Summary

Overview – This project is a continuation of our previous NSF-funded research (DEB 98-05722 and DEB-98-08504). A three-year research program is proposed to determine how a novel stressor – atmospheric deposition of nutrients – is changing the dynamics of the detritus-based food web that has co-evolved with its host, the northern pitcher-plant *Sarracenia purpurea*. Three null hypotheses will be tested:

1) Nitrogen derived from atmospheric sources and nitrogen derived from captured prey are used equivalently by the *Sarracenia* food web and by the plant itself;
2) The trajectory of assembly of the *Sarracenia* food web is independent of initial starting composition, habitat type, and the type of, and rate at which, nutrients are supplied;
3) Host plant growth morphology is independent of food web structure and nutrient supply.

In field "pulse" experiments, both the initial species composition of the *Sarracenia* food web and the source of nitrogen input will be manipulated. The trajectory of community assembly will be followed for an entire growing season. Nitrogen isotope ratios will reveal the movement of nitrogen derived from anthropogenic sources and from shredded prey through the food web. In a reciprocal greenhouse "press" experiment, the effects of different food web structures on nutrient uptake and growth of pitcher plants will be measured. Experimental results will be used to calibrate Markov models of community assembly and coupled differential equation models of food web dynamics and plant responses. These models will be used to predict the responses of integrated communities to environmental stress. The proposed research will reveal the importance of anthropogenic stressors on co-evolved systems, and contribute to a deeper understanding of the contrasting effects of top-down and bottom-up forces on the dynamics of non-equilibrial assemblages.

Intrinsic merit – A major challenge for ecologists is to understand the role of stressors on community structure and function. Responses of many individual species to natural and anthropogenic stresses have been studied in great detail, but far less is known about how species interactions within integrated communities will respond to stress. Environmental cycles with lengthy return times, natural and anthropogenically-induced climate change, and unintentional or deliberate alterations of the environment may modify the types, frequencies, or intensities of stressors. The consequences of such stressors for species interactions and community structure are unknown, and may be especially severe for communities of strongly co-evolved species. The focus of this research is on a detritus-based food web, because 70-90% of all primary productivity enters food webs as detritus. However, the development of model systems for understanding the structure and dynamics of detritus-based food webs has not paralleled similar developments in studies of grazing food webs. The proposed research will lead to an appropriate model system for the experimental study of detritus-based food webs.

Broader impacts – This proposal addresses ecological phenomena at the interface of "basic" and "applied" ecology. Ecological systems increasingly are affected by anthropogenic activities, and the proposed research explicitly seeks to understand the responses of stressors resulting from transportation, agriculture, and industrial activities on a tightly co-evolved, "natural" community. The proposed research expands on previously-funded research by the principal investigators that identified a simple, inexpensive method for assessing the response of bogs to nitrogen deposition. The proposed research will result in general models that can be applied to other ecological systems experiencing novel stressors of anthropogenic origin. The proposed research will also involve graduate students as well as undergraduate interns in supervised and independent research. The undergraduates will be involved fully in REU site activities at the Harvard Forest. All data will be catalogued with complete metadata and permanently archived in the Harvard Forest Archives (**http://harvardforest.fas.harvard.edu**).

Project Description

I. Objective

A major challenge for ecologists is to understand the role of stressors on community structure and function (Underwood 1989). Although responses of many individual species and whole ecosystems to natural and anthropogenic stresses have been studied (*e.g.,* Spink & Parsons 1995, Doak & Morris 1999, Aber *et al.* 1998, Carpenter *et al.* 1998), far less is known about how webs of interactions among species will respond to stress. Species in a community have evolved in response to particular types, frequencies, and intensities of stress and disturbance (*e.g.,* Pickett & White 1985, Chesson 1986, Davis 1986). Environmental cycles with lengthy return times, natural and anthropogenically-induced climate change, and unintentional or deliberate alterations of the environment may modify the types, frequencies or intensities of stressors, with unexpected consequences for species interactions and community structure. These consequences may be especially severe for communities of strongly co-evolved species. We propose a set of manipulative field and greenhouse experiments aimed at determining how a novel stressor – atmospheric deposition of nutrients – is changing the dynamics of the detritus-based food web that has co-evolved with its host, the northern pitcher-plant *Sarracenia purpurea*. The results will be used to develop models of community assembly and food web dynamics that can be used to predict the responses of integrated communities to environmental stress. The proposed research will reveal the importance of anthropogenic stressors on co-evolved systems, and contribute to our understanding of the assembly of food webs by contrasting effects of top-down and bottom-up forces on the dynamics of non-equilibrial assemblages.

II. Theoretical motivation

The relative importance of stressors, such as nutrient enrichment and changes in predator abundance (*i.e.,* "bottom-up" and "top-down" control) on the structure and dynamics of food webs has been investigated in detail in the last 25 years or so (see *e.g.,* reviews in DeAngelis 1992, Power 1992, Polis & Winemiller 1996, Carpenter *et al.* 2001). This topic has taken on renewed urgency as human activities worldwide cause eutrophication of aquatic systems and removal of top predators on land and sea. For example, large international collaborations have been formed to address the impacts of nutrient loading on coastal food webs (Skei *et al.* 2000, Olsen *et al.* 2001) and the results of these studies have been linked to trends in global climate change (*e.g.,* Legendre & Rivkin 2002). However, the vast majority of these studies, both "basic" and "applied", have focused on "grazing food webs", in which the basal trophic level is an autotroph (terrestrial plant or phytoplankton) or on soil ecosystem processes such as rates of N mineralization (*e.g.,* reviews in Matson *et al.* 2002, Rabalais 2002). Only in the last few years have ecologists turned their attention to determining how nutrient supply or predator abundance influences detritus-based or donor-controlled food webs (Bengtsson *et al.* 1996, De Ruiter *et al.* 1996, Batzer 1998, Wallace *et al.* 1999, Berg *et al.* 2001 Rosemond *et al.* 2001, 2002, Liiri *et al.* 2002). Understanding the dynamics of detritus-based food webs is especially important because it has been estimated that 70-90% of all primary productivity enters food webs as detritus (O'Neill & Reichle 1980, Pomeroy 1991, Wetzel & Ward 1992). Model systems are needed to explore in detail how stressors affect food web dynamics and the structure of entire communities.

In our research, we will use the invertebrate food web that occurs within the rainwater-filled leaves of *Sarracenia purpurea* (Fig. 1) for our experimental studies of the dynamics of stressed food webs. With NSF support during the last four years, we have developed this "*Sarracenia* food web" as a model system for exploring: community assembly in dynamic habitats; interactions between the food web and its host plant;

Figure 1 –*Sarracenia purpurea*

and effects of chronic N deposition on plant physiology, morphology, and population dynamics. Pitcher plants (families Sarraceniaceae, Nepenthaceae, Cephalotaceae) support well-described food webs of specialized species that have evolved to take advantage of the discrete aquatic habitat in rain-filled living pitcher plant leaves (reviews in Fish 1983, Kitching 2000, 2001, Ellison *et al.* 2002). The *Sarracenia* food web is an excellent system to use for studying the effects of environmental stressors on food webs. This food web is characterized by strong interactions among a small set of species that are obligate inhabitants of the pitchers (e.g., Fish 1983, Ellison *et al*. 2002). It can be manipulated and replicated easily, both in the greenhouse and in the field (*e.g.,* Addicott 1974, Cochran-Stafira & von Ende 1998, Ellison *et al.* 2002). We can experimentally contrast the effects of natural and anthropogenic nutrient inputs and evaluate the relative importance of top-down and bottom-up effects on food web assembly and dynamics (*cf.* Miller *et al*. 2002). The food web structure and species composition is remarkably consistent across the entire range of *S. purpurea* (Buckley *et al. in review*). Thus, results from one or few sites can be generalized to larger geographic scales.

