LETTER

Reverse latitudinal trends in species richness of pitcher-plant food webs

Hannah L. Buckley[1,4], Thomas
E. Miller[1]*, Aaron M. Ellison[2] and
Nicholas J. Gotelli[3]

[1]*Department of Biological
Science, Florida State University,
Tallahassee, FL 32306-1100, USA*
[2]*Harvard University, Harvard
Forest, P.O. Box 68, Petersham,
MA 01366, USA*
[3]*Department of Biology,
University of Vermont,
Burlington, VT 05405, USA*
[4]*Present addresss: Ecology and
Entomology Group, P.O. Box 84,
Lincoln University, Canterbury,
New Zealand*
*Correspondence: E-mail:
miller@bio.fsu.edu*

Abstract

Latitudinal patterns in species richness have been well documented for guilds and individual trophic groups, but comparable patterns for entire, multitrophic communities have not been described. We studied the entire food web that inhabits the water-filled leaves of the pitcher plant *Sarracenia purpurea* across North America at two spatial scales: among sites and among leaves within sites. Contrary to the expectation, total species richness at both scales increased with latitude, because of increasing species richness at the lower trophic levels. This latitudinal pattern may be driven by a top-down effect. The abundance of the mosquito *Wyeomyia smithii*, a ubiquitous top predator in this system, decreases from south to north and may permit greater species richness of prey trophic levels at higher latitudes.

Keywords

Biogeography, carnivorous plants, community, inquilines, *Sarracenia purpurea*, species diversity, *Wyeomyia smithii*.

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INTRODUCTION

Geographical variation in the diversity of biological assemblages is one of the earliest recognized ecological patterns (Darwin 1859). Diversity patterns have been studied in a variety of systems and at a variety of spatial scales and generally have been reported to show a significant decrease in species richness as latitude increases (Rosenzweig 1995). However, such studies are usually restricted to particular taxonomic or ecological guilds, such as mammals or birds. There is a semantic problem in that 'community' has been used to refer to trophic levels or guilds rather than as suites of interacting species across all trophic levels. Whole multitrophic communities might be expected to follow the same overall trend as do single taxa or guilds, but this expectation has never been tested.

We studied geographical variation in species richness of the entire food web of invertebrates, protozoa and bacteria that inhabits the water-filled leaves (pitchers) of the purple pitcher plant, *Sarracenia purpurea* L. Variation in community patterns was partitioned into two spatial scales: among populations of *S. purpurea* across North America (hereafter 'site' scale) and among water-filled pitcher leaves within sites ('pitcher' scale). Whereas both scales are affected by climate and biogeography of the component species, the site scale

reflects factors that affect a large area such as the rate of leaf production and loss, and migration rates among pitchers, while the pitcher scale reflects productivity and species interactions occurring within the individual pitcher communities. Each pitcher contains an entire community, so diversity can be quantified both within trophic levels and for the whole community. Although several previous studies have documented geographical patterns of diversity within trophic levels (e.g. Perelman *et al.* 2001) or taxonomic groups (e.g. Tramer 1974; Stevens & Willig 2002), surprisingly no previous study has quantified spatial patterns in richness for an entire, discrete multitrophic community throughout its entire geographical range.

