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RESEARCH PAPER

Local- to continental-scale variation in the richness and composition of an aquatic food web

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ABSTRACT

Aim We investigated patterns of species richness and composition of the aquatic food web found in the liquid-filled leaves of the North American purple pitcher plant, *Sarracenia purpurea* (Sarraceniaceae), from local to continental scales.

Location We sampled 20 pitcher-plant communities at each of 39 sites spanning the geographic range of *S. purpurea* – from northern Florida to Newfoundland and westward to eastern British Columbia.

Methods Environmental predictors of variation in species composition and species richness were measured at two different spatial scales: among pitchers within sites and among sites. Hierarchical Bayesian models were used to examine correlates and similarities of species richness and abundance within and among sites.

Results Ninety-two taxa of arthropods, protozoa and bacteria were identified in the 780 pitcher samples. The variation in the species composition of this multi-trophic level community across the broad geographic range of the host plant was lower than the variation among pitchers within host-plant populations. Variation among food webs in richness and composition was related to climate, pore-water chemistry, pitcher-plant morphology and leaf age. Variation in the abundance of the five most common invertebrates was also strongly related to pitcher morphology and site-specific climatic and other environmental variables.

Main conclusions The surprising result that these communities are more variable within their host-plant populations than across North America suggests that the food web in *S. purpurea* leaves consists of two groups of species: (1) a core group of mostly obligate pitcher-plant residents that have evolved strong requirements for the host plant and that co-occur consistently across North America, and (2) a larger set of relatively uncommon, generalist taxa that co-occur patchily.

Keywords

Food web, hierarchical Bayesian modelling, latitudinal gradients, North America, *Sarracenia purpurea*, species composition, species richness.

INTRODUCTION

Theories that attempt to explain patterns of community structure generally operate at three spatial scales: local habitats, metacommunities and larger scales that encompass entire biogeographic ranges. At the scale of local habitats, many theories addresses how small-scale processes, such as environmental conditions and species interactions (especially competition and predation), determine population and community patterns (Case, 1999). Empirical tests at this spatial scale show that interactions among species, and the responses of species to environmental conditions, should be most important in the distributions and abundances of species. At the metacommunity scale, dispersal limitation and species saturation are thought to affect species diversity within the constituent habitats and may even override the effects of local interactions (see, e.g., Cornell & Lawton, 1992). The metacommunity concept has contributed to the development of significant theory (see Leibold *et al.*, 2004; Holyoak *et al.*, 2005), and a growing number of experiments at this scale confirms that species interactions (see, e.g. Miller &

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Kneitel, 2005), habitat structure and resource availability (see, e.g., Srivastava, 2006), dispersal (see, e.g., Kneitel & Miller, 2003) and, more recently, genetics (see, e.g., Whitham *et al.*, 2006; Crutsinger *et al.*, 2009) can be important determinants of among-community patterns.

Theories predicting community structure at even larger spatial scales are uncommon (Srivastava, 2005). At continental scales, distribution and abundance patterns may reflect broad environmental gradients (Huston, 1994; Rosenzweig, 1995; Hawkins *et al.*, 2003) and historical and evolutionary processes (Ricklefs & Schluter, 1993). Most empirical work at these spatial scales is based on simple correlation analysis of geographic gradients in species richness (Gotelli *et al.*, 2009) and is often restricted to groups of potential competitors or trophic guilds (see, e.g., Rivadeneira *et al.*, 2002) or to single taxonomic groups such as mammals, birds, or trees (see, e.g., Rahbek & Graves, 2001; Stevens & Willig, 2002). Geographic studies incorporating taxa interacting across trophic levels will almost certainly be more revealing than studies that are taxonomically or trophically restricted (Ellingsen & Gray, 2002; Andrew & Hughes, 2004). Further, although most large-scale studies of diversity are conducted at a single spatial grain, for example latitude–longitude blocks of particular size (Rahbek & Graves, 2001; Arita *et al.*, 2005), processes controlling distribution and abundance often operate at multiple spatial scales that may be revealed only by sampling at multiple grain sizes (see, e.g., Levin, 1992; Mittelbach *et al.*, 2001). Teasing apart the influences of regional and local processes therefore requires sampling across trophic levels and at multiple spatial scales (He & Condit, 2007).

Here we describe a study of a complete food web at two spatial scales across the entire geographic range of the community – the bacteria, protozoa, rotifers and arthropods that inhabit water-filled pitchers of the North American purple pitcher plant, *Sarracenia purpurea* L. (see Appendix S1 in Supporting Information and Fig. 1). This detritus-based aquatic food web is restricted to discrete habitat units (rain-filled leaves) of a single host plant that itself occurs in circumscribed habitats such as bogs and pine savannas. This system provides three naturally discrete hierarchical sampling units: pitchers within plants, plants within populations and populations within the plant's geographic range. We compared patterns of food-web species richness and composition in pitchers of similar age within and among *Sarracenia* populations throughout its range. We have previously described simple patterns of species richness in this food web across the geographic range of the host plant (Buckley *et al.*, 2003), but we did not analyse the variation in species composition, the environmental drivers of that variation or the scale dependence of those drivers.

Many studies on this system at local and meso-scales show that, within pitchers, species abundances are controlled by a combination of processes, including interactions, resources and dispersal (Miller & Kneitel, 2005; Gotelli & Ellison, 2006, Hoekman *et al.*, 2009). Our large-scale analysis can provide insight into the relative importance of these factors. For