We propose to study the consequences of altering the type, frequency, and intensity of a major stressor: input of nutrients from anthropogenic sources input into the *Sarracenia* food web. We focus the proposed research on contrasting effects of nutrient inputs from two sources: captured prey and atmospheric deposition. Captured prey is broken down by the *Sarracenia* food web and mineralized by bacteria, which make the nutrients in the prey available to the plant. Captured prey represents the "natural" source of nutrients in this co-evolved mutualism between the plant and its food web (Bradshaw & Creelman 1984). Reactive nitrogen and phosphorus (principally NO_x, NH_4, and PO_4) derived from anthropogenic activities (fossil fuel combustion and agriculture) is dissolved in rainwater, is deposited directly into *Sarracenia* pitchers, and is immediately available for uptake by the plant itself (Ellison & Gotelli 2002) and the basal trophic levels of the *Sarracenia* food web. Atmospheric deposition is a novel stressor (reviewed in Galloway & Cowling 2002, Howarth *et al.* 2002) that has affected the *Sarracenia* assemblage only within the past 50 years (Gotelli & Ellison 2002b).

III. Results from prior NSF support: DEB 98-05722 and DEB 98-08504, "*RUI Collaborative Research: Inquiline communities in changeable pitchers: do nutrients link community assembly to dynamic habitats?*"

A. Goals and key achievements
Our collaborative project had three goals:

(1) The development of a model system for analyzing and predicting community assembly and persistence in a habitat that changes on the same time scale as that governing the assembly of the community. We proposed to use the community of arthropods and rotifers that inhabit the rain-filled pitchers of *Sarracenia purpurea* as this model system.
(2) Experimental manipulations of this system to determine how the invertebrate community and the plant interact. We proposed to explore the importance of nutrients for plant leaf allocation patterns, growth, and reproduction, and the effects of plant structure on the *Sarracenia* food web.
(3) The construction of models to describe the assembly and persistence of the invertebrate community and its link to the demography of *S. purpurea*.

We proposed and successfully completed eight manipulative and observational experiments, and developed appropriate models to address these goals. Specifically:
- We conducted three-year greenhouse and field *press* experiments (3 experiments total) to quantify the effects of nutrients on plant growth (Ellison & Gotelli 2002).
- We completed 2 field seasons of each of two experiments examining the assembly of the *Sarracenia* food web in leaves of different sizes and ages (Ellison & Gotelli *in review* a).

- Based on several cohorts of permanently marked plants, we constructed demographic models for plant population growth (Gotelli & Ellison 2002a), and began the development of individual-based models that will allow us to link the community dynamics, leaf morphology, and plant population dynamics (Ellison & Gotelli *in review* b).
- Plant reproductive dynamics were characterized separately, in a series of two additional experiments that we had not initially proposed (Ellison 2001, Ellison & Parker 2002).
- Lastly, we conducted two experiments examining prey capture rates as a function of habitat characteristics and plant morphology (Ellison & Gotelli *unpublished*, Hart *et al. in review*).
- In the course of these prey capture experiments, we discovered that the dominant prey item, the ant *Myrmica lobifrons* Pergande, was not known previously from New England. With additional support from the Massachusetts Natural Heritage and Endangered Species Program, we explored ant diversity and assembly rules in pitcher-plant bogs throughout New England (Gotelli & Ellison 2002b, 2002c, Ellison *et al. in press*).

Our results and models have provided a more complete picture of linkages between pitcher-plant invertebrate communities and their host plants, at individual leaf, whole-plant, and regional (across bog) scales. Our focus on measures of plant performance filled a lacuna in prior studies of the *Sarracenia* food web (reviewed by Ellison *et al.* 2002), which, with few exceptions, emphasized population dynamics and interspecific interactions among the invertebrates. An example of this bias is reflected in the common use of the term *inquiline* for the inhabitants of the pitchers. Inquilines literally are "tenants", organisms that live in the body space of another organism but that do not have any effects on their host. In contrast, our work has supported a handful of earlier studies (Judd 1959, Plummer & Kethley 1964, Fish & Hall 1978, Bradshaw 1983, Bradshaw & Creelman 1984) that demonstrated that the invertebrates that live within pitcher plants are involved in intricate reciprocal interactions with the plants themselves.

B. Human resource development
We focused intensively on supporting undergraduates through this RUI award and associated REU supplements to both PIs. In total, we supported 9 undergraduates at Mount Holyoke and 7 at the University of Vermont. Three of the Mount Holyoke students are pursuing graduate degrees in ecology, two work in the private sector, and four are still undergraduates. Two of the Vermont students are pursuing graduate degrees in ecology, two are in the Peace Corps, and three are still undergraduates. To date, we have published one paper with an undergraduate (Ellison & Parker 2002) and submitted one co-written with two undergraduates (Hart *et al. in review*). This award also supported a senior research associate (L. Bledzki) in Ellison's laboratory; he has submitted two manuscripts to date.

## C. Publications resulting from DEB 98-05722 and DEB 98-08504
To date, 15 papers have resulted from this award (listed below). Of these 15, 11 have already been published or will be published by the end of 2002, including a primary research article in *Proceedings of the National Academy of Sciences* and review papers in *Trends in Ecology & Evolution* and *Advances in Ecological Research*. The *PNAS* paper was highlighted in the News & Comments section of *Trends in Ecology & Evolution* (17: 305). We also organized a well-attended symposium on carnivorous plants as model ecological systems for ESA's annual meeting in 2000, which resulted not only in the two review papers, but also in a request from an editor at Springer-Verlag for us to write a book on carnivorous plants for their Ecological Studies series. We expect to write that book in 2004 or 2005.

1. Ellison, A. M. 2001. Interspecific and intraspecific variation in seed size and germination requirements of *Sarracenia* (Sarraceniaceae). **American Journal of Botany** 88: 429-437.
2. Ellison, A. M., & N. J. Gotelli. 2001. Evolutionary ecology of carnivorous plants. **Trends in Ecology & Evolution** 16: 623-629.
3. Ellison, A. M. & N. J. Gotelli. 2002. A fine-scale indicator of nitrogen saturation in northern ecosystems. **Proceedings of the National Academy of Sciences, USA** 99: 4409-4412.

4. Ellison, A. M. 2002. Food for thought: a review of recent research on pitcher-plant bogs in New England. *Conservation Perspectives* http://www.MassSCB.org/epublications/ (Spring 2002).

5. Bledzki, L. A. & A. M. Ellison. 2001. Nutrient regeneration by rotifers in New England (USA) bogs. **Verhandlung Internationale Vereinigung Limnologie** 28: (*in press*).

6. Ellison, A. M., N. J. Gotelli, J. S. Brewer, L. Cochran-Stafira, J. Kneitel, T. E. Miller, A. S. Worley, and R. Zamora. 2002. The evolutionary ecology of carnivorous plants. **Advances in Ecological Research** 33: (*in press*).

7. Gotelli, N. J. & A. M. Ellison. 2002a. Biogeography at a regional scale: determinants of ant species density in bogs and forests of New England. **Ecology** 83: 1604-1609.

8. Gotelli, N. J. & A. M. Ellison. 2002b. Nitrogen deposition and extinction risk in the northern pitcher plant *Sarracenia purpurea*. **Ecology** 83: (*in press*).

9. Gotelli, N. J. & A. M. Ellison. 2002c. Assembly rules for New England ant assemblages. **Oikos** (*in press*).

10. Ellison, A. M. & J. N. Parker. 2002. Seed dispersal and seedling establishment of *Sarracenia purpurea* (Sarraceniaceae). **American Journal of Botany** 89: 1024-1026.

11. Ellison, A. M., E. J. Farnsworth & N. J. Gotelli. *in press.* Ant diversity in pitcher-plant bogs of Massachusetts. **Northeastern Naturalist**.

12. Ellison, A. M. & N. J. Gotelli. *in review* a. Community assembly in a dynamic habitat. Submitted to **The American Naturalist**.

13. Ellison, A. M. & N. J. Gotelli. *in review* b. Demography of the northern pitcher plant *Sarracenia purpurea*: population dynamics from individual trait-based models. Submitted to **Ecological Monographs**.

14. Bledzki, L. A. & A. M. Ellison. *in review*. Diversity of rotifers from northeastern USA bogs with new species records for North America and New England. Submitted to **Hydrobiologia**.

15. Hart, C. M., C. Ordoyne & A. M. Ellison. *in review*. Competition for prey between spiders and pitcher plants. Submitted to **Ecology**.

