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

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16 Running title: Pitcher-plant food webs from local to continental scales

17

1 **ABSTRACT**

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

5 **Location:** We sampled twenty pitcher-plant communities at each of thirty-nine sites spanning the
6 geographic range of *S. purpurea*—from northern Florida to Newfoundland and westward to eastern
7 British Columbia.

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

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

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

6

7 **KEYWORDS**

8 Food web, hierarchical Bayesian modeling, latitudinal gradients, *Sarracenia purpurea*, species
9 composition, species richness.

10

1 INTRODUCTION

2 Theories that attempt to explain patterns of community structure generally operate at three spatial scales:
3 local habitats, metacommunities, and larger scales that encompass entire biogeographic ranges. At the
4 scale of local habitats, many theories addresses how small-scale processes, such as environmental
5 conditions and species interactions (especially competition and predation), determine population and
6 community patterns (Case, 1999). Empirical tests at this spatial scale show that interactions among
7 species and responses of species to environmental conditions should be most important in the
8 distributions and abundances of species. At the metacommunity scale, dispersal limitation and species
9 saturation are thought to affect species diversity within the constituent habitats and may even override
10 the effects of local interactions (see, e.g., Cornell & Lawton, 1992). The metacommunity concept has
11 contributed to the development of significant theory (see Leibold *et al.*, 2004; Holyoak *et al.*, 2005), and
12 a growing number of experiments at this scale confirms that species interactions (see, e.g., Miller &
13 Kneitel, 2005), habitat structure and resource availability (see, e.g., Srivastava, 2006), dispersal (see,
14 e.g., Kneitel & Miller, 2003), and, more recently, genetics (see, e.g. Whitham *et al.*, 2006; Crutsinger *et*
15 *al.*, 2009) can be important determinants of among-community patterns.

16 Theories predicting community structure at even larger spatial scales are uncommon (Srivastava,
17 2005). At continental scales, distribution and abundance patterns may reflect broad environmental
18 gradients (Huston, 1994; Rosenzweig, 1995; Hawkins *et al.*, 2003) and historical and evolutionary
19 processes (Ricklefs & Schluter, 1993). Most empirical work at these spatial scales is based on simple

1 correlation analysis of geographic gradients in species richness (Gotelli *et al.*, 2009) and is often
2 restricted to groups of potential competitors or trophic guilds (see, e.g. Rivadeneira *et al.*, 2002) or to
3 single taxonomic groups such as mammals, birds, or trees (see, e.g., Rahbek & Graves, 2001; Stevens &
4 Willig, 2002). Geographic studies incorporating taxa interacting across trophic levels will almost
5 certainly be more revealing than studies that are taxonomically or trophically restricted (Ellingsen &
6 Gray, 2002; Andrew & Hughes, 2004). Further, although most large-scale studies of diversity are
7 conducted at a single spatial grain, for example, latitude-longitude blocks of particular size (Rahbek &
8 Graves, 2001; Arita *et al.*, 2005), processes controlling distribution and abundance often operate at
9 multiple spatial scales that may be revealed only by sampling at multiple grain sizes (see, e.g., Levin,
10 1992; Mittelbach *et al.*, 2001). Teasing apart the influences of regional and local processes therefore
11 requires sampling across trophic levels and at multiple spatial scales (He & Condit, 2007).

12 Here, we describe a study of a complete food web at two spatial scales across the entire
13 geographic range of the community: the bacteria, protozoans, rotifers, and arthropods that inhabit water-
14 filled pitchers of the North American purple pitcher plant *Sarracenia purpurea* L. (see Appendix S1 in
15 Supporting Information and Fig. 1). This detritus-based aquatic food web is restricted to discrete habitat
16 units (rain-filled leaves) of a single host plant that itself occurs in circumscribed habitats such as bogs
17 and pine savannas. This system provides three naturally discrete hierarchical sampling units: pitchers
18 within plants, plants within populations, and populations within the plant's geographic range. We
19 compared patterns of food-web species richness and composition in pitchers of similar age within and

1 among *Sarracenia* populations throughout its range. We have previously described simple patterns of
2 species richness in this food web across the geographic range of the host plant (Buckley *et al.*, 2003), but
3 we did not analyse the variation in species composition, environmental drivers of that variation, or scale
4 dependence of those drivers.

