Recent developments in community ecology reflect a shift from equilibrium, niche-based concepts to a more pluralistic view which incorporates species interactions, nonequilibrium dynamics, migration and evolutionary history. This creates a much more complex perspective of the forces determining patterns of species abundance and distribution in communities: dealing with the complexity itself has become a major hurdle in conceptual and experimental community ecology. We propose to organize a group of ecologists, evolutionary biologists, mathematical modelers, and systematists to conduct a comparative observational and experimental study of the metazoan community inhabiting leaves of the pitcher plant *Sarracenia purpurea*. This community is remarkably consistent and widespread across much of North America and provides model microcosm for experimental studies. The incubation activities will bring together a working group of scientists to plan a set of coordinated field studies to investigate this community throughout North America, to collect pilot data from these studies, to develop macroecological hypotheses that can be tested with these data, and to formalize models of community structure based on these data. The long-term goal is the development and execution of a comprehensive set of field experiments and phylogeographic studies of ecological and evolutionary determinants of community structure from local to continental scales.

OBJECTIVE

We propose to organize a group of ecologists, evolutionary biologists, mathematical modelers, and systematists to conduct a comparative observational and experimental study of the metazoan community inhabiting leaves of the pitcher plant *Sarracenia purpurea*. The incubation activities will bring together a working group of scientists to plan a set of coordinated field studies to study this community throughout North America, to collect pilot data from these studies, to flesh out macroecological hypotheses that can be tested with these data, and to formalize models of community structure based on these data. The long-term goal is the development and execution of a comprehensive set of field experiments and phylogeographic studies of ecological and evolutionary determinants of community structure at continental scales.

Thomas E. Miller (Florida State University) is serving as the formal PI for administrative purposes only. All three scientists, Aaron M. Ellison (Mount Holyoke College), Nicholas J. Gotelli (University of Vermont) and Miller will be involved in all aspects of this incubation project.

INTRODUCTION

The last three decades have seen a major reevaluation of processes thought to determine patterns of distribution and abundance of individual species within ecological communities (e.g., Strong et al. 1984, Diamond & Case 1986, Gotelli & Graves 1996, Polis & Winemiller 1996, Morin 1999). This reevaluation has reflected a shift from an emphasis on equilibrium, niche-based, and competition-driven models (e.g., Diamond 1975) to a more pluralistic set of approaches that incorporate nonequilibrium models and a recognition that many different types of interspecific interactions can regulate community structure. Four broad factors encompass many of the complex forces determining distribution and abundances of species in communities. First, **species interactions** through “top-down” and “bottom-up” forces interact within defined food webs (see, e.g., Leibold 1996). Second, communities are generally **open, nonequlibrium systems**. Regional, historical, and stochastic factors that affect immigration and extinction of component species intersect with species interactions to generate patterns in communities at a broad range of spatial and temporal scales (see, e.g., Ricklefs & Schluter 1993). Third, **evolutionary histories** of component species within communities constrain responses to both abiotic and biotic factors (see, e.g., Harvey & Pagel 1991, McPeek & Miller 1996). Finally, many ecologically identifiable communities span broad **geographic ranges** (e.g., bogs, salt marshes, mixed deciduous forests), and species composition is often correlated with geography (see, e.g., Colwell & Lees 2000). Among-population comparative approaches have been used to elucidate geographic distributions of related species in an evolutionary context (“phylogeography”; Losos 1996). The macroecological research program (Brown 1995, Maurer 1999) suggests that the complexity in community structure engendered by the intersection of these four factors can be resolved through large-scale comparative studies across the geographic ranges of entire species and community types.

Species are the fundamental, interacting units within an ecological community, yet if species composition changes, then the relative importance of these four factors in determining community structure is also likely to change. Fundamental advances in our understanding of how natural communities are structured could occur if we could hold species composition constant within a single habitat or community type across a broad geographic range and then study the changes in species interactions that occur across this geographic range. We propose a series of incubation activities, through NSF’s Biocomplexity Initiative, to begin such a macroecological study of a discrete, well-defined community type — the set of invertebrates, protozoa, and bacteria that inhabit fluid-filled leaves of *Sarracenia purpurea* — whose species composition is constant from Newfoundland south to Florida and west to British Columbia. The proposed activities will allow us to sample this community type systematically throughout North America, generate a comparative data set that can be analyzed with new null models for macroecology (Gotelli & Entsminger 2000), and begin planning comparative field experiments that will be conducted across the continent to understand the ecological and evolutionary determinants of local community structure.