IV. The *Sarracenia* – invertebrate food web system

Sarracenia purpurea is the most widespread of the twelve species in this genus of carnivorous plants (Schnell 1976). This long-lived rosette-forming perennial grows in seepage swamps and *Sphagnum* bogs along the east coast of North America from Georgia north to Newfoundland and Labrador, and westward across Canada and the upper Midwestern United States. In New England, the plant produces new leaves approximately every 20 days during the growing season (Fish and Hall, 1978), and each leaf holds ≤ 50 ml of water. Many arthropods— including ants, flies, collembola, spiders, millipedes, and grasshoppers— are attracted to the extrafloral nectaries around the pitcher's lip; some enter the leaves and drown in the standing water (Newell & Nastase 1998).
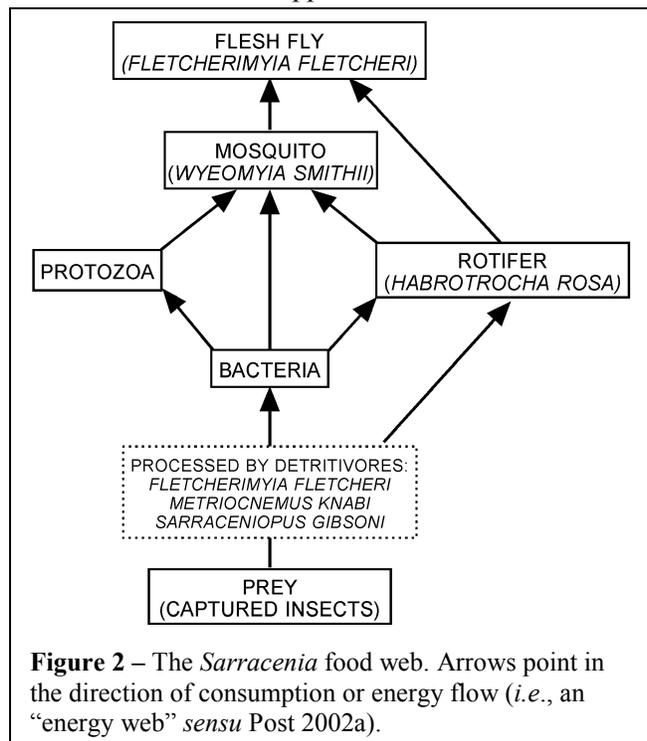
Unlike its congeners that digest prey directly with plant-secreted proteolytic enzymes (Juniper *et al.* 1989), *S. purpurea* depends on a relatively simple food web of obligate pitcher-inhabitants (Folkerts 1999), including bacteria, protozoa, and invertebrates (Fig. 2), to decompose and mineralize captured prey (Bradshaw 1983, Bradshaw & Creelman 1984, Heard 1994b, Chapin & Pastor 1995). Throughout its entire geographic range, the species composition of the *Sarracenia* food web is surprisingly constant (Fig. 2; Buckley *et al. in review*). Because of winter freezes and annual pitcher senescence,

Figure 2 – The *Sarracenia* food web. Arrows point in the direction of consumption or energy flow (*i.e.*, an "energy web" *sensu* Post 2002a).

the *Sarracenia* food web is re-assembled anew each year.

This food web has four trophic levels (Fish 1983, Bledzki & Ellison 1998, Kneitel & Miller 2002). Three detritivores – the slime mite *Sarraceniopus gibsonii* Nesbitt, and larvae of the midge *Metriocnemus knabi* Coq.and the sarcophagid fly *Fletcherimyia fletcheri* (Aldrich) – shred prey. The shredded remains are further decomposed by bacteria (Buckley *et al. in review*, Ellison *et al.* 2002, Miller *et al.* 2002). These bacteria serve as the primary source of food for the rest of the community. Protozoa (Cochran-Stafira & von Ende 1998) and rotifers (usually *Habrotrocha rosa* Donner; Petersen *et al.* 1997, Bledzki & Ellison 1998) make up the second trophic level and consume bacteria as well as small detrital particles. The third trophic level is occupied by the omnivorous mosquito larvae *Wyeomyia smithii* (Coq.), which consumes protozoa, rotifers, and bacteria. *Fletcherimyia fletcheri*, also functions as a top predator, as it consumes rotifers and first and second instar *W. smithii* (Bledzki and Ellison 1998). Addicott (1974) showed experimentally that species richness of protozoa and rotifers declined with abundance of *W. smithii*. Heard (1994b) demonstrated that *W. smithii* and *M. knabi* are involved in a processing-chain commensalisms. Cochran-Stafira & von Ende (1998) studied tritrophic interactions among mosquito larvae, protozoa and bacteria. They found a trophic cascade among these taxa mediated by the composition and abundance of the protozoa, and further suggested that *W. smithii* is a keystone predator in this system. More recent work has expanded the focus of these studies to include the rotifer (Petersen *et al*, 1997; Bledzki & Ellison 1998) and bacterial (Miller *et al.* 2002; N. Ward, A.M. Ellison, & N.J. Gotelli *unpublished data*) assemblages within the pitchers. The plant itself regulates the pCO_2 and pO_2 of the water in the pitcher so that the *Sarracenia* food web can function throughout the season (Cameron 1977, Bradshaw 1983, Joel & Gepstein 1985, Joel & Heide-Jørgensen 1985, Meir *et al.* 1991).

Kitching (2001) asserted that the discrete nature of the *Sarracenia* food web (bordered by the walls of the pitcher-plant leaf) also defines the scale at which local dynamics occur, but the dynamics of prey capture, the life history of the macroinvertebrates and their host plant, and the temporal variability in nutrient inputs "open up" this system. First, nutrient input into this system is entirely allochthonous. Prey capture rate depends on leaf size and age – most prey are caught by large leaves that are between 10 and 30 days old (Fish & Hall 1978, Creswell 1993) – as well as on density of spiders in the surrounding area (Hart *et al. in review*). Release of prey nitrogen to the plant is controlled by the rate of shredding and mineralization, although quantitative rates are currently unknown (we propose to quantify them; see experiment in **§VI.A.**, below).

Second, although all members of the *Sarracenia* food web must recruit into new pitchers, only the mites, bacteria, protozoa, and rotifers reproduce within the pitchers. Both detritivores (*Fletcherimyia* and *Metriocnemus*) and top predators (*Wyeomyia* and *Fletcherimyia*) are larvae of flies that reproduce outside of the plant. Recruitment of these species into pitchers and subsequent assembly of the food web depends on pitcher morphology and age (Forsyth & Robertson 1975, Fish & Hall 1978, Ellison *et al.* 2002, Ellison & Gotelli *in review* a) and their effects on oviposition choices by adult female flies (Heard 1994a). In New England, both top predators are univoltine. Consequently, pitchers produced later in the season have food webs that are missing the top trophic levels because they lack *Fletcherimyia* and have few or no *Wyeomyia* (see Fig. 5, in **§VI.C.**, below).

Third, chronic nitrogen deposition is a stressor in this system that has changed the type, intensity, and frequency with which primary nutrients are available for community assembly (Table 1). Since the 1950s, nitrogen deposition has increased dramatically (Vitousek *et al.* 1997, Galloway & Cowling 2002), and the *Sarracenia* food web now receives nearly as much N from atmospheric sources as it does from shredded prey (Table 1). Unlike nitrogen from prey, which must be processed by the *Sarracenia* food web, reactive nitrogen dissolved in rainwater is available immediately both to the plant and to the *Sarracenia* food web. In the set of experiments we propose here, we take advantage of the "openness" of this discrete system to

address how a contained food web and its host plant respond separately and interactively to current changes in type, frequency, and intensity of nutrient availability.

V. Hypotheses

We propose to examine how shifting the nutrient input into the *Sarracenia* food web – from a nutrient supply dominated by prey to one dominated by atmospheric deposition – alters the structure and dynamics of *S. purpurea* and its associated food web, and to determine whether variability in nutrient input can be effectively buffered by the plant. We will use a set of manipulative field and greenhouse experiments to test the following null hypotheses that are directly motivated by our prior NSF-supported research:

Table 1 – Contributions of four different nutrient sources to the nutrient budget of *S. purpurea*. Prey data from Chapin & Pastor (1995); Rotifer data from Bledzki & Ellison (1998); Soil data from Ellison, Gotelli & Bledzki (unpublished); Nitrogen in precipitation from National Atmospheric Deposition Program, Quabbin, Massachusetts monitoring station; phosphate in precipitation from Ellison, Gotelli & Bledzki (unpublished).