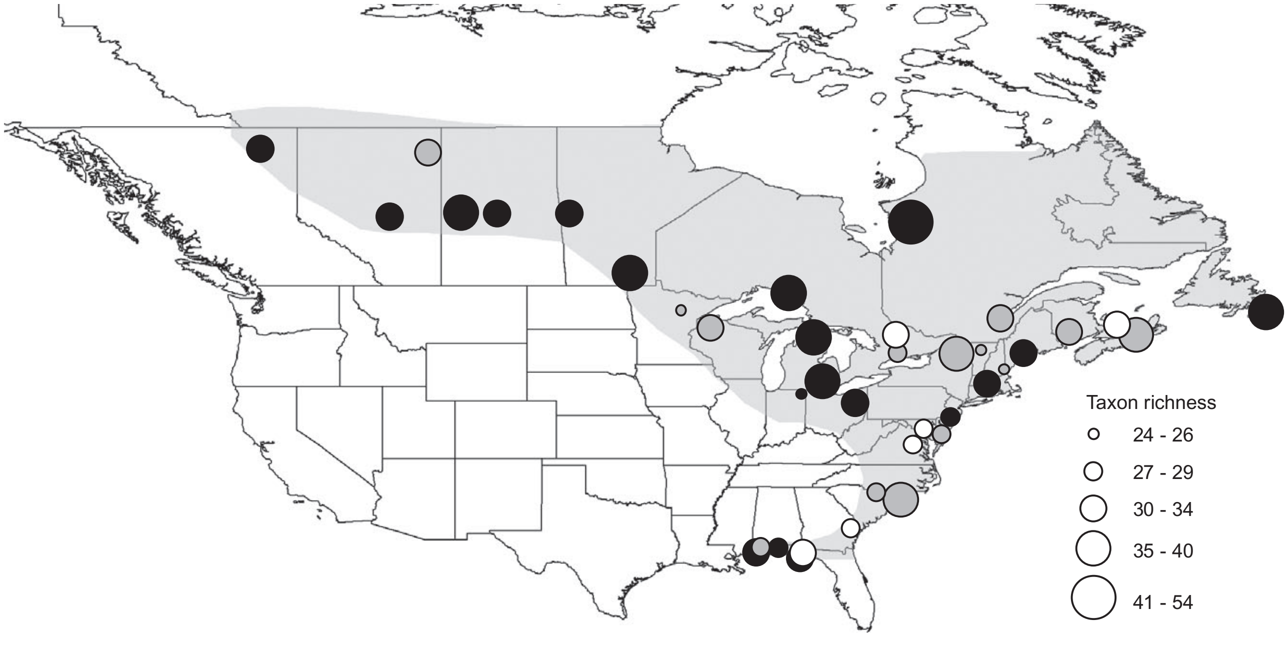

Figure 1 Map showing the locations of the 39 sampled sites (circles) across the geographic range of *Sarracenia purpurea* (shaded area) in North America. The size of each point represents the number of taxa occurring within pitchers at that site out of the 90 encountered across all sites; larger points represent sites with a greater number of taxa. Percentage similarity in species composition of all taxa is represented by the shading of the points: sites with <70% similarity are white, those between 70 and 80% similarity are grey, and those with > 80% are black.

example, higher abundance of the filter-feeding larvae of the pitcher-plant mosquito, *Wyeomyia smithii* (Coq.), is known to reduce the abundances of protozoa and rotifers (Addicott, 1974; Miller *et al.*, 2002; Trzcinski *et al.*, 2005a,b; Hoekman, 2007) but to have more variable effects on the abundance of microbes (Kneitel & Miller, 2002; Hoekman, 2007; Peterson *et al.*, 2008). Therefore, if this pattern scales up to the geographic scale, we should observe a strong relationship among pitchers and among sites between the abundance of *W. smithii* and the composition and richness of protozoa, rotifers and, to a lesser extent, bacteria. On the other hand, the addition of resources to this system has been shown to increase the abundances of mites, rotifers, protozoa and bacteria (Kneitel & Miller, 2002; Hoekman, 2007). Therefore, similarly, if this pattern scales up, we should observe strong correlations between food-web richness and composition and the size and morphology of pitchers, which control habitat volume (Gotelli & Ellison, 2006), and environmental variables related to resource availability.

Ours is the first study of a single community type at a continental scale. Community theory predicts that we should see variation in community patterns with latitude (Buckley *et al.*, 2003), and we expected sites to vary more than individual pitchers within sites in species richness and composition of food webs, because the broad geographic range of *S. purpurea* encompasses large differences in climate, historical factors and bog characteristics. We investigated the following question: What drives the distribution and abundance of species at the within- and among-*Sarracenia* population scales? We answered this question by: (1) comparing variations in the food web at these two spatial scales, and (2) determining the relative effects of resource-based factors, interactions and abiotic and biotic site variation at these two spatial scales on species richness, species composition and the abundance of individual species.

METHODS

Study species

Sarracenia purpurea is a long-lived (> 50 years), carnivorous, perennial plant that grows as a rosette of pitcher-shaped leaves. It occurs in nutrient-poor wetlands – ombrotrophic bogs, poor fens, sand plains and longleaf-pine savannas – along the eastern coastal plain of North America and westward across Canada and the northern mid-western states of the United States (Schnell, 2002; Fig. 1), spanning 30° of latitude and 70° of longitude. In the northernmost portion of its range, the growing season is short, the seasonal temperature variation is large, and *S. purpurea* var. *purpurea* is primarily restricted to sphagnum peat bogs. In the south-eastern coastal plain, the growing season is long, seasonal temperature variation is small, and *S. purpurea* var. *venosa* grows in pine savannas and seepage swamps. In the southernmost part of the range (the Florida Panhandle, Alabama and Mississippi), *S. purpurea* ssp. *venosa* var. *burkii* (= *Sarracenia rosea*, *sensu* Naczi *et al.*, 1999) grows year-round, experiences relatively little seasonal temperature variation and occurs mostly in the sandy soils of pine savannas.

Unlike those of other Sarraceniaceae, the pitcher-shaped leaves of *S. purpurea* are open to the sky and fill with rainwater and snow. The plants attract a variety of prey, primarily ants and other small arthropods, which fall into the water-filled pitchers and drown. These aquatic microhabitats (generally 3–50 ml of fluid) are also colonized by a variety of arthropods, rotifers, protozoa and bacteria that form a detritus-based food web (Appendix S1; see also Addicott, 1974; Bradshaw & Creelman, 1984; Miller & Kneitel, 2005). Obligate inhabitants of *S. purpurea* pitchers include larvae of three dipterans – *Wyeomyia smithii*, the midge *Metriocnemus knabi* Coq., and the sarcophagid *Fletcherimyia fletcheri* (Aldrich) – and one histiostomatid mite, *Sarraceniopus gibsoni* (Nesbitt). Bacteriovores include the bdelloid rotifer *Habrotrocha rosa* Donner and numerous protozoan species (Addicott, 1974; Cochran-Stafira & von Ende, 1998). Bacterial abundances are generally high (10^4–10^9 ml^{-1}; Kneitel & Miller, 2002) and can vary at different spatial scales (Harvey & Miller, 1996; Peterson *et al.*, 2008). Less common members of this community include loricate rotifers, cladocerans, copepods, amphipods, nematodes and multi-cellular algae (Addicott, 1974; Miller *et al.*, 1994; Bledzki & Ellison 2003). The resource base of this community is the prey captured by the leaf, which is first shredded by the flesh flies and midges and then decomposed and mineralized by the microbes. The plant takes up phosphorus and nitrogen (and possibly small proteins and amino acids) from the pitcher fluid (Bradshaw & Creelman, 1984; Butler *et al.*, 2008). Bacteria are themselves fed on by a host of bacteriovorus protozoa and rotifers, primarily *H. rosa*, and the mite (Kneitel & Miller, 2002; Butler *et al.*, 2008; Karagatzides *et al.*, 2009). The mosquito larvae are omnivorous filter feeders that ingest pieces of dead prey, small protozoa and bacteria (Addicott, 1974). The flesh fly is an omnivorous top predator that feeds on the mosquito larvae (Butler *et al.*, 2008), shreds prey and also cannibalizes conspecifics (Forsyth & Robertson, 1975).

