PROJECT SUMMARY

Overview
Most theoretical models of species coexistence assume that habitat patches are spatially fixed in size and constant in quality. How communities are organized in systems with dynamic habitat patches – those that are neither spatially fixed in size nor temporally constant in quality – is a crucial yet unresolved ecological question. The proposed research uses realistic field manipulations to understand the creation of dynamic habitat patches and how associated communities interact with them. The research takes advantage of a model ecological system: the carnivorous pitcher plant *Sarracenia purpurea*, its associated aquatic food web, its prey, and its herbivores. In this system, the tubular leaves of the plant fill with rainwater and function as dynamic habitat patches for a self-contained aquatic food web. Changes in patch location, quantity, and quality may be mediated by reciprocal interactions and feedback loops among patches (the plant and its growing leaves), its primary prey (ants), and its herbivores (moth larvae that feed on the plants’ leaves). A set of field experiments are proposed in which patch size, density, and spatial pattern, and levels of herbivory are manipulated. These experiments address the following questions:

1. Do the feedback loops between the moth, the plant, and the ant result in local aggregations of plants and spatial association between ant nests and plants?
2. Does spatial clustering of moth larva attacks leads to “traveling waves” of suitable and unsuitable patches?
3. How does the structure of the aquatic food web in a pitcher respond to changes in patch structure (leaf size and number of plants)?

Intellectual Merit
The research proposed here is a novel experimental study of species interactions in dynamic habitats, which change in size, quality, and spatial arrangement. The *Sarracenia* system is a well-used model for studies of ecological stoichiometry, population dynamics in changing environments, community assembly and metacommunity dynamics at local, regional, and continental scales, and food web structure. The proposed research broadly expands the theoretical context of patch dynamics and the scope of *Sarracenia* research by exploring mechanisms responsible for creating and maintaining dynamic habitats, and testing their role in structuring multi-trophic communities.

Broader Impacts
There are three broader impacts of the proposed research. First, undergraduates, graduate students, teachers, research assistants, and post-docs will be educated and mentored through continuous involvement in theory and methods of basic ecological research and in fundamentals of natural history. Second, the proposed research will yield a general framework for understanding how multi-trophic communities assemble and disassemble in changing environments. Third, an established model ecological system – the *Sarracenia* system - will be propelled to a new level, where it can be used to explore mechanisms driving food web dynamics at the landscape scale.
I. Objective

The goal of this research is to experimentally elucidate how interactions among prey, predators, and herbivores control the spatial pattern of dynamic habitat patches, and to understand how these interactions indirectly affect multi-trophic communities inhabiting these patches.

Community ecology seeks to explain the distribution and abundance of interacting species, but general yet realistic models of coexistence remain elusive. For analytical convenience, models of species coexistence in patchy landscapes (e.g., Hanski 1985, Mouquet & Loreau 2002) use an important simplification – stable patches of fixed sizes with constant attributes. In the research proposed here, we will move beyond this simplification and study species interactions in dynamic habitats, which change in size, quality, and spatial arrangement.

We will continue to use the *Sarracenia* model system (Fig. 1) for the proposed research. *Sarracenia purpurea* is a long-lived perennial carnivorous plant that grows in bogs, poor fens, and seepage swamps throughout the eastern U.S. and Canada. *Sarracenia purpurea* serves three important ecological functions. First, it is a predator; its tube-shaped leaves fill with water and capture arthropod prey (mostly ants and flies). Second, *Sarracenia* is prey for noctuid moth larvae that feed on leaves, inflorescences, and rhizomes. Finally, *Sarracenia* is a dynamic habitat patch; a specialized, co-evolved micro-ecosystem develops in each intact *Sarracenia* leaf. The captured prey are the inputs for this detritus-based ecosystem.

Past NSF funding to the PIs, along with research by several other groups, has led to the emergence of this system as a model for: studies of ecological stoichiometry (Ellison & Gotelli 2002, Wakefield *et al.* 2005); population dynamics in changing environments (Bradshaw and Holzapfel 2001, Gotelli & Ellison 2002c, 2005); community assembly and metacommunity dynamics at local, regional, and continental scales (Ellison *et al.* 2003, Buckley *et al.* 2003, Trzcinski *et al.* 2003, Krawchuk & Taylor 2003, Miller & Kneitel 2005); and...

Research on the Sarracenia system to date has focused primarily on structure and dynamics of Sarracenia’s aquatic food web, and on the interplay between the food web and the plant. We now have a rich picture of the dynamics of this food web, but we have not yet addressed the fact that its habitat – the plant population itself – is not simply a static landscape of green “test-tubes” in which food web dynamics play out. Rather, it is a spatially structured, dynamic system. The organization of this dynamic system appears to be controlled by interactions between Sarracenia, the ants that are its primary prey, and herbivores that kill leaves or entire plants. Our proposed research into these interactions will move this model system to a new level – where it can be used to explore mechanisms driving food web dynamics at the landscape scale.

II. Theoretical Background and Motivation

Many theoretical models predict that two or more species competing for a single (or similar) resource can stably coexist in a landscape if there is sufficient dispersal, immigration, and emigration among habitat patches (Skellam 1951, Hutchinson 1951, Horn & MacArthur 1972). Recent expansion of food web theory into a broader landscape context (Polis et al. 1997, 2005) explicitly acknowledges that fluxes of material resources, organisms, and energy can control trophic dynamics and can both respond to and drive ecosystem processes (Holt 2005). Both metacommunity models (Mouquet & Loreau 2002) and landscape analyses of food webs incorporate a set of assumptions about the structure of the “landscape” and the meaning of spatial heterogeneity: a landscape is viewed as a mosaic of fixed patches connected by immigration and emigration of organisms, and exchange of resources and energy (Horn & MacArthur 1972, Forman & Godron 1986). Patches differ in their fixed attributes, such as vegetation, soil, water, or geology (Cadenasso et al. 2005).