Source	$NO_3 + NH_4$	PO_4
Prey	3.8 mg/pitcher/yr	4.7 mg/pitcher/yr
Rotifer	8 mg/pitcher/yr	16 mg/pitcher/yr
Soil	0.26 mg/L	0.15 mg/L
Precipitation	1.53 mg/L	0.5 mg/L

1) Nitrogen derived from atmospheric sources and nitrogen from captured prey are used equivalently by the *Sarracenia* food web and the plant itself;
2) The trajectory of assembly of the *Sarracenia* food web is independent of initial starting composition, habitat type, and the type of, and rate at which, nutrients are supplied;
3) Host plant growth morphology is independent of food web structure and nutrient supply.

VI. Proposed Research

A. How do atmospheric and prey N move through the *Sarracenia* food web?

PROBLEM STATEMENT

Two types of allochthonous nutrient input provide the resource base for the *Sarracenia* food web: (1) shredded and mineralized prey; and (2) inorganic nutrients (principally NO_x, NH_4, and PO_4) dissolved in precipitation. Prey nutrients are released gradually, and this input is part and parcel of the co-evolved *Sarracenia* food web. Nutrients dissolved in rainwater reflect recent anthropogenic activities and have a profound effect on plant morphology (Fig. 3). Reactive nutrients dissolved in rainwater are immediately available, and the pitcher plant and its food web have been exposed to them at high levels for only the past 50 years (the lifespan of a single plant). With two experiments, we propose to examine how these different nutrient types move through the *Sarracenia* food web and into the plant. One experiment measures the decomposition and mineralization rate of prey by different combinations of shredders, and the other traces nutrients from the
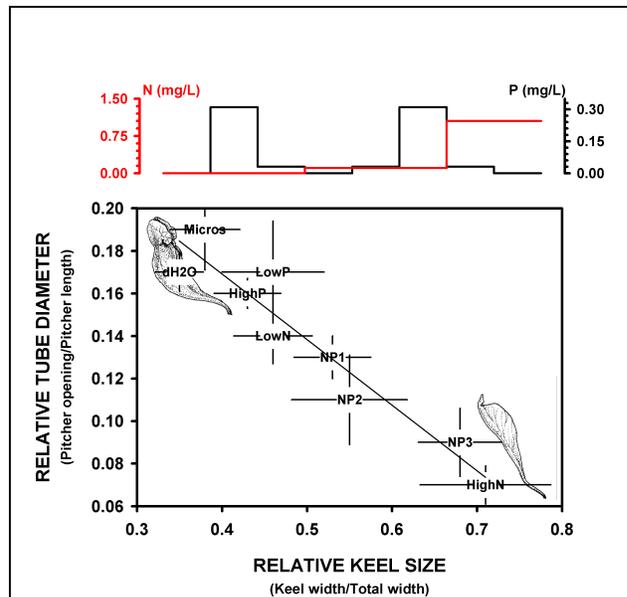

Figure 3 - Morphological response of *Sarracenia purpurea* to direct nutrient additions. On the main plot, each point represents the joint mean of two composite morphological variables and their 95% confidence intervals. Means are labeled with the nutrient addition treatment. The plot at top illustrates the N and P concentrations added at each treatment. The red line illustrates the N concentration and the black line the P concentration in each treatment as ordered from left to right along the regression line. The results suggest that morphology is responsive to N concentration, but not to P concentration. Figure from Ellison & Gotelli (2002).

two different sources through the food web and into the plant. In these and subsequent experiments proposed here, we focus our attention on nitrogen (N), because we have already shown that *Sarracenia* is N-limited, and because plant morphology and physiology respond dramatically to changes in N input but respond little to changes in P input (Fig. 3; Ellison & Gotelli 2002).

EXPERIMENT 1: RATE OF DECOMPOSITION AND MINERALIZATION OF PREY IN THE *SARRACENIA* FOOD WEB
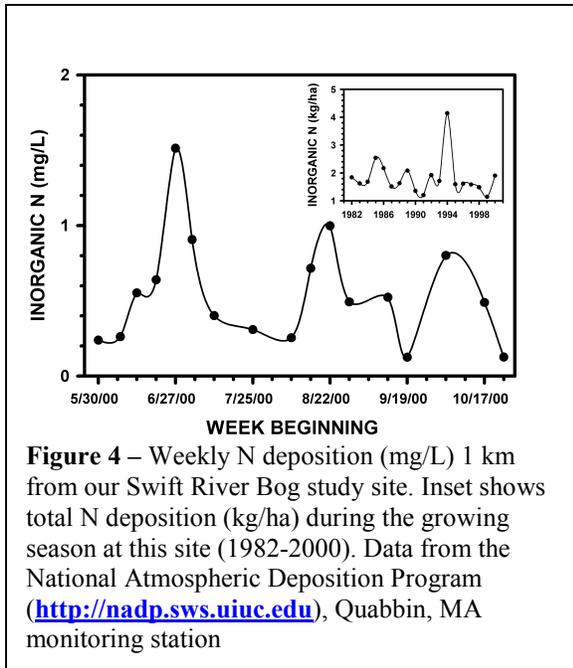Methods – We propose a greenhouse experiment to quantify the rates of decomposition and mineralization of prey. This experiment is a necessary prelude to understanding the impacts of changes in intensity and frequency of nutrient input to the *Sarracenia* food web. There are three shredders in the *Sarracenia* food web: mites, midge larvae, and sarcophagid larvae (Fig. 2, above), yielding 8 (= 2^3) possible combinations of shredders (including the control of no shredders). We will establish 10 replicates of each combination of shredders (including controls) in 20 ml of distilled H_2O in 2-week-old first (largest) leaves of mature *S. purpurea* plants in the Harvard Forest greenhouse (total *n* = 80 plants). Plants to be used in this experiment are four years old and were grown from seed as part of our previous NSF-funded research. Initial population sizes for each shredder taxon will be established at average values observed in field assemblages (30 midge larvae, 1 sarcophagid larva, 1 mite/ml); Ellison & Gotelli *unpublished*). Pitchers will be seeded with bacterial populations by adding 1 ml of natural pitcher water that has been filtered to remove protozoa and rotifers. Prior to adding the shredders, initial NO_3 and NH_4 concentrations of the pitcher fluid will be measured *in situ* with Orion ion-sensitive electrodes. Each pitcher will then be fed 5 ants (*Myrmica lobifrons*, which accounts for >50% of the prey captured in the field; Ellison & Gotelli *unpublished*) collected from the nearby bog at Tom Swamp. NO_3 and NH_4 concentrations will then be measured *in situ* with ion-sensitive electrodes at 12-hr intervals for 1 wk (field experience has shown that after one week, only head capsules remain of captured prey). Ant carcasses will be wet weighed before being fed to the plants, and then extracted daily with pipettes and re-weighed wet as an index of decomposition. After weighing, carcasses (and parts) will be returned to the plant. We will also dry and weigh a set of ants to determine an appropriate wet-to-dry weight conversion.

Because subsequent field experiments will use *Drosophila* as a food source (because it is easy to rear and it may be difficult to collect sufficient *M. lobifrons* for all the field experiments), this experiment will be repeated with 5 *Myrmica* equivalents worth of *Drosophila* as a food source. We will analyze the tissue N content of *M. lobifrons* on a Fison C-H-N analyzer, and then do the same for a standardized sample of frozen adult *Drosophila*. These calculations will allow us to determine the equivalent number of *Drosophila* (in terms of N content) for a fixed number of *Myrmica*.

Predictions and Analysis – The null hypothesis for this experiment is that prey decomposition and mineralization rates will not differ for different combinations of shredders. We will test this hypothesis by comparing rates of prey decomposition and mineralization (expressed as the slope of ant dry mass and N concentration regressed against time) among the eight different treatments. The estimates of prey decomposition and mineralization rates by different shredder combinations will be used subsequently in our models of interactions between the plant and its food web under changing frequencies and intensities of nutrient inputs (see **§VI.D.**, below).