Data collection

Between May and mid-September 2001 we sampled food webs in *Sarracenia purpurea* pitchers at 39 sites throughout the plant's geographic range (Fig. 1). Site-selection criteria included a minimum plant population size (at least 50 plants), accessibility, availability of sampling permits and the use of only native populations. Each food web was sampled only once at a site; we standardized for seasonal effects by sampling each population approximately 4 weeks after spring flowering; widely separated sites were sampled at similar times by different research teams that all followed identical sampling protocols.

The latitude and longitude of each sampled *S. purpurea* population were determined by a global positioning system (Magellan GPS 315). Spatially referenced elevation and climate data for all sites were obtained from the Landscape Analysis and Application Section of the Canadian Forest Service (McKenney *et al.*, 2006). Elevation and climate data for points nearest to the study site locations were queried in ArcGIS 9.0. The area covered by each population was estimated in the field with transect tapes.

Vegetation cover was visually estimated in a 1-m^2 quadrat centred on each sampled pitcher plant; the percentage covers of sphagnum, trees, shrubs, forbs and graminoids were recorded.

At each site, one transect was established through the longest axis of the highest density of plants (that could be reached on foot); transect length therefore varied with population areal extent. Along this transect, the closest plant to each of 20 evenly spaced points was selected, and, on this plant, the oldest pitcher produced during the current season was sampled. As leaf production begins immediately after flowering, most sampled communities should therefore have been 3–5 weeks old. Where the pitcher of the current season could not be sampled because of leaf damage, we sampled the youngest pitcher from the previous growing season. Wolfe (1981) showed that younger leaves captured more prey than leaves more than 30 days old, so pitcher age in our analyses may be correlated with prey-capture frequency.

We collected pitcher contents with sterile plastic pipettes, recorded their total volume and then divided the fluid into a Diptera-free, 1.5-ml sample, placed in a sterile microcentrifuge tube, and the remainder, which was placed in a 50-ml sterile macrocentrifuge tube. Both portions were refrigerated and returned to the lab, where arthropods and other large species in the large sample were counted and identified to the lowest taxonomic resolution possible (10× magnification for arthropod identification, 100× magnification for the identification of rotifers and large protozoa; identification and nomenclature followed Pennak, 1989). A 0.1-ml subsample of the smaller sample was serially diluted (10^{-3} and 10^{-5}) by sterile techniques. Three replicates from each dilution were plated on full-strength PCB agar plates. Emergent bacterial colonies were separated into morphotypes based on colour, texture and transparency. After both 3 and 10 days, for the plate from each dilution on which colony number was closest to being between 30 and 300, the number of colonies of each bacterial morphotype was recorded. The counts from the three replicate plates at that dilution were then averaged to yield relative abundance of each bacterial morphotype within individual pitchers. Some of these culturable morphotypes were later tentatively identified by standard sequencing of 16S rDNA (Pepper & Gerba, 2005).

Plant measurements made in the field included rosette diameter along the widest axis and the number of pitchers with and without water. The length, width at the widest point, keel width and lip width of each sampled pitcher were measured with digital callipers (Ellison *et al.*, 2004).

To quantify the environmental characteristics of sites, we used a clean Tygon tube to extract five 50-ml pore-water samples from capped and perforated PVC tubes (50 cm long × 2.5 cm in diameter) that were sunk into the peat at even intervals along our sample transect. For each water sample, we measured pH and calcium content (mg l^{-1}) with Orion ion-sensitive electrodes (Thermo Electron Corp, Woburn, MA, USA) and phosphate (PO_4-P), nitrate (NO_3-N), and ammonium (NH_4-N) (all in mg l^{-1}) spectrophotometrically according to US Environmental Protection Agency (EPA) standard methods (Clesceri *et al.*, 1998). Pore-water samples were not taken at the eight southern sites with dry sandy soils.

Data analysis

Variation in species composition

We assessed variation in food-web species composition among sites and pitchers by calculating a mean similarity from presence data using the Jaccard similarity index, which represents the average similarity in species composition of each sampled community to every other community. High mean similarity indicates that samples within the matrix are compositionally homogeneous and that species turnover among samples is low; a mean similarity of 1.0 would mean that all samples were identical (Scheiner, 1992). Mean similarity was generated both for the site-by-species matrix and for all 39 of the pitcher-by-species matrices (one matrix for each site). The average of the mean pitcher similarities yielded a mean pitcher similarity for sites.

Data reduction

The presence of arthropods (including rotifers for the purposes of these analyses), protozoa and bacterial morphotypes that occurred in more than 1% of the 592 pitchers across 30 sites (those sites for which pore-water samples were taken) were analysed separately by principal coordinates analysis (PCoA) implemented in the labdsv package version 1.3.1 in R (R Development Core Team, 2006) on the basis of a Steinhaus distance matrix. The Steinhaus metric, which is similar to the Sorenson distance metric, is suitable for presence data and resulted in the best spread of pitchers in the ordination space (Legendre & Legendre, 1998). The site scores for the first two axes of each PCoA (PCoA-1 and PCoA-2) were used as measures of variation in 'species' composition for arthropods, protozoa and bacteria because they explained the most variation in each case.

Because many of the explanatory variables were correlated with each other, we used principal components analysis (PCA) (Legendre & Legendre, 1998) implemented in PC-ORD version 5 (McCune & Mefford, 2006) to reduce the number of pitcher-plant morphology variables, vegetation-cover variables and site-level variables for the 30 sites. For the pitcher-plant morphology variables we extracted the first three PCs, and for the vegetation-cover variables and the site-level variables we extracted only the first two principal components; these PC axes were used as predictor variables in subsequent analyses.