5 Many studies on this system at the local and meso-scales show that, within pitchers, species
6 abundances are controlled by a combination of processes, including interactions, resources, and dispersal
7 (Miller & Kneitel, 2005; Gotelli & Ellison, 2006, Hoekman *et al.*, 2009). Our large-scale analysis can
8 provide insight into the relative importance of these factors. For example, higher abundance of the
9 filter-feeding larvae of the pitcher-plant mosquito, *Wyeomyia smithii* (Coq.), is known to reduce the
10 abundances of protozoans and rotifers (Addicott, 1974; Miller *et al.*, 2002; Trzcinski *et al.*, 2005a, b;
11 Hoekman, 2007) but to have more variable effects on the abundance of microbes (Kneitel & Miller,
12 2002; Hoekman, 2007; Peterson *et al.*, 2008). Therefore, if this pattern scales up to the geographic
13 scale, we should observe a strong relationship among pitchers and among sites between the abundance
14 of *W. smithii* and the composition and richness of protozoans, rotifers, and, to a lesser extent, bacteria.
15 On the other hand, the addition of resources to this system has been shown to increase the abundances of
16 mites, rotifers, protozoans, and bacteria (Kneitel & Miller, 2002; Hoekman, 2007). Therefore, similarly,
17 if this pattern scales up, we should observe strong correlations between food-web richness and
18 composition and the size and morphology of pitchers, which control habitat volume (Gotelli & Ellison,
19 2006), and environmental variables related to resource availability.

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

10 **METHODS**

11 **Study species**

12 *Sarracenia purpurea* is a long-lived (>50 years), carnivorous, perennial plant that grows as a rosette of
13 pitcher-shaped leaves. It occurs in nutrient-poor wetlands—ombrotrophic bogs, poor fens, sand plains,
14 and longleaf-pine savannas—along the eastern coastal plain of North America and westward across
15 Canada and the northern mid-western states of the United States (Schnell, 2002; Fig. 1), spanning 30° of
16 latitude and 70° of longitude. In the northernmost portion of its range, the growing season is short, the
17 seasonal temperature variation is large, and *S. purpurea* var. *purpurea* is primarily restricted to
18 *Sphagnum*-peat bogs. In the south-eastern coastal plain, the growing season is long, seasonal
19 temperature variation is small, and *S. purpurea* var. *venosa* grows in pine savannas and seepage swamps.

1 In the southernmost part of the range (the Florida Panhandle, Alabama, and Mississippi), *S. purpurea*
2 ssp. *venosa* var. *burkii* (= *S. rosea*, sensu Naczi *et al.*, 1999) grows year-round, experiences relatively
3 little seasonal temperature variation, and occurs mostly in the sandy soils of pine savannas.

4 Unlike those of other Sarraceniaceae, the pitcher-shaped leaves of *S. purpurea* are open to the
5 sky and fill with rainwater and snow. The plants attract a variety of prey, primarily ants and other small
6 arthropods, which fall into the water-filled pitchers and drown. These aquatic microhabitats (generally 3
7 to 50 mL of fluid) are also colonized by a variety of arthropods, rotifers, protozoans, and bacteria that
8 form a detritus-based food web (Appendix S1; see also Addicott, 1974; Bradshaw & Creelman, 1984;
9 Miller & Kneitel, 2005). Obligate inhabitants of *S. purpurea* pitchers include larvae of three dipterans—
10 *Wyeomyia smithii*, the midge *Metriocnemus knabi* Coq., and the sarcophagid *Fletcherimyia fletcheri*
11 (Aldrich)—and one histiostomatid mite, *Sarraceniopus gibsoni* (Nesbitt). Bacteriovores include the
12 bdelloid rotifer *Habrotrocha rosa* Donner and numerous protozoan species (Addicott, 1974; Cochran-
13 Stafira & von Ende, 1998). Bacterial abundances are generally high (10^4 to 10^9 per mL; Kneitel &
14 Miller, 2002) and can vary at different spatial scales (Harvey & Miller, 1996; Petersen *et al.*, 2008).
15 Less common members of this community include loricate rotifers, cladocerans, copepods, amphipods,
16 nematodes, and multi-cellular algae (Addicott, 1974; Miller *et al.*, 1994; Bledzki & Ellison 2003). The
17 resource base of this community is the prey captured by the leaf, which is first shredded by the flesh
18 flies and midges and then decomposed and mineralized by the microbes. The plant takes up phosphorus
19 and nitrogen (and possibly small proteins and amino acids) from the pitcher fluid (Bradshaw &