EXPERIMENT 2: FATE OF PREY AND ATMOSPHERIC NUTRIENTS
Methods – We propose a 2-factor field experiment in which we will simultaneously manipulate prey availability and atmospheric deposition of reactive N. Additions of *Drosophila* will be used to simulate different levels of prey, and pre-mixed nutrient concentrations will be substituted for pitcher water to simulate different levels of atmospheric deposition. Average prey capture rates for *S. purpurea* at our sites are 0.75 ± 0.71 (range = 1 – 5) ants per day (Ellison & Gotelli *unpublished*). Atmospheric deposition rates of NO_3 + NH_4 vary considerably in the field, with a weekly average (the time-scale for community assembly and rearrangment; see **§VI.B.**, below) during the 2000 growing season of 0.55 ± 0.35 mg/L (Fig. 4).

Figure 4 – Weekly N deposition (mg/L) 1 km from our Swift River Bog study site. Inset shows total N deposition (kg/ha) during the growing season at this site (1982-2000). Data from the National Atmospheric Deposition Program (**http://nadp.sws.uiuc.edu**), Quabbin, MA monitoring station

We will use a two-way regression design to assess simultaneously the effects of a wide range of concentrations of prey and precipitation N on this system. Ten levels of rainwater N concentrations (0 mg/L [distilled H_2O] to 10 mg/L N as NH_4NO_3 in equal $\log_{10}$ intervals) will be crossed with 10 levels of prey concentration (0 to 18 ant equivalents in intervals of 2 ant equivalents) for a total of 100 plants, each receiving a unique nutrient × prey combination. This design can be analyzed as a regression response surface, which allows for efficient hypothesis tests, parameter estimation, and detection of non-linear responses. Two sets of 100 plants each will be established at the start of the season in early June. These two hundred non-reproductive plants will be haphazardly chosen at Swift River Bog and each assigned randomly to a treatment. To prevent nutrient contamination by rainwater, each plant will be covered with a clear plastic roof of optically neutral lexan (20 cm × 20 cm, placed 20 cm above the ground) that will exclude rainwater, but allow entry by adult inquilines for oviposition. All treatments will be maintained throughout the growing season as a press experiment (*sensu* Bender et al. 1984); fruit flies will be added twice weekly, and the pitcher water volume will be maintained to a constant level by topping up with liquid of the specified N concentration. Previous data suggest that root uptake of N contributes insignificantly to plant growth (Ellison & Gotelli *unpublished*).

The first set of 100 plants will be harvested in mid July, to catch the phenological peak abundance of the top predator (*Fletcherimyia*). The second set of 100 plants will be harvested in late August. For each plant, we will quantify inquiline abundance in the primary leaf, and measure $\delta^{15}N$ and $\delta^{13}C$ in plant and tissues of larval predators, and in the pitcher plant liquid. We will use the two-end-member-mixing method of Post (2002b) to determine the relative contributions of prey N and atmospheric N to higher trophic levels of the food web and to plant tissues. Post (2002b) showed that for food webs where elements such as N come from two sources (here, prey and atmospheric deposition), trophic position (here, of top predators and the plant itself) can be calculated as:

$$\text{trophic position} = \lambda + (\delta^{15}N_{\text{secondary consumer}} - [\delta^{15}N_{\text{source1}} \times \alpha + \delta^{15}N_{\text{source2}} \times (1 - \alpha)]) / \Delta_n$$
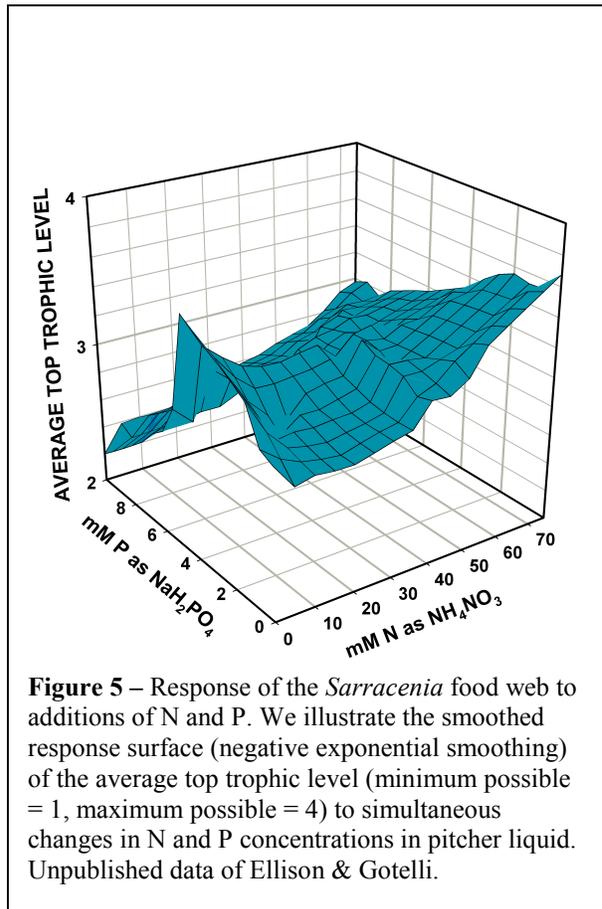
where λ is the trophic position used to estimate $\delta^{15}N_{\text{source}}$ (e.g., 1 for lowest levels of the food web), the $\delta^{15}N$ are measured directly, Δ_n is the enrichment of $\delta^{15}N$ per trophic level (3.4%; Post 2002b), and α is the proportion of N in the consumer ultimately derived from the base of the food web. Post (2002b) showed that α can be estimated using from measurements of $\delta^{13}C$:

$$\alpha = (\delta^{13}C_{\text{secondary consumer}} - \delta^{13}C_{\text{source2}}) / (\delta^{13}C_{\text{xource1}} - \delta^{13}C_{\text{xource2}}).$$

Assays of $\delta^{15}N$ and $\delta^{13}C$ in prey, pitcher water and leaf tissues of the experimental plants will be conducted at the isotope laboratory at the Marine Biological Laboratory, Woods Hole. We will also quantify plant biomass response, and changes in plant morphology, as measured by the relative keel width of pitchers (a reliable indicator of ambient available nitrogen Ellison & Gotelli 2002; Fig. 3, above).

Analysis and Predictions – The null hypothesis is that atmospheric and prey N are used equivalently by the food webs and the pitchers. The alternative hypothesis is that N dissolved in precipitation and deposited directly into pitchers moves more rapidly through higher trophic levels; thus *Wyeomyia*, *Fletcherimyia*, and the plants themselves would have relatively lower trophic positions in systems enriched with atmospheric N. We will also test whether plant biomass, morphology, and within plant translocation of nutrients responds differentially to prey versus atmospheric N. In other experiments (Fig. 3, above), we have already established that atmospheric N can quickly alter pitcher plant morphology; it remains to be seen whether changes in ambient prey can induce similar responses. Non-additive effects of prey and atmospheric nitrogen will be evaluated by testing for a statistically significant interaction term in the multiple regression model.

Preliminary Data – Atmospheric N deposition dramatically alters pitcher plant morphology (Fig. 3, above), and this morphological shift even can be used as an inexpensive biological indicator for nitrogen deposition rates and saturation in New England bogs (Ellison & Gotelli 2002). In the summer of 2001, we conducted a pilot study in which we manipulated the chemical composition of the pitcher liquid and measured changes in the structure of the *Sarracenia* food web (Fig. 5). Six nutrient concentrations in pitcher liquid (0 to 54 mM N as NH_4NO_3 and 0 to 10 mM P as Na_2HPO_4) were maintained in a crossed, orthogonal press experiment; prey levels were not manipulated. In this pilot study, food web complexity, measured as the average top trophic level attained by a food web during the growing season, tended to increase with increasing N ($P = 0.10$) and tended to decrease with increasing P ($P = 0.13$). The trends are intriguing, and warrant additional experimental study as proposed herein.

Figure 5 – Response of the *Sarracenia* food web to additions of N and P. We illustrate the smoothed response surface (negative exponential smoothing) of the average top trophic level (minimum possible = 1, maximum possible = 4) to simultaneous changes in N and P concentrations in pitcher liquid. Unpublished data of Ellison & Gotelli.

B. How do changes in type, frequency and intensity of nutrient input, and associated changes in plant physiology modify community assembly of the *Sarracenia* food web?