Sarracenia purpurea is a carnivorous perennial herb, which is widely distributed across low-nutrient North American wetlands (Fig. 1). Individual plants consist of up to 10 pitcher-shaped leaves and obtain nutrients primarily from insect prey that fall into the rainwater that collects in each pitcher. *Sarracenia purpurea* ranges from the south-eastern United States up through Atlantic Canada and across to northern British Columbia, spanning 30° of latitude and 70° of longitude and encompassing a broad variation in both climatic and habitat conditions (Cody & Talbot 1973; Godt & Hamrick 1998; Naczi *et al.* 1999). In the southern part of the range (the Florida Panhandle), *S. purpurea* grows all the
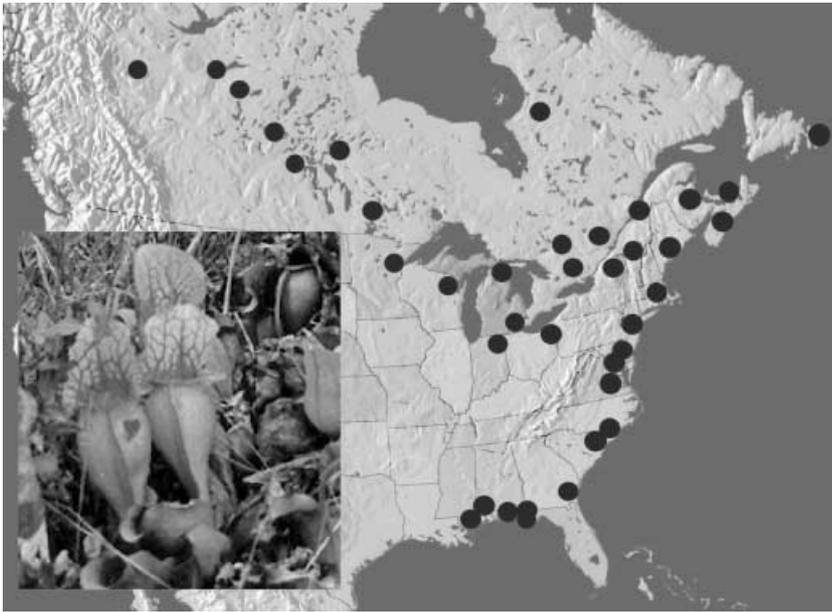
year round and is usually found in the sandy soils of pine savannahs. In its northern range (northern New England and across Canada), the growing season is shorter, the temperature extremes are greater and *S. purpurea* primarily grows in *Sphagnum*-peat bogs.

Despite the broad climatic and habitat variation experienced by the plant throughout its geographical range, a relatively constant set of species lives within its water-filled pitchers (Addicott 1974; Bradshaw & Creelman 1984; Petersen *et al.* 1997; Folkerts 1999; Giberson & Hardwick 1999; Bradshaw & Holzapfel 2001; Kneitel & Miller 2002). The species composing a typical pitcher-plant food web across North America include various bacteria and protozoa, the bdelloid rotifer *Habrotrocha rosa* Donner (Bledzki & Ellison 2003), and a suite of apparently obligate members: the mite *Sarraceniopus gibsoni* (Nesbitt), and aquatic larvae of the pitcher-plant mosquito *Wyeomyia smithii* (Coq.), a midge [*Metriocnemus knabi* (Coq.)] and a flesh fly [*Fletcherimyia fletcheri* (Aldrich)] (Addicott 1974). Less common members of this assemblage include loricate rotifers, cladocerans, copepods, amphipods, nematodes and multicellular algae. Most of the published work on this system has reported experiments in individual pitchers that address questions of competition, predation and the structure of the local community. These experiments at small spatial scales (within individual pitchers) and short time scales (days to weeks) show that community composition is affected by levels of predation (by mosquito larvae) and resources (insects captured by the pitcher) (Addicott 1974; Cochran-Stafira & von Ende 1998; Kneitel & Miller 2002; Miller *et al.* 2002). At larger spatial scales, however, the relatively constant species pool presents a unique opportunity to examine how the structure of an

entire food web changes over a broad climatic gradient spanning many North American wetlands.

We quantified the spatial patterns in species richness of this inquiline community across the range of the host plant *S. purpurea*. Concurrently, we quantified patterns in a number of associated environmental variables that could be associated with the observed spatial patterns.

METHODS

Data collection

We selected 39 known, undisturbed populations haphazardly distributed throughout the range of *S. purpurea* (Fig. 1). Site-selection criteria included population size (more than 50 plants), ability of the population to sustain the damage of destructive sampling and accessibility. Only natural, rather than introduced, populations were sampled. The latitude, longitude and elevation of each population were determined using the satellite global positioning system.

New pitchers are produced during the summer following flowering and then throughout the fall. When leaves initially open, they capture more prey and tend to have higher abundances of some species, especially bacteria and mosquitoes. However, after the initial 2–3 weeks, age of the pitcher has little effect on the component community (Miller *et al.* 1994). We chose to standardize our sampling at different sites by choosing leaves that were *c.* 4 weeks old, by visiting each site *c.* 1 month following flowering and choosing the first, usually largest pitcher, of the new season's growth. Flowering time was determined through herbarium or other records for each area or estimated from

sites at similar latitudes. Using consistent sampling protocols, several research teams collected samples at widely separated sites, so that temporal biases introduced by travel schedules were minimized.