INQUILINE COMMUNITIES ASSOCIATED WITH *SARRACENIA PURPUREA*

Sarracenia purpurea is a carnivorous plant that grows in low-pH bogs in eastern North America from Florida to Newfoundland and across southern Canada to British Columbia (Schnell 1976). The morphology of this species varies little over its entire geographic range. The plant forms rosettes with 1 to 20 distinctive cup-shaped leaves that collect rainwater (0-50 ml) in which they capture a large variety of invertebrate prey (Addicott 1974), especially dipterans, collembolans (Cresswell 1991), and ants (Heard 1994, Miller et al. 1994). The individual leaves of *S. purpurea* host a community of nonprey invertebrates, protozoa, and bacteria (termed "inquilines" or "phytotelmata"; Fish 1983). Obligate inquiline species include three larval dipterans (Fish & Hall 1978) — a mosquito (*Wyeomyia smithii*), a midge (*Metriocnemus knabi*), and a sarcophagid (*Blaesoxipha fletcheri*) — a mite *Sarraceniopus gibsoni* (Fashing & O'Connor 1984), and a bdelloid rotifer, *Habrotrocha rosa* (Bateman 1987). Other species common in this community include protozoans (Addicott 1974, Cochran-Stafira & von Ende 1998), copepods and cladocerans (Miller et al. 1994), and bacteria (Prankevicius & Cameron 1989, 1991, Cochran-Stafira & von Ende 1998).

The energetic basis for the inquiline community is the prey captured by each leaf. These prey may disintegrate as a result of bacterial activity or may be ripped apart and partially eaten by *M. knabi* and *B. fletcheri*. The disintegrating remains provide particulate matter, which is further broken down by bacteria and, if small enough, taken up by the filter-feeding species (*W. smithii* and *H. rosa*) and the copepods. The bacteria themselves are eaten by these filter feeders and protozoa. At the top of this "donor-controlled" food web, filter-feeding larvae of *W. smithii* feed on rotifers and protozoa (Cochran-Stafira & von Ende 1998). The waste products of these inquilines, principally NO_3-N, NH_4-N, and PO_4-P, are taken up by the pitcher plant and are its primary source of nutrients. Within-pitcher interactions among inquiline species have been demonstrated in a number of studies (Addicott 1974, Istock et al. 1975, Bradshaw & Holzapfel 1986, 1992, Heard 1994, 1995, Miller et al. 1994, Broberg & Bradshaw 1995, Bledzki & Ellison 1998, Cochran-Stafira & von Ende 1998), but virtually all of these studies have been conducted within single populations of *S. purpurea*, and it is not clear whether conclusions drawn from single studies at single locations are applicable across the range of this community.

The broad geographic range of *S. purpurea*, and the relatively consistent species richness of its inquiline community across this geographic range, together create an exceptional opportunity for detailed ecological and evolutionary studies of community structure. First, the spatial scale of local to regional interactions ranges in an easily defined manner from the level of individual pitchers to pitchers on the same plant, to plants in the same population, to populations across a large geographic range (e.g. Harvey & Miller 1996). Whereas the habitat (low-pH bogs), pitcher morphology, and inquiline species pool remain constant across the entire range of *S. purpurea*, life histories of the inquilines vary with latitude. For example, in the northeastern U.S. and Canada, *S. purpurea* has relatively short-lived leaves (1-2 yrs; Fish & Hall 1978), and most of the insect inquilines are univoltine or undergo very few generations per year. At the southern extreme of its range, individual leaves (and potentially their inquiline community) may persist for several years, and insect species may undergo a shorter diapause or no diapause and produce multiple generations annually. This situation creates an interesting scenario in which the **identical** species cooccur across a gradient in seasonality and annual productivity. Evolutionary implications of this gradient for the mosquito *Wyeomyia smithii* have been explored by Bradshaw & Holzapfel (1986, 1989, 1992; see also Broberg and Bradshaw 1995, Istock et al. 1975), who studied latitudinal differences in life-history traits related to density. There are, however, no large-scale studies of variation in the entire community structure of *S. purpurea* inquilines.