PROBLEM STATEMENT

Community assembly rules describe mechanisms that control entry and establishment of species in an assemblage (Diamond 1975, Post & Pimm 1983, Drake 1990, Law & Morton 1996). In spite of long historical interest in this problem (Samuels and Drake 1997, Gotelli 1999), most empirical studies of community assembly are not experimental. Instead, community assembly rules have been inferred from statistical analyses of static patterns of community structure (*e.g.,* Keddy and Weiher 1999, Gotelli & McCabe 2002, Gotelli and Ellison 2002c), or from historical records of species introductions (Moulton and Pimm 1983, Duncan 1997, Lockwood *et al.* 1999). There is also a long tradition of experimentally adding and removing species from communities, both in field and laboratory experiments (reviews in Hairston 1989, Goldberg and Barton 1992, Beyers & Odum 1993, Paine 1994, Resetarits & Bernardo 1998). However, few of these manipulations have been analyzed in the context of community assembly rules (Cole 1983, Abele 1984, Gilpin *et al.* 1986, Drake 1991, Weiher & Keddy 1995, Sait *et al.* 2000)

With the exception of our studies on the *Sarracenia* food web (Ellison & Gotelli *in review* a; see Fig. 6, below), these studies also have ignored biological interactions between the assembling community and its habitat. Normally, the habitat is treated as a passive inert structure, even though in two notable field studies the habitats were living coral heads (Abele 1984) or mangrove islands (Cole 1983). Recognizing *Sarracenia purpurea* as a living habitat allows us to examine the importance of biotic feedback between the habitat and the assemblage, and to determine how assembly rules change when the food web is altered through bottom-up (*i.e.*, changes in type, frequency, or intensity of nutrient input; Balčiūnas & Lawlor 1995) or top-down (*i.e.,* changes in predator species abundance or composition; Sait *et al.* 2000) effects. Stressors such as changes in nutrient input and abundance of predators not only could exert both bottom-up and top-down effects on the dynamics of the *Sarracenia* food web, but also could affect plant growth dynamics (= changes in the habitat) and subsequent interactions between the food web and its host plant.

Because we can establish *Sarracenia* food webs with predetermined initial compositions, we can carry out experimental tests of community assembly rules in changing environments. In our previously-funded research, we examined how pitcher age affected temporal and spatial patterns of species co-occurrence patterns (the classical metric of community assembly: Diamond 1975) within the *Sarracenia* food web (Ellison *et al.* 2002). Here, we propose to ask three new questions. First, to what extent do priority effects (Wilbur & Alford 1985, Shorrocks & Bingley 1994) determine the dynamic trajectory of community assembly? This question will be answered by establishing replicated communities with different initial combinations of species and then following their development in a *pulse* experiment. Second, to what extent does nutrient stress modify these biotic effects (Dunson & Travis 1991)? This question will be answered by establishing all of the species combinations in 3 different nutrient regimes. Finally, to what extent is community assembly modified by interactions of nutrient stress with physiological responses of the pitcher plant? This question will be answered by seeding a parallel set of assemblages in plastic tubes in the field. These tubes mimic the physical structure of the pitcher plant leaf, but they are physiologically inert.

EXPERIMENTAL DESIGN
<u>Methods</u> – The five macroinvertebrates in the *Sarracenia* food web (midge, mosquito, and sarcophagid larvae, mites, and rotifers) will be manipulated in field populations of *S. purpurea* to establish all possible species combinations as starting points for community assembly. With 5 taxa, there are $2^5 = 32$ species combinations, including the combination of no species initially. Initial population sizes for each taxon will be established at average values observed in assemblages at our field sites (10 mosquito larvae, 30 midge larvae, 1 sarcophagid larva, 1 mite/ml, 10 rotifers/ml; A.M. Ellison & N.J. Gotelli *unpublished*). Although some experimental designs in competition studies have controlled for intra- and interspecific density differences (Underwood 1986, Bernardo et al. 1995, Gotelli 1997), we have not used this approach because we are interested in the effect of the presence or absence of entire populations on the structure and dynamics of the food web (Schluter 1994, 1995). Furthermore, because the species differ by orders of magnitude in their body sizes, and vary in trophic status and life histories, it does not seem appropriate to "equilibrate" the system for differences in density.

Each treatment will consist of the specified number of inquilines and 25 ml of pitcher fluid (distilled H_2O and two nutrient levels bracketing observed deposition: 0.15, 1.5 mg/L of N added as NH_4NO_3). Pitchers will be allowed to trap prey at ambient levels (which we will monitor) and additional input of atmospheric nutrients will be monitored automatically (NADP monitoring station at Quabbin, MA, 1km from Swift River Bog, and EMS tower at Harvard Forest, 2 km from Tom Swamp). We expect rapid colonization of bacteria and protozoa as prey are shredded by inquilines and decomposition begins. For each of the three nutrient levels, three replicates of each treatment will be established in the first (= largest) leaf of the growing season (total sample size = 32 combinations × 3 replicates × 3 nutrient levels = 288 plants). This is an ecological *pulse* experiment, in which community assembly will be initiated from different starting points, but no further manipulations are applied. Once a week each invertebrate assemblage will be

censused non-destructively. A 1 ml subsample of liquid will be collected to estimate sizes of bacterial, protozoan, and rotifer populations (methods described in detail in Ellison *et al.* 2002). In our pilot study described below, 12 person-hours per week were required to sample the food web of each of 120 plants; we estimate that 30 person-hours per week will be required to maintain this experiment.

In parallel with the manipulations of living plants, we will establish the same treatment combinations in a set of 288 plastic centrifuge tubes painted dark green and placed in the field adjacent to the pitchers of the same treatment combination (an additional 30 person-hours per week). Plastic tubes have been used in other experiments with the *Sarracenia* food web (e.g., Cochran-Stafira & von Ende 1998); the assumption has been that these containers are adequate mimics of *S. purpurea* pitchers. However, experiments on the trophic structure of *Sarracenia* food webs in living leaves (Addicott 1974, Kneitel & Miller 2002) and test tubes (Cochran-Stafira & von Ende 1998) have yielded contrasting results (strong *vs.* weak top-down control of the *Sarracenia* food web). Although Kneitel & Miller (2002) hypothesized that the differences were due to experimental setting, experimental duration, natural levels of protozoan species richness, prey capture rate, or predator density, we suggest that the differences result from the fundamental effects of a living habitat on the food web. Specifically, we predict that photosynthesis, respiration, and nutrient uptake by the plant itself (*e.g.,* Cameron 1977, Joel & Gepstein 1985, Joel & Heide-Jørgensen 1985, Meir *et al.* 1991) substantially alter community assembly in living pitchers versus inert plastic tubes. We will use weekly measurements of pitcher and test-tube nutrient concentrations (*in situ* with ion-sensitive electrodes) and monthly measurements of pitcher photosynthetic rates (with a Li-Cor 6200 photosynthesis system and custom cuvette; Ellison & Gotelli 2002) as co-variates in our analysis of the response of the *Sarracenia* food web to habitat and nutrient loading.

Analysis and Predictions – Our null hypothesis is that the trajectory of community assembly is independent of initial starting composition, nutrient input, and habitat type. This would be the case if: (1) community assembly is dominated by stochastic extinction and colonization; (2) buffering of the pitcher plant liquid by plant respiration and nutrient uptake has no effect on trophic dynamics of the *Sarracenia* food web; and (3) oviposition by the dipterans is insensitive to plant characteristics. The alternatives are that priority effects are important (*i.e.,* the trajectory of community assembly is sensitive to the initial species composition) and/or that colonization sequence is determined by interactions between colonizing invertebrates and ovipositing flies on the one hand and a living *Sarracenia* leaf on the other.