1 Creelman, 1984; Butler *et al.*, 2008). Bacteria are themselves fed on by a host of bacteriovorous
2 protozoans and rotifers, primarily *H. rosa*, and the mite (Kneitel & Miller, 2002; Butler *et al.*, 2008;
3 Karagatzides *et al.*, in press). The mosquito larvae are omnivorous filter feeders that ingest pieces of
4 dead prey, small protozoans, and bacteria (Addicott, 1974). The flesh fly is an omnivorous top predator
5 that feeds on the mosquito larvae (Butler *et al.*, 2008), shreds prey, and also cannibalizes conspecifics
6 (Forsyth & Robertson, 1975).

7 **Data collection**

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

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

1 tapes. Vegetation cover was visually estimated in a 1-m² quadrat centered on each sampled pitcher
2 plant; the percentage covers of sphagnum, trees, shrubs, forbs, and graminoids were recorded.

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

11 We collected pitcher contents with sterile plastic pipettes, recorded their total volume, and then
12 divided the fluid into a Diptera-free, 1.5-mL sample, placed in a sterile microcentrifuge tube, and the
13 remainder, which was placed in a 50-mL sterile macrocentrifuge tube. Both portions were refrigerated
14 and returned to the lab, where arthropods and other large species in the large sample were counted and
15 identified to the lowest taxonomic resolution possible (10× magnification for arthropod identification,
16 100× magnification for the identification of rotifers and large protozoans; identification and
17 nomenclature followed Pennak, 1989). A 0.1-mL subsample of the smaller sample was serially diluted
18 (10⁻³ and 10⁻⁵) by sterile techniques. Three replicates from each dilution were plated on full-strength
19 PCB agar plates. Emergent bacterial colonies were separated into morphotypes based on color, texture,

1 and transparency. After both 3 and 10 days, for the plate from each dilution on which colony number
2 was closest to being between thirty and 300, the number colonies of each bacterial morphotype was
3 recorded. The counts from the three replicate plates at that dilution were then averaged to yield relative
4 abundance of each bacterial morphotype within individual pitchers. Some of these culturable
5 morphotypes were later tentatively identified by standard sequencing of 16S rDNA (Pepper & Gerba,
6 2005).

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

10 To quantify environmental characteristics of sites, we used a clean Tygon tube to extract five 50-
11 mL pore-water samples from capped and perforated PVC tubes (50 cm long \times 2.5 cm in diameter) that
12 were sunk into the peat at even intervals along our sample transect. For each water sample, we
13 measured pH and calcium content (mg/L) with Orion ion-sensitive electrodes (Thermo Electron Corp,
14 Woburn, Massachusetts, USA) and phosphate (PO₄-P), nitrate (NO₃-N), and ammonium (NH₄-N) (all in
15 mg/L) spectrophotometrically according to U.S. EPA standard methods (Clesceri *et al.*, 1998). Pore-
16 water samples were not taken at the eight southern sites with dry sandy soils.