The inquiline community of *S. purpurea* is a model system for studying community structure, as most features of this community are very general. Similar small aquatic ecosystems, from tree holes to small ponds, have been used for a number of classic studies in community ecology (e.g., Werner & Hall 1976, Wilbur 1987). The basic processes studied in inquiline communities to date, such as predation and nutrient flow, do not differ in any significant way from those of most other communities. What makes this an ideal study system is the large number of replicate communities (multiple leaves within plants, multiple plants within bogs) within each population of *S. purpurea*, the ease of doing manipulative experiments in these natural microcosms, and their large geographic range. In particular, the constancy of the plant and the inquiline community across broad gradients in temperature, seasonality, rainfall, etc., will allow us on the one hand to explore how communities are structured independently from abiotic gradients and on the other to explore how large abiotic gradients affect life histories and community dynamics of a single, naturally occurring system. Such a study is unprecedented in community ecology, as communities and the abiotic environment generally covary in parallel.

In sum, the *Sarracenia purpurea* – inquiline system offers four clear advantages for studies aimed at untangling the complex of factors that control community structure:

> *Sarracenia purpurea* represents a discrete natural habitat for inquilines that is hierarchically organized at three distinct spatial scales: leaves within pitchers, pitchers within bogs, bogs within regions.
>
> The inquiline community contains a diversity of predators, producers, omnivores, and detritivores that are linked through shared resources and habitat affinities, allowing us to study an entire interacting assemblage, not merely a guild of closely related species.
>
> The system is small enough for realistic field manipulations but occurs over a huge geographic range, so we can document continent-wide patterns in community structure.
>
> The geographic consistency and relatively closed nature of inquiline communities allow us to address questions about both ecological and evolutionary forces structuring communities.

GOALS OF THE INCUBATION ACTIVITIES

We propose to bring together a group of ecologists, systematists, and evolutionary biologists, most of whom have some experience with *S. purpurea* and its inquilines. We have four goals for the incubation activities:

I. **To define realistic questions and testable hypotheses concerning mechanisms of community structure in the *Sarracenia purpurea* – inquiline system that can be addressed by means of a comparative descriptive and experimental approach.** A partial list might include:

   a. Is this really a continuous community across the entire geographic range, or are some species absent or replaced in specific locales?
   b. Do the relative abundances of species in the community change in any predictable way with abiotic factors such as temperature or photoperiod?
   c. Do species interactions vary among geographic locations, especially with regard to environmental gradients?
   d. Do macroecological patterns of body size, species richness, range area, or abundance emerge at larger geographic scales?
   e. Is there evidence of evolutionary changes in life histories of inquilines other than *W. smithii* that are consistent with changes in the abiotic (or biotic) conditions?
   f. Is there evidence of coevolutionary patterns, such as Thompson's (1999) geographic mosaic hypothesis? If so, there will be predictable variation in "compatibility" between species pairs across communities.

II. **To develop consistent methods for collection, experimental design, and data analysis.** Pilot projects using these methods will be done to determine technical and logistical needs, feasibility, and statistical power and sample sizes required for a continental-scale study.

III. **To develop quantitative models (analytical, simulation, and statistical) using these data to predict community structure and community assembly across a broad geographical range.** These models should incorporate variability at multiple spatial scales (leaves within plants, plants within bogs, bogs widely separated across the landscape) and account for geographic variability in selective pressures, food-web properties of the inquiline assemblage, and interactions between the inquilines and their host plants.

IV. **To determine appropriate project organization, data management, and dissemination of results.**

PROPOSED ACTIVITIES

We propose four primary activities designed to “incubate” and develop the ideas in this proposal:

First, a conference will be held in at Florida State University, Tallahassee, Florida, to bring together appropriate ecologists, biogeographers, evolutionary biologists, systematists, and modelers to discuss, and further refine the set of questions and hypotheses to be tested. We will invite both scientists who can contribute generally to discussions on community biogeography and researchers actively studying *S. purpurea* inquilines. Possible invitees include W. E. Bradshaw (*Wyeomyia*), C. M. Holzapfel (*Wyeomyia*), L. Cochran-Stafira (protozoa), N. Ward-Rainey (bacteria), M. A. McPeek (evolution of communities), M. A. Leibold (community structure), J. H. Brown (macroecology) and J. Losos (phylogeography). An appropriate set of methods for addressing these questions for the *S. purpurea* inquiline community will be discussed simultaneously.

Second, a working group from among the conference participants will design an observational and experimental protocol for eight *S. purpurea* communities from north Florida to southern Canada (sites to be identified by the working group). This group will help guide the pilot descriptive and experimental studies at the eight field sites using standardized methods. The resulting database and protocol will serve as a the working example for the remaining portion of the incubation activities.

Third, we will develop a formal, spatially explicit database structure for managing these community-level data. The database will be linked to a geographic information system that can be used to explore issues of connectivity and dispersal between bogs (landscape scale). We will also begin development of predictive mathematical and statistical models that can be applied to our dataset.