Predictors of variation in species richness and composition

Because pitchers were nested within sites and because we wanted to relate pitcher species richness and composition to variables measured at both the pitcher and site scales, we constructed two-level hierarchical Bayesian models (Gelman & Hill, 2007) for three groups: arthropods + rotifers, protozoa and bacteria. We used varying intercept models without interactions terms because ours was an exploratory study with many predictor variables. Species richnesses of the three groups were normalized by a natural log transformation. Species composition, as measured by PCoA axis scores, was normally distributed for the three groups. Both species richness and composition were modelled as Gaussian processes with identity-link functions. Although richness is a count variable and therefore more correctly modelled as untransformed values with a Poisson distribution, the methods for calculating the variance explained (see below) are only available for models that assume a Gaussian distribution. We used non-informative priors for all parameters in all models (Gelman & Hill, 2007). Species richness and composition were modelled separately for the three different groups. Each dependent variable (y), richness or composition at the pitcher level, was modelled as a function of pitcher-level predictor variables, x, and site-level predictor variables, u. The pitcher-level model takes the form $y_i \sim N(\alpha_j + \beta x_i, \sigma^2_y)$, for $i = 1,\ldots, n_j$, where y_i is the richness or composition of the ith pitcher, α_j is the regression intercept for the jth site, β is the matrix of coefficients for the pitcher-level predictors, σ^2_y is the pitcher-level regression error and n is the total number of pitchers. The hierarchical model treats the pitcher-level intercept terms, α, as though they come from a normal distribution across sites and models them as $\alpha_j \sim N(\gamma + \theta u_j, \sigma^2_\alpha)$, for $j = 1,\ldots, J$, where γ is the site-level regression intercept and θ is the matrix of coefficients for the site-level predictors, σ^2_α is the site-level regression error and J is the total number of sites.

In all models, the same set of environmental predictor variables was used (pitcher age, pitcher PCs 1–3, vegetation PCs 1–2 and site PCs 1–2). The models for protozoa and bacteria also contained abundances of mosquitoes and midges as additional pitcher-level predictors. Fully conditional models that included all predictors were taken as the final result in all cases because methods for determining the importance of predictor variables, model comparison and model reduction using hierarchical Bayesian methods are still controversial (Gelman & Hill, 2007).

Models were fitted by Markov chain Monte Carlo iteration with the BRugs package (Thomas *et al.*, 2006) of R version 2.7.1 (R Development Core Team, 2006). We assessed model convergence visually for three simultaneously running Markov chains of at least 50,000 iterations, after a 10,000-iteration burn-in period, and thinned it at every tenth value to reduce the effects of autocorrelation on parameter estimates.

To obtain the relative amount of variance in the data at the pitcher level and the site level, we calculated the intra-class correlation coefficient as the ratio of pitcher-level variance to the sum of the pitcher-level variance and the site-level variance from an unconditional model that did not contain predictor variables (Gelman & Hill, 2007). The variance explained by the predictor variables for the full model was calculated as $R^2 = 1 - \{\text{mean}[\text{var}(y_i - \hat{y}_{ik})]/\text{var}(y_i)\}$. In other words, we took the residuals for each pitcher from each iteration and calculated the variance across iterations for each pitcher. We then divided the mean of these variances by the variance in the dependent variable and subtracted the result from 1 to obtain the variance explained.

Predictors of variation in the presence of obligate pitcher-plant residents

The presence of the four obligate pitcher-plant residents – *W. smithii*, *M. knabi*, *F. fletcheri* and *Sarraceniopus gibsoni* – together with that of *H. rosa*, was modelled with two-level hierarchical Bayesian models with varying intercept terms without interaction terms. The presence of each species was modelled as a Bernoulli process with a logit link function and non-informative priors for all parameters in all models. Each dependent variable (y), the presence of each species at the pitcher level, was modelled as a function of pitcher-level predictor variables, x, and site-level predictor variables, u. The pitcher-level model takes the form $y_i \sim \text{Bern}(\alpha_j + \beta x_i)$, for $i = 1,\ldots, n_j$, where y_i is the presence or absence of the species in the ith pitcher, α_j is the regression intercept for the jth site, β is the matrix of coefficients for the pitcher-level predictors and n is the total number of pitchers. The second level of the hierarchical model was the same as that described above for species richness and composition, as were the predictor variables.

RESULTS

Species composition of all trophic levels

Across all sites, we found a total of 13 arthropod + rotifer species, 48 protozoan morphospecies and 29 bacterial morphotypes (the most common are listed in Appendix S2). Individual pitchers contained a mean of 3 ± 1.2 (SD) arthropod species (*W. smithii* and *M. knabi* were most common), 2 ± 1.4 protozoan morphospecies (most abundant were *Poterioochromonas malhamensis*, *Bodo* sp., and *Colpoda* near sp. *insula*), and 6 ± 2.1 bacterial morphotypes. At the site level, we recorded 6 ± 1.4 arthropods, 9 ± 3.8 protozoan morphospecies and 17 ± 2.6 bacterial morphotypes. Three of the four obligate pitcher-plant species (*W. smithii*, *M. knabi* and *S. gibsoni*) and the rotifer *H. rosa* were found at virtually all sites, whereas *F. fletcheri* was found at only 27 of the 39 sites. The number of rare taxa was very large; of the 90 taxa encountered, only 56 occurred in more than 1% of pitchers. Plots of the number of individuals versus the number of occupied sites (Appendix S3) illustrate that most taxa were relatively rare and occurred at < 50% of the sampled sites.

Mean similarity in species composition among sites was 0.54 ± 0.04. In other words, on average, for any given site, just over half the species were the same as at any other given site. The similarity of sites varied geographically; sites in western and central Canada had consistently higher among-site similarity (and richness) than eastern sites (Fig. 1). Contrary to our initial prediction, the mean similarity among pitchers within sites was much lower (0.36 ± 0.04) than the similarity among sites.

Data reduction

The first two axes of the PCoA of the 56 species occurring in at least 1% of pitchers sampled at the 30 sites without missing data and for which pore-water data were available accounted for 47%

of the variation in occurrence of arthropods + rotifers, 40% in occurrence of protozoa and 21% in occurrence of bacteria. The variation accounted for by these first two axes primarily reflected variation in the presence of the more common species within pitchers. For example, for the arthropods + rotifers, the loadings on the first PCoA axis were positively related to the presence of *W. smithii* and *M. knabi* and negatively related to the presence of *S. gibsoni* and *H. rosa*. The loadings on the second axis were negatively related only to the presence of *W. smithii*. For protozoa, the loadings on the first axis were negatively related to the presence of *Bodo* sp. and those on the second to the presence of *Poterioochromonas* sp. For bacteria, the loadings on the first axis were strongly and positively related to the presence of *Klebsiella pneumoniae*, a species of Cytophagales, and to the presence of unidentified morphotype number 46. Loadings on this axis were strongly negatively related to presence of *Flectobacillus* sp. Those on the second axis were strongly positively related to the presence of *K. pneumoniae*, *Flectobacillus* sp. and morphotype number 46 and negatively to that of *Pseudomonas* sp.

