
- Tilman, D. (1990) Constraints and tradeoffs: towards a predictive theory of competition and succession. *Oikos* **58**, 3–15.

- Tilman, D. and Pacala, S. (1993) The maintenance of species richness in plant communities. In: *Species Diversity in Ecological Communities: Historical and Geographical Perspectives* (Ed. by R.E. Ricklefs and D. Schluter), pp. 13–25. University of Chicago Press, Chicago.
- Tilman, D., May, R.M., Lehman, C.L. and Nowak, M.A. (1994) Habitat destruction and the extinction debt. *Nature* **371**, 65–66.
- Travis, J. (1996) Ecology and evolution of geographical variation in species interaction. *Am. Nat.* **148**, S1–S8.
- Tuljapurkar, S. (1990) *Population Dynamics in Variable Environments*. Springer-Verlag, New York.
- Twolan-Strutt, L. and Keddy, P.A. (1996) Above- and belowground competition intensity in two contrasting wetland plant communities. *Ecology* **77**, 259–270.
- Urban, N.R. and Eisenreich, S.J. (1988) Nitrogen cycling in a forested Minnesota bog. *Can. J. Bot.* **66**, 435–449.
- Van Dijk, H.F.G. and Roeloffs, J.G.M. (1988) Effects of excessive ammonium deposition on the nutritional status and condition of pine needles. *Physiol. Plant.* **23**, 494–501.
- van Groenendael, J., de Kroon, H., Kalisz, S. and Tuljapurkar, S. (1994) Loop analysis: evaluating life history pathways in population projection matrices. *Ecology* **75**, 2410–2415.
- van Tienderen, P.H. (1995) Life cycle trade-offs in matrix population models. *Ecology* **76**, 2482–2489.
- Vandermeer, J.H. (1969) The community structure of communities, an experimental approach with protozoa. *Ecology* **50**, 362–371.
- Warren P.H. (1996) The effects of between-habitat dispersal rate on protist communities and metacommunities in microcosms at two spatial scales. *Oecologia* **105**, 132–140.
- Weiher, E. and Keddy, P.A. (1995) The assembly of experimental wetland plant communities. *Oikos* **73**, 323–335.
- Weiher, E. and Keddy, P.A., eds. (1999) *Ecological Assembly Rules: Perspectives, Advances, Retreats*. Cambridge University Press.
- Weiss, T.E., Jr. (1980) *The Effects of Fire and Nutrient Availability on the Pitcher Plant Sarracenia flava L.* Ph.D. dissertation, University of Georgia, Athens.
- Wilson, J.B. and Roxburgh, S.H. (1994) A demonstration of guild-based assembly rules for a plant community, and determination of intrinsic guilds. *Oikos* **69**, 267–276.
- Wilson, J. B., Allen, R.B. and Lee, W.G. (1995) An assembly rule in the ground and herbaceous strata of a New Zealand rain forest. *Func. Ecol.* **9**, 61–64.
- Wilson, S.D. and Tilman, D. (1995) Competitive responses of eight old-field plant communities in four environments. *Ecology* **76**, 1169–1180.
- Wisdom, M.J., Mills, L.S. and Doak, D.F. (2000) Life stage simulation analysis: estimating vital-rate effects on population growth for conservation. *Ecology* **81**, 628–641.
- Wolfe, L.M. (1981) Feeding behavior of a plant: differential prey capture in old and new leaves of the pitcher plant (*Sarracenia purpurea*). *Am. Midl. Nat.* **106**, 352–359.
- Woodin, S.J. and Farmer, A.M. (1993) Impacts of sulphur and nitrogen deposition on sites and species of nature conservation importance in Great Britain. *Biol. Cons.* **63**, 23–30.
- Worley, A.C. and Harder, L.D. (1999) Consequences of preformation for dynamic resource allocation by a carnivorous herb, *Pinguicula vulgaris* (Lentibulariaceae). *Am. J. Bot.* **86**, 1136–1145.

- Zamora, R. (1995) The trapping success of a carnivorous plant (*Pinguicula vallisneriifolia*), the cumulative effects of availability, attraction, retention, and robbery of prey. *Oikos* **73**, 309–322.
- Zamora, R. (1999) Conditional outcomes of interactions: the pollinator-prey conflict of an insectivorous plant. *Ecology* **80**, 786–795.
- Zamora, R., Gómez, J.M. and Hódar, J.A. (1997) Responses of a carnivorous plant to prey and inorganic nutrients in a Mediterranean environment. *Oecologia* **111**, 443–451.
- Zamora, R., Gómez, J.M. and Hódar, J.A. (1998) Fitness responses of a carnivorous plant in contrasting ecological scenarios. *Ecology* **79**, 1630–1644.
- Zamora, R., Jamilena, M., Rejón, M.R. and Blanca, G. (1996) Two new species of the carnivorous genus *Pinguicula* (Lentibulariaceae) from Mediterranean habitats. *Plant Syst. Evol.* **200**, 41–60.