Fourth, a second conference involving this working group will be held one year later at Mount Holyoke College, South Hadley, Massachusetts. Participants will discuss the pilot data and reevaluate the questions and approaches set out in the first conference. They will produce a working paper, appropriate for publication in *Ecology* or *American Naturalist*, on the subject of comparative community analyses. This second conference will also be used to determine the appropriateness of further funding from the Biocomplexity Initiative and, presumably, to begin to organize a larger, multi-PI proposal for such research.

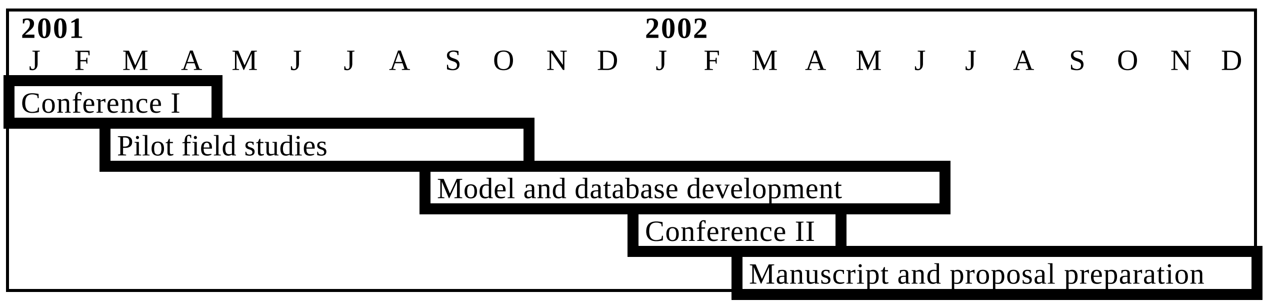
CONTRIBUTIONS AND RESPONSIBILITIES OF THE PIS

Thomas E. Miller will be responsible for overall coordination of this incubation project. He has extensive field experience with the *S. purpurea* – inquiline community in northern Florida and is developing models for these inquiline communities that incorporate the effects of stochastic migration on the assembly of communities. Aaron M. Ellison and Nicholas J.

Gotelli are currently studying interactions between *S. purpurea* and the inquilines in bogs of Massachusetts and Vermont (with support from NSF-DEB). They have also been studying the biogeography of *S. purpurea*, its inquilines (including protozoa, rotifers, and bacteria), and its principal prey (ants) at 22 sites in Massachusetts, Vermont, and Connecticut. Ellison has primary responsibility for coordinating this project, and for field experimental design, and will take the lead on experimental design components of this incubation activity. Gotelli is developing scale-dependent models of *S. purpurea* demography and inquiline community assembly. He has also developed an extensive set of software tools for null-model analysis of community structure (Gotelli & Entsminger 2000). Gotelli will take the lead on the modeling components of this incubation activity.

As part of this incubation activity, we propose to hire a postdoctoral scientist to supervise all field work and database development. The postdoc will be responsible for all field work and working with the PI's to process and analyze this data. This will involve a substantial amount of work in eight field sites, as well as working at the institutions of all three PIs. The postdoc will also be help to organize and run the second conference and will help in the production of the resulting manuscript.

TIMETABLE



RELEVANCE TO THE BIOCOMPLEXITY INITIATIVE

Support is requested from the Biocomplexity Initiative for two reasons. First, we feel that disentangling the forces structuring communities is one of the most important questions in ecology today. Arguably, progress in community ecology has been limited by our current inability to understand direct and indirect effects of different forces such as species interactions, immigration, evolutionary history, disturbance, and productivity. Nevertheless, ecologists are increasingly being asked to predict community patterns well into the future. Conservation work involving habitat degradation (including global warming), invasibility, and restoration all require a more predictive community ecology than our current knowledge allows.

Second, the proposed investigation requires an entirely new scale of investigation, opening up new questions and hypotheses, and a new level of cooperation between scientists from different fields: such a scale of investigation is similar to that called for by Brown (1995) and others (e.g., Ricklefs & Schluter 1993). Collecting such a wide variety of organisms and then distributing appropriate samples to specific experts is daunting. Investigating even a significant portion of a single community is very difficult (cf. Polis 1991), even in relatively closed, easily described communities such as those associated with *S. purpurea*. Studying entire communities at a multiplicity of spatial scales, and incorporating field observations, process-oriented experiments, and mathematical modeling, as we propose to do here, seems exactly what is envisioned by the Biocomplexity Initiative.

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