Horn & MacArthur (1972) recognized that patches of fixed sizes with constant attributes were but an analytical convenience. If habitats appear, change, or disappear locally, a set of separate equations are required to link their dynamics with those of their dependent communities (Horn & MacArthur 1972). Spatial and landscape models of population dynamics of single species (e.g., Clark 1991a, 1991b) or several competing species (e.g., Ellison & Bedford 1995, Olff et al. 2000, Kennedy & Storer 2000, Ricketts 2001, Zavala & Zea 2004, Fuhlendorf & Engle 2004) have taken up Horn & MacArthur’s challenge and extended patch dynamic models to the shifting mosaics of what we refer to as dynamic habitats. These models all illustrate that coexistence and persistence of species depend on the timescale at which habitats change and the spatial linkages among them. However, experimental confirmation of processes that create dynamic habitats and the roles of dynamic habitats in structuring ecological communities are lacking. Further, these models have mostly focused on communities consisting of competing species within a single trophic level. Extensions of these models to encompass multi-trophic communities are required to comprehend the dynamics of complete food webs on landscapes.

The Sarracenia system (Fig. 1) offers both a unique opportunity and a generalizable model with which to examine mechanisms responsible for creating and maintaining dynamic habitats, and exploring their role in structuring multi-trophic communities. In a series of experiments focused on three trophic levels – ants (prey); plants (intermediate predator and habitat patches for the aquatic food web); moths (herbivore and “top predator” in this three-level system) – we address the following questions and associated hypotheses:
1. **WHAT SETS THE INITIAL CONDITIONS?** We hypothesize that temporal feedbacks between mobile prey and sessile predators result in spatial segregation of different prey species, spatial association of prey and predators, and local aggregations of habitat patches.

2. **WHAT CREATES AND MAINTAINS DYNAMIC HABITATS?** We hypothesize that the spatial clustering of herbivores leads to “traveling waves” of suitable and unsuitable patches.

3. **HOW DO THESE PATCH DYNAMICS CONTROL STRUCTURE OF THE ASSOCIATED AQUATIC FOOD WEB?** We hypothesize that the structure of the aquatic food web in any given patch (*i.e.*, pitcher) is a function of number of patches, creation of new groups of patches (*i.e.*, plants), and distance among groups of patches.

### III. The *Sarracenia* system

#### A. Background

In the last decade, our research (see §IX. Results from Prior NSF Support, below), together with work by several other research groups, has firmly established the *Sarracenia* system (Fig. 1) as a model for exploring a wide range of ecological questions (reviews in Ellison & Gotelli 2001, Ellison *et al.* 2003, Srivastava *et al.* 2004, Miller & Kneitel 2005). Until the mid-1990s, research on this system focused on dynamics of aquatic food webs in single pitchers (*e.g.*, Addicott 1974, Bradshaw & Creelman 1984, Heard 1994b, Błędzki & Ellison 1998), but more recent work has emphasized the importance of scale-dependence on the composition and structure of the *Sarracenia* food web (Harvey & Miller 1996, Miner & Taylor 2002, Ellison *et al.* 2003, Kneitel & Miller 2003, Trzcinski *et al.* 2003, Krawchuk & Taylor 2003, Srivastava *et al.* 2004, Miller & Kneitel 2005). We now can map dynamics of the *Sarracenia* system directly onto a three-level hierarchy (Table 1) that theorists (Leibold *et al.* 2004, Amarasekare *et al.* 2004) have

<table>
<thead>
<tr>
<th>Definition in a:</th>
<th>Metacommunity</th>
<th>Food web</th>
<th><em>Sarracenia</em> system</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Patch</strong></td>
<td>Occupied by a single individual</td>
<td>A habitat occupied by a single food web</td>
<td>A single pitcher with its food web whose existence is contingent on draining of the pitcher by <em>herbivorous moths (Exyra)</em>, and whose structure depends on prey inputs.</td>
</tr>
<tr>
<td><strong>Locality</strong></td>
<td>A community consisting of a collection of identical patches</td>
<td>A collection of identical habitats with similar food webs</td>
<td>A single plant, consisting of a collection of <em>n</em> pitchers. Plant growth and new pitcher production is controlled by nutrients mineralized by food webs and shared among pitchers. <em>These processes are modulated by spatial and temporal distribution of prey (ants) and removal of pitchers by moth larvae (Exyra).</em></td>
</tr>
<tr>
<td><strong>Region</strong></td>
<td>A metacommunity consisting of a collection of localities linked by dispersal</td>
<td>A collection of disparate food webs linked by allochthonous energy flow</td>
<td>A collection of plants whose food webs are linked by energy/nutrient flow from the surrounding bog into the pitchers; migration of bacteria, protozoa, rotifers and, mites; oviposition dynamics of adult Diptera; foraging behavior of ant colonies, and dispersal and oviposition dynamics of herbivorous moths.</td>
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defined as the theater in which metacommunity dynamics play out. Relevant nested scales include individual pitchers (“patches”), multiple pitchers within single plants (“localities”), clumps of plants and groups of clumps in single bogs (“regions”), and multiple bogs in the landscape.