The first three axes from the PCA of the pitcher and plant morphology data accounted for 75% of the variation among pitchers in their morphological characteristics (Appendix S4). The loadings on the first pitcher PCA axis (‘size’) increased with rosette diameter, pitcher height and pitcher volume. Those on the second (‘habitat area’) increased with pitcher volume. Those on the third (‘pitcherness’) were positively associated with smaller keels and greater lip widths.

The first two axes from the PCA of the vegetation data accounted for 64% of the variation in local habitat characteristics (Appendix S4). High site scores for the first vegetation PCA indicated sites at which pitchers were surrounded by a higher percentage cover of sphagnum and a lower percentage cover of forbs. High site scores on the second indicated sites with a higher percentage cover of trees and a lower percentage cover of graminoids.

The first two axes from the PCA of environmental characteristics accounted for 74% of the variation among the 30 sites with pore-water data (Appendix S4). The loadings on the first axis described a geographic gradient in a whole range of spatially structured environmental conditions moving from west to east and north to south across the distribution of sites. Sites with high scores on this axis were at low elevations in the south-east United States, had long growing seasons with high mean temperatures and precipitation, and had low annual variation in both of these variables. Sites with high scores were more acidic and had lower levels of calcium and ammonium in pore water. Sites with high values on the second axis had more basic pore water that contained more phosphorus but less ammonium.

Hierarchical modelling of food-web richness and composition at the 30 pore-water sites

Species richness

Between 70 and 84% of the variation in richness of arthropods, rotifers, protozoa and bacteria was at the pitcher level rather than at the site level (Table 1). The hierarchical models revealed that richness of arthropods + rotifers was higher in larger, older pitchers (pitcher PC 1) that were not flattened (pitcher PC 3), were surrounded by more sphagnum (vegetation PC 1) and occurred at sites in the north-western part of the host-plant range, where pH and PO_4 are lower (site PCs 1 and 2; Fig. 2a). Protozoan richness was positively associated with midge abundance and pitcher age and negatively associated with older, flatter pitchers (pitcher PC 3) that occurred at higher-latitude sites (Fig. 2b). Pitchers that contained greater richness of bacterial morphotypes were older and larger (pitcher PC 1) and occurred at sites at higher latitudes (site PC 1) (Fig. 2c). Despite these patterns, the predictor variables did not account for much of the observed variation in species richness (maximum $R^2 = 0.32$; Table 1).

Table 1 Proportion of variance calculated from variance partitioning showing the relative amount of variation in the data for each hierarchical Bayesian model at the pitcher and site levels.

	Proportion of variation		
Model	Pitcher level	Site level	R^2
Arthropod richness	0.70	0.30	0.32
Protozoan richness	0.84	0.15	0.15
Bacterial richness	0.77	0.23	0.21
Arthropod composition axis 1	0.64	0.36	0.35
Arthropod composition axis 2	0.81	0.19	0.19
Protozoan composition axis 1	0.84	0.16	0.15
Protozoan composition axis 2	0.61	0.39	0.36
Bacterial composition axis 1	0.81	0.19	0.18
Bacterial composition axis 2	0.64	0.36	0.33

R^2 values give the amount of variation explained by all predictors for each model.

Species composition

The first PCoA axis describing variation in arthropod + rotifer species composition was positively related to geographic location (site PC 1) and negatively to pitcher size (pitcher PC 1; Fig. 3a). The second was related to geographic location (site PC 1), pitcher size (pitcher PC 1) and pitcher age and was marginally related to the relative cover of sphagnum (vegetation PC 1) (Fig. 3b). Composition of protozoan taxa (PCoA 1) was related positively to pitcher age and negatively to midge density, mosquito density and sphagnum cover (vegetation PC 1; Fig. 3c). Protozoan PCoA 2 was positively associated with plants that had greater numbers of water-filled leaves (pitcher PC 2) and that occurred at sites in the north-western part of the host-plant range, with lower PO_4 concentration in the pore water and lower pH (site PC 1; Fig. 3d). Finally, variation in bacterial composition (PCoA 1) was positively related to the density of midge larvae in pitchers, pitcher age and plants that had greater numbers of water-filled leaves (pitcher PC 2). This bacterial-composition axis was also marginally positively related to