We will first use a fixed factor ANOVA (32 levels of species composition × 2 levels of habitat type × 3 levels of nutrient solution) to test for overall differences in invertebrate abundance, average trophic level (large sarcophagid larvare = trophic level 4, mosquito larvae = trophic level 3, rotifers = trophic level 2, small sarcophagid and midge larvae, and mites = trophic level 1), species evenness, and estimated community biomass. Orthogonal contrasts will be used to test for effects of species number, and effects of average trophic level on community structure. Next, we will analyze the data as a 5-way ANOVA testing for main effects and interaction terms for the presence and absence of each taxon (Whittam & Siegel-Causey 1981) for a particular nutrient-habitat combination. Finally, we will use path analysis (Shipley 2001) to determine the relative importance of top-down and bottom-up control on invertebrate abundance. Specifically, we will construct explicit path models (passive sampling, habitat structure, top down, bottom up, mixed trophic) based on the known trophic interactions and natural history of the major component taxa, and assess the relative fit of the models to the data (Burnham & Anderson 1998; Gotelli & Ellison, *unpublished analyses*).

Preliminary Data – We have used this non-destructive census method in a two season-long studies of invertebrate colonization and food web assembly in *Sarracenia* leaves of different ages. Invertebrate assemblages were sampled weekly from 120 pitchers growing at Molly Bog (Vermont) and Hawley Bog (Massachusetts). We summarize the data as directed graphs indicating transitions among different food

webs (Figure 6). These graphs will be developed into a series of Markov models that we will fit to the data from the invertebrate colonization experiment (see **§VI.D. Model Development**, below).
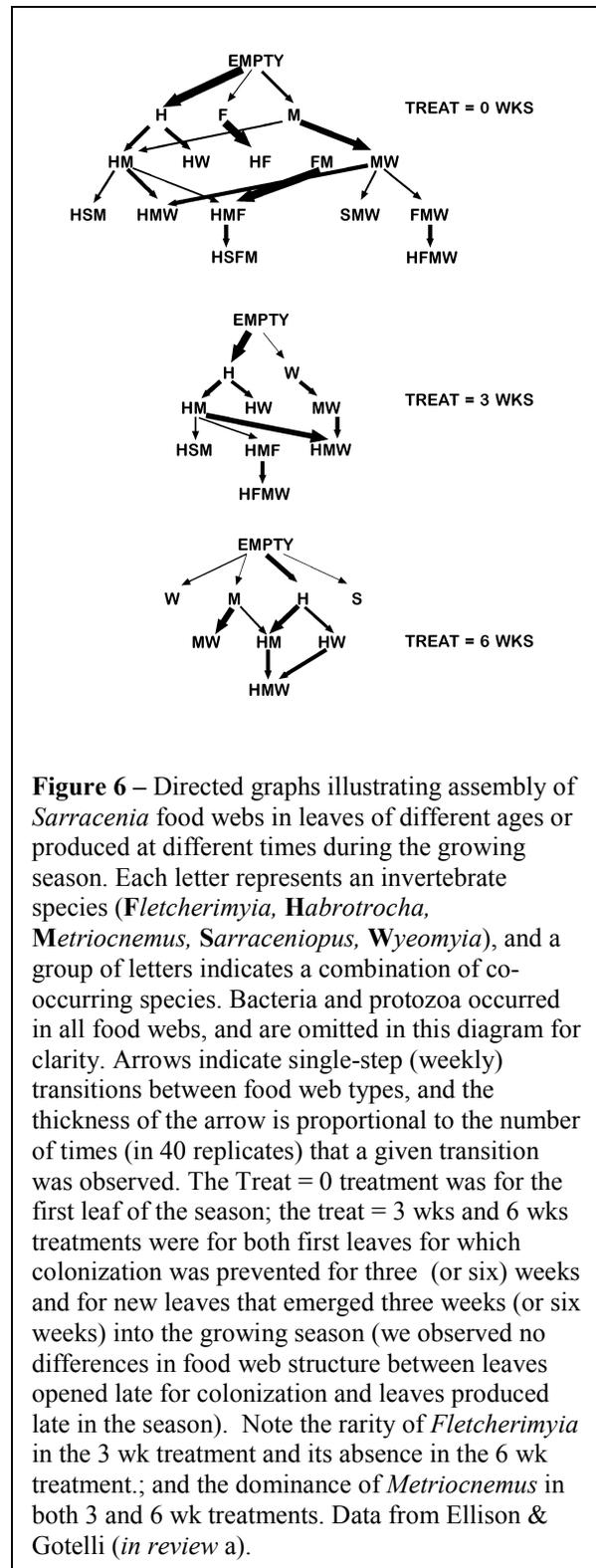
C. How do food web structure and composition affect growth and morphology of the *Sarracenia* leaf?

PROBLEM STATEMENT

In the preceding experiment (**§VI.B.**), comparisons of community development in plastic tubes and *S. purpurea* leaves tested for the effects of the living plant and the nutrient content of the pitcher liquid on the development of the *Sarracenia* food web. In this experiment, we want to examine the flip side of this interaction and document the effects of the food web itself on plant growth and morphology. In our previously-funded research, we established that pitcher growth and morphology is sensitive to reactive nutrients directly deposited into pitchers (Fig. 3, above), but we did not assess the role of the nutrients mineralized by the food web itself on plant growth and production. These effects will depend on the extent to which different assemblages modify the nutrient chemistry of the pitcher plant liquid, which mediates this response.

EXPERIMENTAL DESIGN

Methods – The design here follows that of the preceding experiment, but with two important changes. First, this will be a *press* experiment in which the initial food webs will be maintained through time. Invertebrates will be censused weekly, and replenished as needed to maintain the initial species composition. Second, this experiment will be conducted in the greenhouse, rather than in the field. The greenhouse setting allows us to control more carefully the composition of the food web as well as the growing conditions of the plant. This combination will enable us to directly quantify the effects of the food web on pitcher water chemistry while controlling prey availability and eliminating atmospheric deposition of nutrients into pitchers. Plants to be used in this experiment are four years old.

Figure 6 – Directed graphs illustrating assembly of *Sarracenia* food webs in leaves of different ages or produced at different times during the growing season. Each letter represents an invertebrate species (**F**letcherimyia, **H**abrotrocha, **M**etriocnemus, **S**arraceniopus, **W**yeomyia), and a group of letters indicates a combination of co-occurring species. Bacteria and protozoa occurred in all food webs, and are omitted in this diagram for clarity. Arrows indicate single-step (weekly) transitions between food web types, and the thickness of the arrow is proportional to the number of times (in 40 replicates) that a given transition was observed. The Treat = 0 treatment was for the first leaf of the season; the treat = 3 wks and 6 wks treatments were for both first leaves for which colonization was prevented for three (or six) weeks and for new leaves that emerged three weeks (or six weeks) into the growing season (we observed no differences in food web structure between leaves opened late for colonization and leaves produced late in the season). Note the rarity of *Fletcherimyia* in the 3 wk treatment and its absence in the 6 wk treatment.; and the dominance of *Metriocnemus* in both 3 and 6 wk treatments. Data from Ellison & Gotelli (*in review* a).

In the greenhouse at the Harvard Forest, we will establish 5 replicates each of the 32 possible combinations of invertebrates in the first (largest) leaf of 160 mature plants. Food webs will be seeded

with natural pitcher water to establish bacterial and protozoan populations. The food webs will be maintained by feeding plants *Drosophila* prey, and invertebrates will be replenished as necessary. At the end of the growing season, all leaves of each plant in half the replicates will be harvested, weighted, and measured. The other half of the replicates will be maintained into a 2nd year of experimentation, to account for delayed flowering responses by the plants (Shreve 1906, Ellison *et al.* 2002).

Analysis and Predictions – The statistical analysis will follow that of the preceding experiment, but the response variables will be plant biomass and morphological indices (keel width to plant width; Fig 3, above) that reflect the degree of investment in pitchers and photosynthetic organs (Ellison & Gotelli 2002). We will also measure nutrient concentrations in the pitcher liquid at the end of the experiment using a Lachat autoanalyzer. The null hypothesis is that plant morphology is not dependent on inquiline community structure. The alternative hypothesis is that food webs dominated by shredders (flesh flies, mites, and midges) will induce plants to produce pitchers with smaller tubes and larger keels because these plants will have greater N available to them and will invest less in prey capture and more in photosynthetically efficient flattened leaves (phyllodia) (Ellison & Gotelli 2002).