Within individual patches (pitchers), the presence and abundance of the top predators *Wyeomyia smithii* and *Fletcherimyia fletcheri* exert top-down effects on bacteria, protozoa, and rotifers (Addicott 1974, Błędzki & Ellison 1998, Kneitel & Miller 2002, Trzcinski et al. 2005). Prey availability has bottom-up effects on bacteria, protozoa, rotifers, and mite population dynamics and species richness of protozoa (Kneitel & Miller 2002, Miller & Kneitel 2005, Trzcinski et al. 2005). Oviposition rates of both predators and of the midge *Metriocnemus knabi*, which shreds captured prey, vary with pitcher size, and adult emergence is synchronized with the availability of newly-opened pitchers (Mogi & Mokry 1980, Istock et al. 1983, Heard 1994a, 1994c, Krawchuk & Taylor 1999). Prey contribute ~10% of the plant’s nutrient budget (Chapin & Pastor 1995, Newell & Nastase 1998, Dixon et al. 2005); in the northern portion of its range, *S. purpurea* receives 20-50% of its N budget from atmospheric deposition (Błędzki & Ellison 1998). Excess N input shifts leaf morphology from pitchers to non-carnivorous phyllodes (Ellison & Gotelli 2002), which do not host food webs, but contribute ~25% more carbon per unit leaf area than do pitchers (Ellison & Gotelli 2002). However, atmospheric deposition may eventually lead to population decline and extinction as root and rhizome reserves are exhausted and seedlings are killed by nitrogen “burn” (Gotelli & Ellison 2002c, Güsewell 2005, Gotelli & Ellison 2005).

Within localities (whole plants, which consist of a set of water-filled leaves), dispersal among patches maintains populations of protozoa and rotifers that suffer high levels of predation in individual pitchers (Błędzki & Ellison 1998, Kneitel & Miller 2003). Larvae of *Fletcherimyia* can track prey by moving among pitchers on a single plant (Trzcinski et al. 2003). Pitcher-plant flowers also provide roosts and mating sites for adult *Fletcherimyia* (Krawchuk and Taylor 1999), which pollinate *S. purpurea* (Burr 1979). Pitcher plants produce only one flower per plant, and at our study sites ~5-30% of the plants flower annually.

Within a region (an entire bog), plant distribution and bog physiognomy affect oviposition dynamics of *Wyeomyia*, *Metriocnemus*, and *Fletcherimyia* (Heard 1994a, 1994c, Miner & Taylor 2002). Plants are rarely randomly arrayed in a bog, but rather tend to form clumps (Fig. 2; Ellison & Parker 2002, Krawchuk & Taylor 2003), in part because of the extremely limited seed dispersal of *Sarracenia* (Ellison & Parker 2002). Krawchuk & Taylor (2003) showed that the limited movement distances of adult *Wyeomyia* and *Metriocnemus* (10s of m) and *Fletcherimyia* (ca. 100m) resulted in positive effects of leaves, plants, or clumps of plants on density of larvae of these

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**Figure 2.** Spatial arrangement of *Sarracenia purpurea* adults (large circles) and seedlings (small circles) in a 500 × 500 cm mapped plot at Hawley Bog, in 2001. Spatial clustering is significant up at scales up to 200cm (P < 0.05, Monte Carlo simulations on Ripley’s K); adult plants are clustered with adult plants, and seedlings are clustered with seedlings (Moran’s I = 3.4, P = 0.006). Figure from Ellison and Parker (2002). Tick labels are cm.
three species, and generally negative effects of isolation of clumps of plants (Fletcherimyia only) or peatlands (Wyeomyia and Fletcherimyia) on larval density.

**B. Preliminary data**

ANTS are the primary prey of pitcher plants; they account for the majority of individual prey items and total prey biomass (Newell & Nastase 1998, Ellison et al. 2002, and unpublished). In northern bogs, the most common ants are Myrmica lobifrons (sensu Francoeur 1997), Formica subaenescens (sensu Francoeur 1973), and Dolichoderus pustulatus (Ellison et al. 2002, Gotelli & Ellison 2002b). The first two and species nest in Sphagnum moss, whereas D. pustulatus builds carton nests, often in old or moth-damaged S. purpurea pitchers (Fig. 1). Plants show distinct spatial clustering (Fig. 2; Ellison & Parker 2002), but ant occurrences appear to be randomly arrayed in space (Fig. 3). The ant data illustrated in Fig. 3 are counts of individuals collected in pitfall traps; detailed mapping of nests, as proposed below, is required to test the hypotheses that ant nests are spatially associated with plants, if different species of ants are spatially segregated, and how spatial distributions of nests of different ant species are related to plant population structure.

**Moth** larvae are among the few organisms that feed on the unpalatable leaves of Sarracenia purpurea (Rymal & Folkerts 1982). Papaipema appassionata is a root-borer that kills entire plants. It is rare throughout its range (it is listed as “threatened” in Massachusetts), and will not be examined in detail in this proposal. Exyra fax eats pitcher leaves, and occurs in > 30% of the plants at our study sites in Massachusetts (Atwater et al. 2006). Each larva chews a drainage hole at the base of the pitcher. The damaged leaf cannot capture prey or host a food web, but it does not kill the plant outright (Fish 1976, Rymal & Folkerts 1982, Folkerts & Folkerts 1996). After draining the pitcher, the larva seals the top of the leaf either with a web of silken threads or by girdling and closing the leaf just under the pitcher lip. The larva then feeds on...
the interior surface of the pitcher chamber (Jones 1921, Rymal & Folkerts 1982, Folkerts & Folkerts 1996). Larvae can move among pitchers; we observed a single larva feeding on three pitchers/plant in a single season. In our region, *Exyra* is univoltine. Larvae overwinter as third instars, pupate in early spring, and eclose in late June.