Using standardized sampling methods, we determined the relative abundances of all species of invertebrates, protozoa and bacteria within 20 pitchers at each of the 39 sites. At each site, the 20 pitchers and their contents were collected across the population, each from a different plant. We counted and identified all invertebrates in each pitcher and rotifers in a 0.1-mL subsample. The protozoa in a standard 0.1-mL subsample of pitcher fluid were counted, and each was identified to genus where possible. Bacteria grown on Plate Count Agar using three replicate plates at two dilutions were grouped into morphological colony types. For each site, two measures of species richness were generated: (1) site richness, which was calculated as the total number of species encountered across all 20 sampled plants, and (2) pitcher richness, which was calculated as the average number of species encountered in pitchers within each site.

Data analysis

First, to ensure that the estimates of species richness were not biased or confounded by variation in abundance or sampling intensity (Gotelli & Colwell 2001), species richness was standardized in all samples using rarefaction (EcoSim version 7; Gotelli & Entsminger 2002). In all analyses, standardization of species richness did not change relationships with latitude and produced results qualitatively similar to the unstandardized results reported in the study.

Second, to examine spatial pattern in species richness at the two scales across the host-plant range, generalized linear models were used with the assumption of Poisson-error distribution (S-PLUS; MathSoft, Seattle, WA, USA) to relate site and pitcher richness to a spatial matrix that consisted of all terms for a cubic trend surface regression, i.e. longitude (x), latitude (y), x^2, y^2, xy, x^3, y^3, x^2y and xy^2. This method ensured that not only could we extract linear patterns in the richness data but also the more complex spatial patterns such as patches and gaps could be tested. We also analysed the latitudinal regression models using abundance as an additional predictor variable. These analyses were repeated for the species richness of the three major groups found within these food webs (invertebrates, protozoa and bacteria) and for the abundance of *W. smithii*, the top predator in this system.

RESULTS

Species richness at the site scale increased linearly with latitude; more species were encountered at sites that were farther north (Fig. 2a, open circles). Pitcher richness was
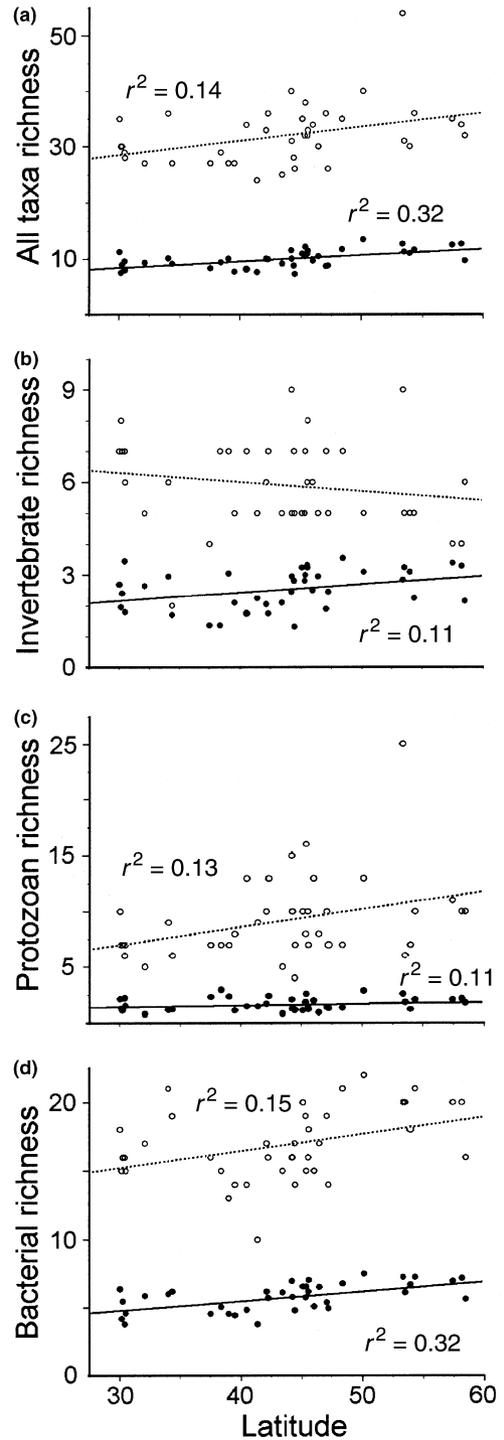

Figure 2 Scatterplots showing the relationships between latitude and species richness for (a) all species, (b) invertebrates, (c) protozoa and (d) bacteria at the site scale (open circles) and the pitcher scale (filled circles). Solid lines represent significant relationships, and the r^2 values are given. Dashed lines represent non-significant relationships.

c. 30% of the site richness and also increased linearly with latitude (Fig. 2a, filled circles).