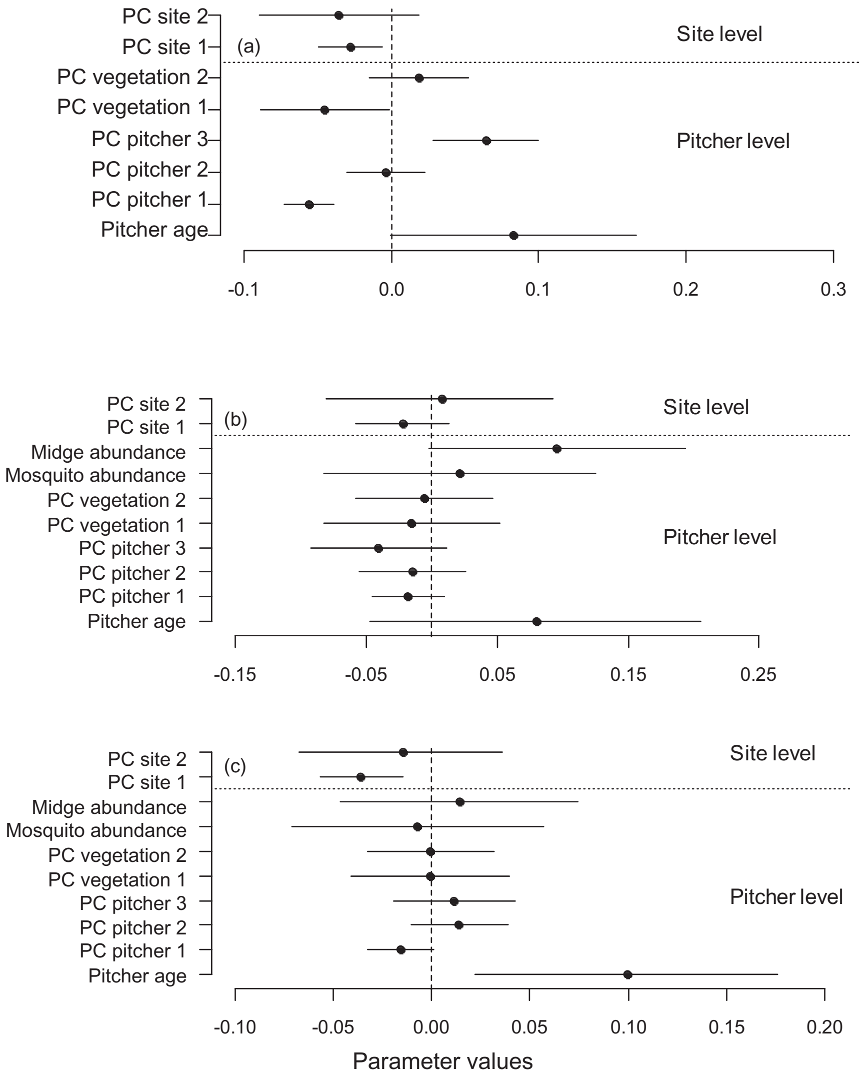

Figure 2 Plots showing the mean values (filled circles) and 95% posterior credibility intervals (lines) for parameter estimates from hierarchical Bayesian models for the pitcher richness of (a) arthropods + rotifers, (b) protozoa, and (c) bacteria. Intervals that do not overlap zero are considered to be significantly different from zero. For protozoan and bacterial richness, the two additional predictors were the number of mosquito larvae and the number of midge larvae present in pitchers. Models do not include data from seven southern sites at which pore-water data were not collected or two sites with missing environmental data. PC, principal component.

sphagnum cover surrounding pitchers (vegetation PC 1; Fig. 3e). Bacterial PCoA 2 was negatively related to the density of midge larvae in pitchers and positively associated with pitchers that were pitcher-like in morphology (pitcher PC 3) and greater tree cover surrounding the plant (vegetation PC 2). This axis was also marginally negatively related to plant size (pitcher PC 1; Fig. 3). As with the species-richness models, the variance explained by the hierarchical models was low and never exceeded 36% (Table 1).

Presence of the four obligate pitcher-plant residents and Habrotrocha rosa

Wyeomyia smithii was more likely to occur in pitchers that were more pitcher-like in morphology (pitcher PC 3) and on plants surrounded by higher tree cover (vegetation PC 2) and less likely to occur in older, smaller pitchers (pitcher PC 1; Fig. 4a). *Fletcherimyia fletcheri* was more likely to occur in younger pitchers from the current season and in pitchers on plants surrounded by greater sphagnum cover (vegetation PC 1) and was marginally associated with geographic location (site PC 1; Fig. 4b). *Metriocnemus knabi* was more likely to occur in larger (pitcher PC 1), older pitchers from previous seasons and was marginally associated with pitchers that were pitcher-like in morphology (pitcher PC 3) on plants surrounded by higher tree cover (vegetation PC 2) and lower sphagnum cover (vegetation PC 1; Fig. 4c). The mite *S. gibsoni* was more likely to occur in larger (pitcher PC 1), younger pitchers that were more pitcher-like (pitcher PC 3; Fig. 4d). *Habrotrocha rosa* was more likely to occur in older pitchers that were more pitcher-like (pitcher PC 3) on plants that were surrounded by lower sphagnum cover (vegetation PC 1) at higher-latitude sites (site PC 1; Fig. 4e).

DISCUSSION

We found significant variation in the composition of the food web among *Sarracenia* populations; our ability to explain that variation, and the variation in species richness, using measured predictor variables, was limited (Table 1). This result is not surprising because we were considering a community that is highly

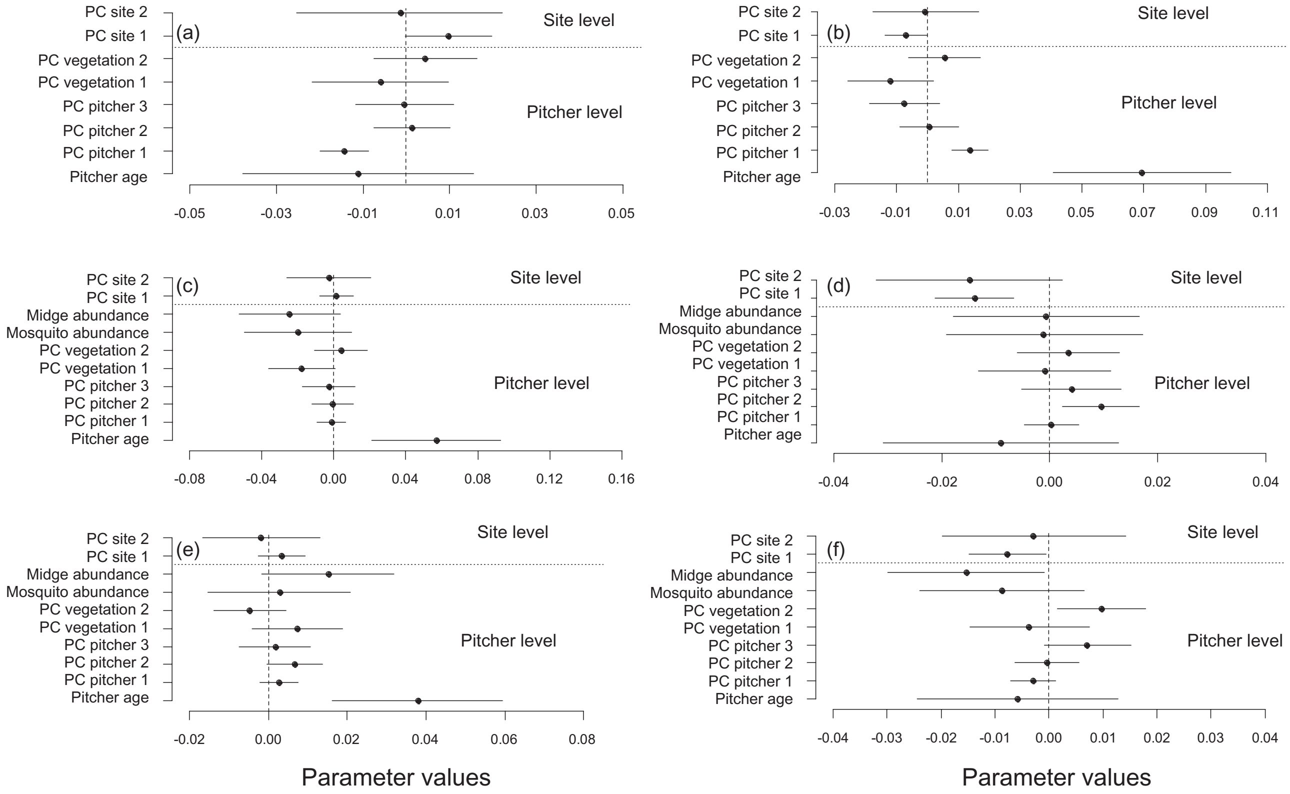

Figure 3 Plots showing the mean values (filled circles) and 95% posterior credibility intervals (lines) for parameter estimates from hierarchical Bayesian models for the pitcher composition of (a) arthropod + rotifer composition axis 1, (b) arthropod + rotifer composition axis 2, (c) protozoan axis 1, (d) protozoan axis 2, (e) bacterial composition axis 1, and (f) bacterial composition axis 2. Intervals that do not overlap zero are considered to be significantly different from zero. For protozoan and bacterial composition, the two additional predictors were the number of mosquito larvae and the number of midge larvae present in pitchers. Models do not include data from seven southern sites at which pore-water data were not collected or two sites with missing environmental data. PC, principal component.