REU student Dan Atwater studied the distribution of *Sarracenia* and the moth larvae at Tom Swamp, a ~50 ha bog at the Harvard Forest LTER site (Atwater et al. 2006). He found that moths fed preferentially on larger plants, and that larvae are spatially aggregated (Fig. 4). Given the apparent selectivity of adults for ovipositing on larger plants and their low mobility – most fly < 10 m from their eclosion site – we hypothesize that the temporal distribution of larvae would lead to a “traveling wave” of attack. Once an individual within a cluster of adult plants is attacked, larvae would inhabit all suitable plants. Plants may then be reduced in quality (size, number of leaves) to the point at which the patch is no longer suitable, and ovipositing adults seek other nearby patches. After *Exyra* has migrated out of a patch, the plants in that patch could recover to suitable size until they were attacked again. Our proposed research tests this hypothesis by tracking spatial and temporal distribution of *Exyra* across the bog, and examines the impact of this patterning on interactions among ants, plants, and the plants’ food webs.

IV. Hypotheses and mechanisms

We will test the overall hypothesis that interactions mobile prey, sessile predators, and mobile herbivores yield a shifting mosaic of prey (the allochthonous input to the *Sarracenia* food web), pitchers (predators of ants and the habitat for the food web), and plants (the ultimate producer of new pitchers), and that the structure of this mosaic is controlled in large part by the herbivore. The field observations and experiments that we will conduct will test a set of explicit mechanisms underlying the generation of this mosaic and its consequences for the dynamics of *Sarracenia* and its aquatic food web.

1. Because pitcher plants provide an energy source (carbon via extrafloral nectaries) for foraging ants:
   1.1. the distribution of ant (prey) nests and individual pitcher plants (predator) will be spatially correlated;
   1.2. the strength of the spatial association of plants and ant nests will increase with plant size and density;
   1.3. the three common bog ant species compete for resources provided by *Sarracenia*, and thus their nests will be spatially segregated within bogs.

2. Because pitcher plants prey on ants, and prey capture rate increases with plant size and prey encounter rate:
   2.1. growth rate and reproductive effort of individual plants will be positively associated with the size of, and negatively associated with distance to, the nearest ant colony;
   2.2. seed production and seedling distribution will be clumped within the bog and positively associated in space with ant nests;
   2.3. “saturation” (§VI.B, Table 2, below) of the aquatic food web in *Sarracenia* pitchers will be positively associated with both prey capture rate and spatial distribution of ant nests.

3. Herbivory by *Exyra*, which results in loss of entire pitchers and alters the spatial arrangement of available habitat (pitchers and plants) within bogs, will disrupt the spatial association among ants and *Sarracenia* and the dynamics of the aquatic food web:
3.1. limited dispersal rates of adult *Exyra* lead to “traveling waves” of pitcher mortality across bogs;
3.2. growth rate and reproductive effort of individual plants will be negatively associated with loss of pitchers;
3.3. ant colony distribution will be hyperdispersed (negatively associated in space) relative to *Sarracenia* attacked by *Exyra*;
3.4. saturation of the aquatic food web will be hyperdispersed relative to patches of plants attacked by *Exyra*.

V. Proposed Research

We will use a combination of spatial mapping, field experiments and observations, and simulation modeling to understand the relationships between *Sarracenia*, ant colonies, and moth attacks. All experimental manipulations will be conducted at Tom Swamp, a ~50 ha bog at the Harvard Forest LTER site (red square in Fig. 5). This site supports a total *Sarracenia* population of >10,000 individuals, approximately 30% of which are annually attacked by *Exyra* (Atwater et al. 2006). We will also extensively sample spatial patterns at 26 bogs in VT, MA, and CT (Fig. 5) and at 24 additional sites in NY, NH, and ME (Buckley et al. 2003).

A. Spatial and temporal associations of ants, plants, and moths

All three sets of hypotheses in §IV require detailed information on the spatial location of plants, ant nests, and moth larvae, and how these spatial patterns vary through time. We are especially interested in predicting regional patterns that may drive local interactions by scaling up from small-scale spatial processes.

We will first map the distribution of these species in 5 replicated 10 × 10 m plots at Tom Swamp. Plants with and without moths will be permanently tagged, measured (Ellison & Gotelli 2002) and mapped ± 1 cm using a compass, meter tapes, and a Sonin® electronic range-finder (Ellison & Parker 2002, Atwater et al. 2006). Entrances to nests of *Myrmica lobifrons*, *Formica subaenescens*, and *Dolichoderus pustulatus* will be located and mapped by following workers from bait stations placed at 1-m intervals throughout each plot. Plant death, seedling recruitment, moth oviposition patterns, and temporal shifts in ant nests will be documented by repeated sampling of these plots each summer. We will also measure pore water NH4 and vegetation structure, as the distribution of these ants covary with these variables (Ellison & Gotelli 2002, Ellison et al. 2002). Degree of spatial aggregation, regularity, or hyperdispersion within and among taxa will be assessed using nearest-neighbor methods (Dixon 1994); temporal changes in these patterns will be determined using SADIE - spatial analysis by distance indices (Perry et al. 1999, Winder et al. 2001).

This sampling regime will provide detailed information on spatiotemporal patterns of ants, plants, and moths at a single site; will patterns be similar among bogs? In Year 1 and Year 5 of this funding period, we will conduct a snapshot survey of the spatial pattern of plants, ant nests, and moth attacks within each of 50 bogs throughout New England and New York (Fig. 5). At each bog, we will map ants, plants, and moths within a fixed 10 × 10 m plot, measure pore...
water NH₄, vegetation structure, and record latitude, longitude, and bog elevation, all of which will enter our statistical models as covariates (Gotelli and Ellison 2002b).