A separate analysis of each taxonomic group (invertebrates, protozoa and bacteria) at the site scale showed that the increase in species richness with latitude was because of an increase in protozoan and bacterial richness (Fig. 2b–d; open circles); invertebrate richness exhibited no significant relationship with latitude. At the pitcher scale, the relationships between richness and latitude were slightly different: richness of all three components of the community increased with latitude (Fig. 2b–d; filled circles). It is of interest to note that the abundance of the top predator in the system, the pitcher-plant mosquito (*W. smithii*), decreased significantly with latitude ($P < 0.006$, $R^2 = 0.18$).

DISCUSSION

The food web in *S. purpurea* is unusual in demonstrating a latitudinal trend in species richness that is the reverse of that observed most frequently for individual guilds or taxa within trophic levels. Rather than increasing towards the equator as expected (Rosenzweig 1995), species richness in this community increases with increasing latitude. Although inverse patterns have been noted for several taxonomic groups (see Huston 1994), such as parasitic wasps (Janzen 1981) and birds of eastern deciduous forest of North America (Rabenold 1979), the present study is the first demonstration of this pattern for an entire community food web. Further, this pattern was exhibited at both site and pitcher spatial scales (see Kaspari *et al.* 2003).

This unusual pattern could be the result of a single numerically dominant group within the community. It was found that different groups within the food web did exhibit different patterns of richness with latitude. At the site scale, richness of macroinvertebrates (primarily dipterans and mites) was not significantly related to latitude, whereas richness of protozoa and bacteria both increased with latitude.

In an observational study like this, it is difficult to determine as to why species richness generally increased with latitude. One possible explanation is that predation plays an important 'keystone' role in structuring this community (Power *et al.* 1996). As the abundance of the top predator, a filter-feeding mosquito, decreases, a greater number of taxa in lower trophic levels (protozoa and bacteria) were able to persist. This result is supported by results from experimental studies of this system, which have shown that the pitcher-plant mosquito is a keystone predator that can regulate richness of protozoa and bacteria (Addicott 1974; Cochran-Stafira & von Ende 1998; Kneitel & Miller 2002). This hypothesis that predation can generate broad geographical patterns of diversity has been advanced

repeatedly but is difficult to test over these large scales (Brown & Lomolino 1998).

An alternative explanation is that larger-scale environmental variables such as climate, soils and hydrology are important influences on species richness in this community through their effects on mosquito abundance. Unfortunately, these variables themselves are correlated in complex ways and it is difficult to separate their individual effects. We have investigated such correlations in a larger analysis of species-specific patterns, which will be reported elsewhere (H.L. Buckley, in preparation).

No other study has collected data appropriate to examine latitudinal patterns over a large spatial scale within the same multitrophic community. Studies have shown that patterns of richness within a guild or trophic level depend on spatial scale, although scale generally refers to an arbitrary measure of area rather than to any structural aspect of the system; for example in birds (Tramer 1974), bats (Stevens & Willig 2002), fossil evidence of herbivory (Wilf & Labandeira 1999), terrestrial plants (Perelman *et al.* 2001), and density-dependent mortality in trees (Lambers *et al.* 2002). Entire real communities are generally composed of ecologically very different taxa (e.g. generation time, resources, mode of dispersal) and our perception of pattern will be limited by the fact that these different taxa probably respond differently and at different scales to community processes. However, pitcher plants are perhaps a strong system in which to address these types of questions, because the two 'scales' that we examined in this study represent naturally discrete spatial scales for all species in the community, i.e. individual leaves and populations of plants within bogs.

Overall, these results suggest that the commonly observed pattern of decreasing diversity with increasing latitude should be investigated in the context of both spatial scale and in entire multitrophic communities. The study of entire food webs over large geographical scales may help to reveal the ecological and evolutionary forces that determine community structure.

ACKNOWLEDGMENTS

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