variable at small spatial scales (Buckley *et al.*, 2004) and that spans such a large geographical range, but contrary to our initial prediction, variation in food-web composition was greater (species turnover was higher) at the among-pitcher than at the among-site scale. Among-site similarity values were high (Fig. 1), and particular taxa – the obligate pitcher-plant residents and *H. rosa* – were consistently common across the range of the host plant, although *F. fletcheri* had a more north-easterly distribution. These species therefore appear to have stronger associations with the host plant itself than with large-scale variation in environmental conditions. The consistent and somewhat unusual habitat provided by the pitcher itself may have resulted in a highly specialized suite of cohabiting species that have all evolved to use the same habitat provided by the host plant. In fact, some studies have suggested that the plant derives only minor benefits from carnivory (e.g. Chapin & Pastor, 1995; Bott *et al.*, 2008). If the species that use the water-filled leaves of *Sarracenia purpurea* depend on their host plant to a greater degree than each plant or leaf benefits from the presence of these associated species, then the food-web composition may be structured by the consistent environment of the leaf itself and not by the relatively large variation in seasonality, productivity and abiotic factors across the plant's range. Although we do not fully understand the exchanges of resources and other benefits between the host plant and these species and among the species themselves (see, e.g., Bledzki & Ellison, 1998; Mouquet *et al.*, 2008), they appear to represent a community-level mutualism, in which at least some species benefit from the presence of other species in the community and their host plant.

The high among-pitcher variation we observed has also been noted in previous studies of this system (e.g. Addicott, 1974; Harvey & Miller, 1996; Buckley *et al.*, 2004; Peterson *et al.*, 2008) and appears to be due in part to the effects of pitcher 'age' (Fish & Hall, 1978; Trzcinski *et al.*, 2003, 2005a; Miller & Kneitel, 2005). Alone among the environmental variables we measured, pitcher age explained variation in almost all dependent variables modelled, including the species richness of the three groups, species composition and the abundance of the obligate residents (Figs 2–4). Because pitchers from previous growing seasons will have had more time to accumulate species and for competitive exclusion and predation to take effect (especially where the growing season is long), we would expect the older pitchers we sampled to differ significantly from younger pitchers in food-web richness and composition. Pitchers usually provide habitat for up to a year (Miller & Kneitel, 2005), but herbivory,