**B. Manipulating spatial interactions**

We propose a novel manipulation of spatial pattern at the “locality scale” (Table 1, above), for which we can measure shifts in the spatial pattern of associated species. Our experiments focus on experimental manipulations of the spatial arrangement of *Sarracenia*, because moths and ants cannot be directly manipulated in this system. Plants that we have already raised from seed in the greenhouse and growing in plastic pots filled with *Sphagnum* will be transplanted to the field, where they will grow, overwinter, and persist in defined spatial configurations. To avoid genetic contamination of the Tom Swamp population of pitcher plants, we will only use plants grown from seed collected at Tom Swamp for all our manipulations. Thus, we will experimentally establish patches of plants that differ in size and density and then quantify the responses of ants and moths to these manipulations.

**Experiment 1 – Locality-scale manipulations of plant size and density**

Our first experiment addresses the hypotheses that plant size and density alter spatial patterns of ant colonies (foragers and prey) and *Exyra* (herbivores), and examines prey capture rates by, and food web structure in, individual leaves of plants of different sizes growing in different densities.

We will establish replicate plots with 6 categories of plant density (1 to 6 plants in a tight clump), orthogonally crossed with 6 categories of plant size (range 2 – 20 cm rosette diameter). Each plot will consist of 126 plants: 1 – 6 plants per clump × 6 plant size classes (Fig. 6).

Clumps of plants will be placed in an evenly-spaced 6 × 6 m grid, with random assignments of different size × density treatments to each grid location, and a 1-m separation between adjacent clumps. In this experimental regression design (Gotelli & Ellison 2004, Cottingham et al. 2005), there are two continuous predictor variables, plant size and density, and a sample size of \( N = 36 \) plant size × density combinations per plot. We will establish 5 replicate plots, for a total of \( 5 \times 126 = 630 \) plants. Treatment plants will be allowed to persist in the field for the duration of the proposed research (5 field seasons).

To address temporal changes in the system (Winder et al. 2001) we will measure spatial patterns of ants, plants, and moth attacks at the start of the experiment, and at the start and end of each field season. Dead or dying plants will not be replaced during the course of the experiment because they may serve as ant nest habitat and may attract (or repel) moths. The distribution of all naturally occurring plants, ant colonies, and *Exyra* larvae on unmanipulated plants within the 36 m² plot also will be mapped at the start of the experiment.

![Figure 6. Treatment combinations in a 6 × 6 experimental regression design. Six combinations of plant size (small to large circles) are crossed with 6 combinations of plant number per clump (dark blue to light blue). In the field, these plants will be placed in a regular spatial array, but the position of each particular treatment within the grid will be randomized.](image)
At the end of each field season, we will measure the following variables within each plot:

1) Presence and density of *Exyra* on natural and experimental plants;
2) Occurrence and distribution of all ant nest entrances;
3) Prey and invertebrate abundance and food web structure and saturation (Table 2) within the leaves of pitcher plants within each experimental clump, and within the leaves of the naturally-occurring plant nearest to each clump.
4) Occurrence and distribution of any new *Sarracenia* seedlings within the plot;
5) Occurrence and distribution of flowering plants (both experimental and natural);
6) Leaf growth of all plants (both experimental and natural).

The analysis will be based on nearest-neighbor distances and Ripley’s *K* for ant colonies and spatial association of *Exyra* larvae with respect to size × density combinations of *Sarracenia* (Ripley 1976, Harkness and Isham 1983, Dixon 1994). Null expectations of response variables will be derived from computer simulation, with random placement of discs (ant nest entrances) or points (*Exyra* larvae) within a mapped plot (Winder et al. 2001). The occurrence of *Exyra* attacks and flowering plants will be analyzed by simulating the random occurrence of *Exyra* and plant flowering among the established plants (given their fixed spatial distribution), and then measuring nearest neighbor distances and other measures of spatial aggregation and segregation. Logistic regression will be used to assess the effects of plant size and clumping on the probability of flowering and the probability of *Exyra* attack. Regression slope parameters from these analyses will provide inputs for the long-term simulation model (described below).

**EXPERIMENT 2 – REGIONAL-SCALE MANIPULATION OF PLANT SIZE AND DENSITY**

The first experiment will reveal effects of leaf size (“patch”), and plant size and density in each “locality” (Table 1). But do these responses “scale up” to the “region”? To answer this question, we will use a whole-plot experiment in which we will establish 5 plots of 6 × 6 m, each of which will receive a different treatment: The plots will be carefully chosen at the start of the experiment to minimize difference in background vegetation, microtopography, and *Sarracenia* density. Background variation in established plants will be measured as a covariate, but not controlled for experimentally.¹ In the manipulated plots, we will transplant 36 clumps of *the same treatment* in an evenly spaced array within each plot:

1) Control: no manipulations

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¹ We have chosen not to remove background plants in each plot. Removals would destroy bog vegetation unnecessarily and would introduce artificial disturbances that would probably affect ant distributions.
2) Small clumps (1 plant), small plant size (< 5 cm leaf length)
3) Small clumps (1 plant) large plant size (≥ 20 cm leaf length)
4) Large clumps (6 plants), small plant size (≤ 5 cm leaf length)
5) Large clumps (6 plants), large plant size (≥ 20 cm leaf length).

This experiment parallels at the regional (whole-plot) scale the manipulations at the locality scale in EXPERIMENT 1, and we will measure the same set of variables. However, in this experiment we will make initial measurements in Years 1 and 2, make the transplants in Year 3, and monitor post manipulation in Years 3, 4, and 5. Because this is an unreplicated BACI design (Gotelli & Ellison 2004), we will use simple randomization tests to establish trends from the pre-manipulation data and then detect shifts in the response variables after the clumps are added (Stewart-Oaten et al. 1992, Underwood 1994, Stewart-Oaten & Bence 2001).