D. Modeling and Synthesis

We propose to use Markov models to describe the assembly of *Sarracenia* food webs, and coupled differential equations to describe the interactions between the food webs and pitcher plant growth. For both models, parameters will be estimated from the results of our field and laboratory experiments. Models will be tested further by measuring food web structure and plant morphology in control sets of 100 unmanipulated plants at each of two bogs: Swift River Bog and Tom Swamp. We will compare the expected frequencies of species combinations generated by the model with the observed frequencies recorded in unmanipulated pitchers (Usher 1979, Caswell 2001). We can also compare the predicted and observed trajectory of empty pitchers as they approach "equilibrium"[1]. Finally, we will contrast pitcher morphology as a function of food web structure and background N deposition with that predicted by our models and observed in our experimental populations.

ASSEMBLY RULES FOR FOOD WEBS

We will use matrix transition models to describe the changes in species combinations that occur during the growing season. Matrix models have been used to describe successional change in animal and plant communities (Horn 1975, Usher 1979, Mcauliffe 1988), and to incorporate past historical events (Tanner et al. 1996), which are not included in simple first-order models (Facelli & Pickett 1990). However, in all of these models, the "state" of the community represents a single species or dominant successional stage (Gotelli 2001). We will extend matrix succession models in a novel analysis of the *Sarracenia* food web by treating the "states" as distinct species combinations.

For example (Table 2), suppose the community consists of only 2 species, A and B. There are 4 possible species combinations (Ø [no species], A, B, AB), so a 4×4 matrix specifies the transitions among the different states. We further specify that assemblages add only 1 species at a time, which is appropriate for a model with a short time step (one week for the *Sarracenia* matrix). Although Lockwood *et al.* (1997) proposed more general models that allow for addition or subtraction of more than one species at a time, we found that >80% of the observed state transitions (as illustrated in Fig. 6, above) in the *Sarracenia* food web were single species additions or deletions (model time step = 7 days). Thus, we assume all

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[1] Although we use standard mathematical analyses to evaluate equilibrium conditions of these models, we stress that the models are describing non-equilibrial assemblages that undergo chronic disturbance at a measurable frequency. These disturbances are represented by transitions from observed communities to the "open" state (Ø), which is an empty leaf. Although the model predicts (realistically) that each individual leaf is frequently disturbed and dynamically changing, a population of leaves reaches an equilibrium frequency of different species combinations for a particular disturbance regime (Gotelli 2001).

transitions but the collapse of the assemblage to the Ø state will occur as single-step (addition or deletion of a single species) transitions. The collapse of the assemblage to the Ø state from any species combination is allowed because of the possibility of sudden floods (overfilling the pitcher) or severe droughts (drying it out completely).

Non-zero transitions represent possible changes that can occur during a single time step. The matrix columns add to 1.0, as there are no net changes in the number of community states. Using standard matrix theory, this model predicts the equilibrium distribution of species combinations, time to go from a newly opened leaf in which all patch states = Ø to an equilibrium condition, and the relative stability of the equilibrium (as measured by its damping ratio; Caswell 2001). The model can also be extended to include lags of more than one time step (second-order Markov models) and fixed occupancy times for a given state (semi-Markov models; Tanner et all. 1996).

Table 2 – Example of a community matrix for determining assembly rules for food webs. 0s indicate transitions that cannot occur in a single time-step because the assemblage adds new species one at a time.

		Stage at time t			
		Ø	A	B	AB
Stage at time $t+1$	Ø				
	A			0	
	B		0		
	AB	0			

The transitions will be estimated in two ways: first, we can empirically tally the number of transitions among the different states that are recorded in our *pulse* experiment (**§VI.B.**). These will be used to create directed graphs such as those shown in Figure 6 (above). Second, we will consider as a null hypothesis a non-interactive community in which probabilities of colonization and extinction in mixed species combinations are based on independent events as measured in single species assemblages. For example, consider an assemblage of 3 communities, and the transition from state ABC to state AB (species C is lost through an extinction). If colonizations and extinctions are independent then,

P(ABC → AB) = P(Extinction of C).

In other words, the transition from ABC to AB can be predicted by simply knowing the extinction probability of species C. Alternatively, if combination ABC is extremely stable, these two probabilities will not be equivalent, and extinctions will have to be modeled as non-independent:

P(ABC → AB) = P(Extinction of C|ABC).

We will fit both kinds of models, predict the equilibrium state, and then compare the expected frequencies of different species combinations to those found in the final census of the pulse experiment. (**§VI.B.**)

INTERACTIONS BETWEEN *SARRACENIA* AND ITS FOOD WEB
We propose to use the experimental results to construct three coupled differential equations linking plant growth, food web structure, and pitcher nutrient water. Let L = leaf biomass, I = invertebrate biomass (or some other measure of food web structure), and N = concentrations of nutrients in pitcher water. Feedback loops between the three components can be modeled as:

$$dL/dt = f(L,N) \qquad dN/dt = g(N,I,L) \qquad dI/dt = h(N,L,I)$$

where *f, g,* and *h* are three growth functions. In our conceptual model, leaf growth (dL/dt) depends only on leaf size (L) and available nutrients (N), but both nutrient availability (dN/dt) and invertebrate community growth (dI/dt) depend on food web structure or size (I), nutrient availability (N), and leaf size (L). Thus, the nutrient pool mediates changes that occur because of food web and plant physiological

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processes. We will not specify the forms of these equations until data are available, but we expect these will follow simple linear, asymptotic, or unimodal relationships (Abrams 1995). We will use the equation solver in S-Plus 6.0 (Insightful Corporation) to determine the equilibrium solution and evaluate its stability.

VII. Significance of the Proposed Research

Atmospheric deposition of nutrients is a novel stressor that may disrupt the integrity and assembly of co-evolved food webs. The invertebrate food web inhabiting rain-filled leaves of *Sarracenia purpurea* is a model system for studying this problem. We propose to use stable isotopes to trace the movement of nutrients derived from shredded prey and derived from atmospheric deposition through both the detritus-based invertebrate food web and the tissues of the host plant. Experimental manipulations of initial species composition and nutrient regimes will reveal how reciprocal interactions between the co-evolved host plant and its food web are modified by a novel stressor. The results will provide new insights into the effects of environmental stressors of anthropogenic origin on top-down and bottom-up forces in non-equilibrial assemblages and co-evolved systems.

VIII. Responsibilities of the PIs

PI Ellison and a research assistant (RA) to be hired will have responsibility for carrying out the field and greenhouse experiments at Swift River Bog, Tom Swamp, and the greenhouse at the Harvard Forest. We will support two undergraduate interns each summer on this project as well. They will be integrated into the large REU activities at the Harvard Forest (an REU site). Ellison and the RA will also be responsible for data and metadata archiving (in the Harvard Forest archives and in the on-line data catalog at the Harvard Forest) and data analysis. Emery Boose, Information and Computer Systems Manager will also work closely with us to ensure data archiving follows the Harvard Forest LTER data management standards. PI Gotelli will have responsibility for model development, programming, and data analysis. Both PIs will share equally in manuscript preparation.

IX. Feasibility and timetable

We will be able to begin these experiments as soon as we receive funding. More than 1500 mature plants grown from seed are available now, and the greenhouse at the Harvard Forest is adequately equipped for this research. We are permitted from Massachusetts Department of Fisheries and Wildlife for field work at Swift River Bog, and field work at Harvard Forest's Tom Swamp requires only construction of an access boardwalk. In his new position at the Harvard Forest, PI Ellison has neither teaching nor administrative responsibilities, and is devoting full time to research; this project is his primary research endeavor.

Table 3 – Timetable. Each year is divided into two **O**ff-seasons (Jan. – Apr.; Oct. – Dec.) and one **F**ield season (May – Sept.). Proposed grant period is Jan. 1, 2003 – Dec. 31, 2005.

Task	2003			2004			2005		
	O	**F**	**O**	**O**	**F**	**O**	**O**	**F**	**O**
Hire full-time research assistant	▓								
Construct access boardwalk at Harvard Forest Bog	▓								
Prey decomposition rate experiment (**§VI.A.**)		▓							
Fate of prey and nutrients experiment (**§VI.A.**)		▓							
Community stability pulse experiment (**§VI.B.**)					▓				
Food web and plant growth press experiment (**§VI.C.**)					▓			▓	
Model development (**§VI.D.**)	▓		▓	▓		▓	▓		
Model testing (**§VI.D.**)					▓			▓	
Manuscript preparation			▓	▓	▓	▓	▓	▓	▓

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