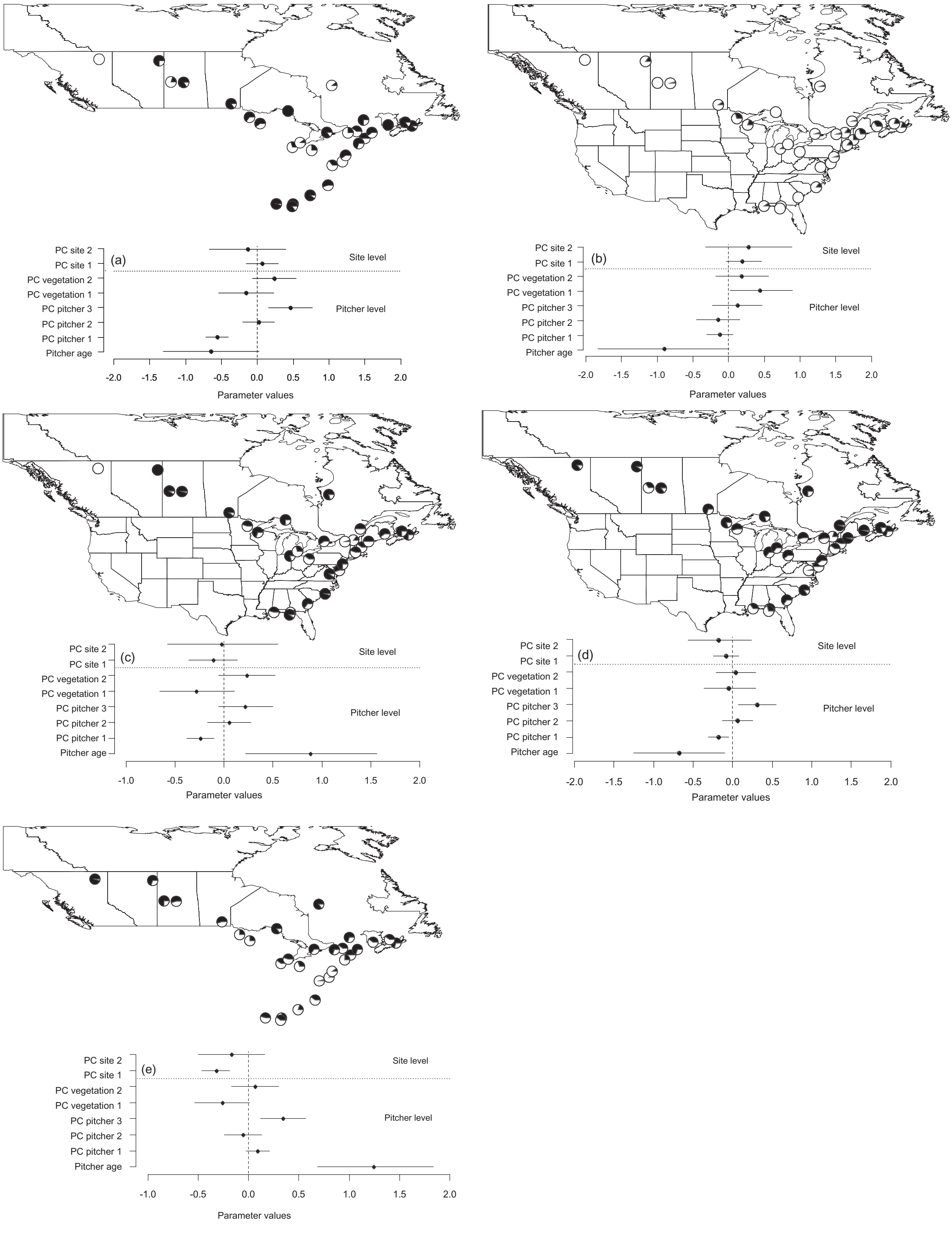

Figure 4 Maps showing the proportion of pitchers occupied (above) and plots (below) showing the mean values (filled circles) and 95% posterior credibility intervals (lines) for parameter estimates from hierarchical Bayesian models for the presence in pitchers of (a) the mosquito *Wyeomyia smithii*, (b) the sarcophagid *Fletcherimyia fletcheri*, (c) the midge *Metriocnemus knabi*, (d) the histiostomatid mite *Sarraceniopus gibsoni*, and (e) the bdelloid rotifer *Habrotrocha rosa*. Intervals that do not overlap zero are considered to be significantly different from zero. Note that the models do not include data from seven southern sites at which pore-water data were not collected or two sites with missing environmental data.

especially by noctuid larvae (Atwater *et al.*, 2006), eventually damages the leaf's ability to hold water.

Few previous studies have found results similar to ours, in which the variance in food-web richness and composition is primarily within, rather than among, sites. Most studies, which have been of single taxonomic groups, have found significant among-site variation associated with climate and latitude (e.g. Rahbek & Graves, 2001; Andrew & Hughes, 2004; Willig & Bloch, 2006), and others have found significant effects of local environmental variables on community structure (e.g. Ellingsen & Gray, 2002). Perhaps the most relevant comparison would be with widespread tree-hole and bromeliad-inhabiting aquatic food webs that are detritus-based and have mosquitoes as top predators. Contrary to our results, tree-hole invertebrate assemblages have high among-site variation (see, e.g., Kitching, 2000; Srivastava, 2005), which may be related to the high variation in the regional pool of available species (Srivastava, 2005). Bromeliads have a comparatively small geographic range, with some variation in trophic structure (Srivastava *et al.*, 2008), but the biogeography of bromeliad food webs has not been well studied (García-Robledo *et al.*, 2005).

The relative homogeneity at large spatial scales of these pitcher-plant inquiline communities, as compared with tree-hole and other similar communities, may be due to the nature of the relationship with their plant host. Many of the component species are obligate inhabitants of the relatively ephemeral habitat provided by *S. purpurea* leaves, and their geographic distributions almost perfectly coincide with that of the host plant. The exact nature of the relationship between the plant and its constituent community is not well understood: it was originally thought to be an obligate mutualism (see, e.g., Bradshaw & Creelman, 1984), but more recent work has suggested that the plant receives no benefit from the aquatic community in its leaves (Butler *et al.*, 2008) or even that some of the species parasitize the host plant (Mouquet *et al.*, 2008). Regardless of the effects on the host plants, many inquiline species appear to have evolved strong requirements for the host plant. This adaptation to the unique habitat found inside the leaves may act to minimize any effects of large-scale variation in environmental conditions.

Interestingly, processes acting at both large and small scales were important in determining the variation in pitcher-level species richness and composition for all taxa and all taxon groups we analysed (Figs 2–4). The among-pitcher variation was in many cases related to the geographic and spatially structured environmental variables represented by 'site PC 1', which summarized a large set of confounded variables (Appendix S4) that may represent a wide range of potential ecological drivers of species distribution and abundance, such as the effects of day length or temperature on behaviour or metabolic rates. When determinants of richness and composition for local communities are considered at small scales, much unexplained variation may be accounted for by processes traditionally seen to be operating at much larger scales, such as the impact of landscape or climatic factors (Ricklefs & Schluter, 1993).

Our previous analysis of latitudinal gradients in species richness for this dataset (Buckley *et al.*, 2003) showed that the abundance of mosquito larvae (*W. smithii*) was correlated with species richness of the lower trophic levels (protozoa and bacteria) and might have resulted in the reverse trend of increasing richness toward the equator. The analysis reported here used only the bog sites where pore water was collected and, surprisingly, found no strong relationship between abundance of mosquito larvae and the richness or composition of the lower trophic levels of the food web. The mean abundance of mosquito larvae at the excluded, mostly southern, pine–savanna sites was 1.7 ± 1.1 individuals ml^{-1} of pitcher fluid (±1 SD), whereas the mean of the sites included in the current analysis was only 0.7 ± 0.5, so habitat factors may drive mosquito abundance and, in turn, influence the lower tropic levels at high densities.

As predicted, the richness and composition of the food webs were related to resource availability and habitat volume. Midge abundance, which has been related to higher resource availability at the lower trophic levels (Hoekman *et al.*, 2009), was related to protozoan richness and the composition of protozoa and bacteria (Figs 2 & 3). Pitcher size (pitcher PC 1), which represents the amount of habitat volume available (Gotelli & Ellison, 2006), explained variation in several aspects of food-web richness and composition. Among-pitcher variation in richness and composition was also associated with differences in pitcher shape and plant size (pitcher PC 2 and PC 3). This result shows that large-scale environmental drivers of plant morphology (Ellison *et al.*, 2004) affect the availability of resources and consequently the structure of these pitcher-plant food webs in such a way as to generate geographic patterns in richness and composition.

Because they can be sampled on distinct spatial scales from pitchers to *Sarracenia* populations, the food webs found in the leaves of pitcher plants provide an important insight into the mechanisms behind geographic variation in food-web species richness and composition. The wide geographic range of the host plant allows us to quantify the interacting effects of local and geographic abiotic and biotic variables on species richness and composition at these multiple spatial scales. Future studies of the biogeography of entire communities must address both the relationship between species and their habitat and the relationships among species within the habitat, by investigating patterns and processes across a wide range of spatial scales.

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SUPPORTING INFORMATION

Additional Supporting Information can be found in the on-line version of this article:

Appendix S1 Diagram of the food web occurring within the pitchers of the North American purple pitcher plant, *Sarracenia purpurea*.
Appendix S2 The 56 taxa that occurred in >1% of 780 pitcher-plant (*Sarracenia purpurea)* leaves sampled at 39 sites throughout the plant's North American range.
Appendix S3 Abundance–occupancy relationships for (a) arthropods + rotifers, (b) protozoa, and (c) bacteria.
Appendix S4 Results from the principal components analysis of pitcher and plant morphology variables (pitcher level), vegetation variables measured within a 1-m^2 quadrat centred on each plant (pitcher level) and site-level environmental variables.

BIOSKETCH

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