In combination, EXPERIMENTS 1 and 2 will allow us to identify processes that set initial conditions for creation and maintenance of dynamic habitats, and how these processes control the structure of a food web in a dynamic habitat. Specifically, these experiments will reveal effects of plant size and density on prey capture, plant growth, and structure of the Sarracenia food web, and on the spatial distribution of ant nests and moth larvae at the locality and regional scales.

EXPERIMENT 3 – IMPACT OF Exyra ON SARRACENIA AND ANTS

Exyra larvae cut holes at the base of Sarracenia pitchers (Fig. 7). These drained leaves contain little or no rainwater, and lack the typical food web associated with S. purpurea. Loss of even a single leaf may have important impacts on the long-term growth and survivorship of the plant. Moreover, dead or dying leaves are used as habitat by the ant Dolichoderus pustulatus, so there are potential direct and indirect effects of Exyra attacks in this system. In our study sites in MA, up to 30% of the plants are attacked by Exyra (Atwater et al. 2006). However, densities can be low at other sites, and it is difficult statistically to tease apart direct effects of Exyra attacks from confounding effects of spatial variation in plant microhabitat. Our proposed experiments allow us to more rigorously quantify the impacts of Exyra on ants and plants.

We will simulate Exyra attacks by cutting a hole in a Sarracenia leaf that mimics the effects of larval feeding. To increase the realism of the experiment, we will rub the inside of the wound with scrapings from real Exyra attacks, to facilitate the transfer of fungi and bacteria that are often associated with natural bore holes. Four experimental treatments will be applied:

1) Control (no plant manipulations)
2) Single Exyra attack (only the first leaf of the season will be cut)
3) Multiple Exyra attacks (all leaves will be cut)
4) Single leaf removal (the first leaf of the season will be entirely removed before it opens).^2

Treatments will be applied to both adult (≥ 10 cm longest leaf) and juvenile (< 5 cm longest leaf) plants. Selected plants will be at least one meter from their nearest experimental

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^2 There is one remaining orthogonal treatment in this design, which would be to removal all leaves of a plant. However, plants with no leaves will not survive more than one year, so we are foregoing this treatment.
neighbor. Ten plants will be assigned randomly to each treatment, for a total sample size of 80 plants. Treatments will be applied at the beginning of the field season in Year 2, and repeated in Year 4. Plant growth, prey capture, and ant-nest distributions will be measured at the end the field season. This is an orthogonal two-way design (treatment × plant size), and we will use *a priori* contrasts to test specific comparisons among the different treatments.

**EXPERIMENT 3** focuses specifically on processes that maintain spatial patterning of dynamic habitats and on temporal shifts in these patterns. Specifically, this experiment tests for direct effects of *Exyra* herbivory and subsequent leaf loss on plant growth, morphology, and survivorship, and will reveal secondary effects of moths on ant nesting behavior and density.

**C. Modeling temporal changes in spatial pattern**

We will develop a spatially explicit simulation model to understand the consequences of species interactions between *Sarracenia*, ants, and *Exyra* (Figure 8; next page). The simulation will randomly place circles (ant nests) in a bounded two-dimensional space, just as in our field sampling and experimental schemes. A simple null model will place these ant occurrences randomly within the plot. The interaction model will choose a random location, but the probability of occurrence will be proportional to a nearest-neighbor distance function that takes into account the existing spatial position of plants and nest entrances. The function itself will be based on the experimental regression results (**EXPERIMENT 1 – §V.B**) or the patterns of covariation among species (**SAMPLING DATA – §V.A**). *Sarracenia* recruitment is rare at this small spatial scale, but we will incorporate a simple random recruitment function to introduce new *Sarracenia* into the model plot. The model will have a discrete time step of one year for plants, which will recruit, grow, or die annually. Thus, the habitat patch – the plant – has its own set of equations in this model, as required for dealing with dynamic habitats. Ant nest movements and *Exyra* attacks will have a semi-annual time step, with movement, growth, or death of ant colonies recorded twice yearly, to reflect within-year variation in these parameters that we will measure from our field data (**EXPERIMENTS 1-3 – §V.B**). The model will reveal how species interactions alter spatial patterns in this system, and how spatial patterns themselves change stochastically through time, in both stationary and non-stationary environments.

**VI. Feasibility and Timetable**

The proposed 5-year project (4/1/2006 – 3/28/2011) spans 5 field seasons (F: April-October) and 5 off-seasons (November-March). Experimental work will begin immediately in Year 1.

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<th>Task</th>
<th>2006-07</th>
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<td>Spatial mapping – Tom Swamp</td>
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<td>Spatial mapping – 50 bogs in New England</td>
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<td>Experiment 1</td>
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<td>Experiment 2 – pre-treatment monitoring</td>
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<td>Experiment 2 – post-treatment monitoring</td>
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<td>Experiment 3</td>
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<td>Simulation model development</td>
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Figure 8. Flow chart of the simulation model of interactions prey (ants), predators/habitat patches (Sarracenia), the aquatic food web that depends on the patches, and herbivores (moths). Parameters for major model pathways will be derived from experiments and surveys that are illustrated. The model will have an annual time step for Sarracenia dynamics and a semi-annual time step for ants, moths, and the food web.

VII. Responsibilities of the Investigators

PI Ellison and research assistant Jessica Butler will be responsible for growing plants for use in the field experiments, and for coordinating the field manipulations at Tom Swamp. PI Gotelli will be responsible for computer modeling work and for coordinating the extensive field sampling in New York and New England. As with our previous awards, both PIs, our students, and our research assistant will share responsibilities for data analysis and manuscript production.

All data will be permanently archived in the Harvard Forest Archives, and in the Harvard Forest LTER on-line data catalog (http://harvardforest.fas.harvard.edu/data.html). We budget ~10% of total direct project costs per year for data management costs at the Harvard Forest.
VIII. Significance of the Proposed Research and Broader Impacts

Ecologists recognize the importance of patchy habitats for species coexistence in models of metacommunities and models of food web structure, but most models and empirical systems continue to treat patches as static elements of the landscape. In nature, community and food web processes interact with biotic habitats and change their spatial distribution at the landscape scale. The overall objective of the proposed research is to understand how species interactions change the spatial distribution of dynamic habitat patches at the landscape scale and affect food web structure within and among those patches. Using the Sarracenia model system, we will experimentally study how the spatial distribution of Sarracenia and the structure of its food web interact with two other taxa: ants, the prey base for the plant and its food web; and herbivorous moth larvae, which drain the pitcher-shaped leaves and remove habitat for the food web. Our results will be integrated into a simulation model that will predict the changes in spatial patterns that occur because of the direct and indirect effect of species interactions among the ants, moths, plants, and the aquatic food web hosted by the plant.

There are three broader impacts of the proposed research. First, we will sustain our commitment to educate and mentor undergraduates, graduate students, teachers, research assistants, and post-docs through continuous involvement in basic ecological research. This commitment is epitomized by the fact that REU students have contributed substantively to the preliminary data undergirding this proposal (§III.B, and Fig. 4), and we currently engage a local K-6 teacher in this research through an RET supplement. Second, we will develop a general framework for understanding how multi-trophic communities assemble and disassemble in changing environments. Third, we will further develop our understanding of the natural history and the architecture of an emerging model system in ecology: the Sarracenia system.

IX. Results from prior NSF support

We have had two previous collaborative awards for our Sarracenia research – DEB 98-05722 / DEB 98-08504 (Inquiline communities in changeable pitchers: do nutrients link community assembly to dynamic habitats?) and DEB 02-35128 / 02-34710 (Effects of nutrient stress on a co-evolved food web).

A. Goals and key achievements of previous proposals

This on-going collaborative project has had three overarching goals:

1. **Analyze and predict assembly and persistence of multi-trophic communities in a habitat that changes on the same time scale as that governing the assembly of the community.**

   Our experimental system is the “Sarracenia model system” (Ellison and Gotelli 2001, Ellison et al. 2003, Buckley et al. 2003).

2. **Construct a nitrogen budget for the Sarracenia system and assess how the dynamics of this system are changing in response to persistent and increasing levels of anthropogenic nitrogen deposition.**

   Sources of N include NH$_4$-N and NO$_3$-N from atmospheric deposition (Ellison and Gotelli 2002), mineralization of captured prey by the arthropod food web (Ellison et al. 2002, Wakefield et al. 2005), direct excretion by rotifers (Błędzki and Ellison 1998, 2002), and organic N absorbed directly by pitchers from prey and by roots from the peat (Karagatzides et al. 2005). We have demonstrated experimentally that plant leaf allocation patterns, growth, and reproduction (Ellison and Gotelli 2002, Ellison et al. 2004), and effects of plant structure on the food web and vice-versa all are driven by nutrient availability (Ellison et al. 2005). We have used stable isotopes – both natural
abundance and \(^{15}\text{N}\)- and \(^{13}\text{C}\)-enriched – to trace organic N, prey N, and N from atmospheric deposition through the plant and the food web (Karagatzides et al. 2005, Butler and Ellison 2006). The whole system is changing rapidly due to persistent nitrogen deposition over much of the range of \(S.\ \text{purpurea}\) (Ellison and Gotelli 2002, Gotelli and Ellison 2002c, Buckley et al. 2003, Ellison et al. 2004, Wakefield et al. 2005).

(3) Develop models that link the assembly and persistence of the food web to the demography of \(S.\ \text{purpurea}\). A unique and central aspect of our work on the \(Sarracenia\) system is the explicit incorporation of habitat (i.e., plant) dynamics on food web assembly, structure, and dynamics. We have developed individual-based, stochastic models of the growth of individual plants (Ellison and Gotelli in prep. b), stochastic matrix models of \(S.\ \text{purpurea}\) population dynamics (Gotelli and Ellison 2002c, 2005), and examined the relationship of these models to the food web (Ellison and Gotelli in prep. a).

We have addressed these goals through a series of 16 manipulative experiments:

- Two 2-year field experiments examined the assembly of the \(Sarracenia\) food web in leaves of different sizes and ages (Ellison et al. 2003, Ellison and Gotelli in prep. a).
- Two 1-year field experiments manipulated nitrogen availability and food web composition and habitat to examine how the food web and the plant interact in processing N (Ellison et al. 2005).
- Four 3-year greenhouse and field press experiments quantified the effects of nutrient additions on plant growth (Ellison and Gotelli 2002, Wakefield et al. 2005);
- A 1-year greenhouse experiment determined the rate at which inorganic nitrogen from atmospheric deposition (as \(^{15}\text{N}\)-NH\(_2\)NO\(_3\)) cycles through the \(Sarracenia\) food web in the presence or absence of a prey source (Butler et al. 2005b)
- Two 2-year experiments measured uptake, translocation, remobilization, and turnover of \(^{15}\text{N}\)-NH\(_2\)NO\(_3\) in \(S.\ \text{purpurea}\) (Butler and Ellison 2006).
- A 72-hour pulse-chase experiment determined that \(S.\ \text{purpurea}\) and its congener \(S.\ \text{flava}\) can directly assimilate organic N (as \(^{15}\text{N}\), \(^{13}\text{C}\)-glycine) and showed that organic N is taken up more slowly than \(^{15}\text{N}\)-NH\(_2\)NO\(_3\) in \(S.\ \text{purpurea}\) (Karagatzides et al. 2005).
- Based on cohorts of permanently marked plants, we constructed demographic models for plant population growth (Gotelli and Ellison 2002c, 2005), and developed individual-based models that will allow us to link food web dynamics, leaf morphology, and plant population dynamics (Ellison and Gotelli in prep. b).
- Plant reproductive dynamics were characterized separately, in a series of two additional experiments that we had not initially proposed (Ellison 2001, Ellison and Parker 2002).
- Two field experiments measured prey capture rates as a function of habitat characteristics and plant morphology (Ellison and Gotelli unpublished, Hart et al. in prep.). These field studies led to three studies focused on structure of prey assemblages and pitcher-plant herbivores:
  1. We discovered that the dominant prey of \(S.\ \text{purpurea}\) in Massachusetts and Vermont is the ant \(Myrmica lobifrons\), which 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 (Ellison et al. 2002, Gotelli and Ellison 2002a, 2002b).
  2. We observed that red spotted newt (\(Notophthalmus viridescens\)) larvae were regularly captured by \(S.\ \text{purpurea}\), and we examined the relationship between plant morphology and newt capture, and the potential contribution of newts to the plant’s N budget (Butler et al. 2005).
  3. We examined spatial distribution of two obligate pitcher-plant herbivores, larvae of the noctuid moths \(Exyra fax\) and \(Papaipema appassionata\), and impacts of herbivory on plant growth (Atwater et al. 2006).
Our results and models have provided a more complete picture of linkages between pitcher-plant food webs and their host plants, at individual leaf, whole-plant, within-bog and among-bog scales. Our studies fill a lacuna in prior studies of the *Sarracenia* food web (reviewed by Ellison *et al.* 2003), which, with few exceptions (Judd 1959, Plummer and Kethley 1964, Fish and Hall 1978, Bradshaw 1983, Joel and Gepstein 1985, Heard 1994b), emphasized population dynamics and interspecific interactions only among the invertebrates and ignored the plant.

**B. Human resource development**

The first award was an RUI award (PI Ellison was then at Mount Holyoke College), and during that award period we focused intensively on supporting undergraduates. The second award, both through the core budget and through two REU supplements, also supported undergraduates. In total, we have supported 20 undergraduates: 9 Mount Holyoke students, 7 University of Vermont students, and REU students from University of Kansas, Haverford College, New College of Florida, and Pueblo (Colorado) Community College. Six of the Mount Holyoke students are pursuing graduate degrees in ecology, and three work in the private sector. Two of the Vermont students are pursuing graduate degrees in ecology, two are in the Peace Corps, and three work in the private sector. Some of the 2003 and 2004 REU students are still in college, one will be starting graduate school in fall 2005, and two are at work as research technicians; the 2005 REU students are still enrolled in college. To date, we have written four papers with undergraduates (Ellison and Parker 2002, Hart *et al.* 2005, Butler *et al.* 2005, Atwater *et al.* 2006). With an RET supplement, we also currently work with a K-6 teacher who is introducing bog ecology to her students in a Winchendon, MA elementary school. These awards also supported Amy Wakefield’s master’s thesis (Wakefield *et al.* 2005) in PI Gotelli’s lab; partially supported two Ph.D. students (Sarah Wittman and Catherine Farrell-Gray) in Gotelli’s lab; supported a visiting post-doctoral fellow (Jim Karagatzides) in Ellison’s lab; and supported research associates Leszek Błędzki (1998-2002) and Jessica Butler (2002-present) in Ellison’s lab. Both research associates have published papers from this research (Błędzki and Ellison 1998, 2002, 2003, Butler *et al.* 2005, Karagatzides *et al.* 2005, Atwater *et al.* 2006, Butler and Ellison 2006). In March 2005, Jim Karagatzides received a 2-year NSERC postdoctoral fellowship to continue his research in Ellison’s lab on cycling of organic N in the *Sarracenia* microecosystem.

**C. Publications resulting from DEB 98-05722 / 98-08504 and DEB 02-35128 / 02-34710**

To date, 30 papers (marked with an * in the Literature Cited section of the proposal) and 15 presentations at national and international meetings have resulted from these awards, including primary research articles in *Proceedings of the National Academy of Sciences* (Ellison and Gotelli 2002), *Ecology* (Gotelli and Ellison 2002b, 2002c, Dixon *et al.* 2005, Wakefield *et al.* 2005), *Ecological Applications* (Gotelli and Ellison 2005), *Ecology Letters* (Buckley *et al.* 2003), and *Oikos* (Gotelli and Ellison 2002a); and review papers in *Trends in Ecology and Evolution* (Ellison and Gotelli 2001), *Advances in Ecological Research* (Ellison *et al.* 2003), and *Ecology Letters* (Ellison 2004). The *PNAS* paper was highlighted in the News and Comments section of *Trends in Ecology and Evolution* (17: 305 [2002]). We also organized a well-attended symposium on carnivorous plants as model ecological systems for ESA’s annual meeting in 2000, which resulted in the two review papers. Ellison will give a keynote address on this work in a symposium on carnivorous plants at the International Botanical Congress in Vienna in July 2005. During this funding period, we published a new textbook for ecologists, *A Primer of Ecological Statistics* (Gotelli and Ellison 2004). Many examples of data analysis and experimental design from our *Sarracenia* research are featured in this book.