17 **Data analysis**

18 *Variation in species composition*

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

9 *Data reduction*

10 The presence of arthropods (including rotifers for the purposes of these analyses), protozoans, and
11 bacterial morphotypes that occurred in more than 1% of the 592 pitchers across thirty sites (those sites
12 for which pore water samples were taken) were analysed separately by principal-coordinates analysis
13 (PCoA) implemented in the labdsv package version 1.3.1 in R (R Development Core Team, 2006) on the
14 basis of a Steinhaus distance matrix. The Steinhaus metric, which is similar to the Sorenson distance
15 metric, is suitable for presence data (Roberts, 2008) and resulted in the best spread of pitchers in the
16 ordination space (Legendre & Legendre, 1998). The site scores for the first two axes of each PCoA
17 (PCoA-1 and PCoA-2) were used as measures of variation in ‘species’ composition for arthropods,
18 protozoans, and bacteria because they explained the most variation in each case.

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

8 *Predictors of variation in species richness and composition*

9 Because pitchers were nested within sites and because we wanted to relate pitcher species richness and
10 composition to variables measured at both the pitcher and site scales, we constructed two-level,
11 hierarchical Bayesian models (Gelman & Hill, 2007) for three groups: arthropods + rotifers, protozoans,
12 and bacteria. We used varying intercept models without interactions terms because ours was an
13 exploratory study with many predictor variables. Species richnesses of the three groups were
14 normalised by a natural-log transformation. Species composition, as measured by PCoA axis scores,
15 was normally distributed for the three groups. Both species richness and composition were modeled as
16 Gaussian processes with identity-link functions. Although richness is a count variable and therefore
17 more correctly modelled as untransformed values with a Poisson distribution, the methods for
18 calculating the variance explained (see below) are only available for models that assume a Gaussian
19 distribution. We used non-informative priors for all parameters in all models (Gelman & Hill, 2007).

1 Species richness and composition were modeled separately for the three different groups. Each
2 dependent variable (y), richness or composition at the pitcher level, was modelled as a function of
3 pitcher-level predictor variables, x , and site-level predictor variables, u . The pitcher-level model takes
4 the form $y_i \sim N(\alpha_j + \beta x_i, \sigma_y^2)$, for $i = 1, \dots, n_j$, where y_i is the richness or composition of the i^{th} pitcher, α_j
5 is the regression intercept for the j^{th} site, β is the matrix of coefficients for the pitcher-level predictors,
6 σ_y^2 is the pitcher-level regression error, and n is the total number of pitchers. The hierarchical model
7 treats the pitcher-level intercept terms, α , as though they come from a normal distribution across sites
8 and models them as $\alpha_j \sim N(\gamma + \theta u_j, \sigma_\alpha^2)$, for $j = 1, \dots, J$, where γ is the site-level regression intercept and θ
9 is the matrix of coefficients for the site-level predictors, σ_α^2 is the site-level regression error, and J is the
10 total number of sites.

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

17 Models were fit by Markov chain Monte Carlo iteration with the BRugs package (Thomas *et al.*,
18 2006) of R version 2.7.1 (R Development Core Team, 2006). We assessed model convergence visually
19 for three simultaneously running Markov chains of at least 50,000 iterations, after a 10,000-iteration

1 burn-in period, and thinned it at every tenth value to reduce the effects of autocorrelation on parameter
2 estimates.

3 To obtain the relative amount of variance in the data at the pitcher level and the site level, we
4 calculated the intraclass correlation coefficient as the ratio of pitcher-level variance to the sum of the
5 pitcher-level variance and the site-level variance from an unconditional model that did not contain
6 predictor variables (Gelman & Hill, 2007). The variance explained by the predictor variables for the full
7 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
8 each pitcher from each iteration and calculated the variance across iterations for each pitcher. We then
9 divided the mean of these variances by the variance in the dependent variable and subtracted the result
10 from 1 to obtain the variance explained.

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

12 The presence of the four obligate pitcher-plant residents—*Wyeomyia smithii*, *Metriocnemus knabi*,
13 *Fletcherimyia fletcheri*, and *Sarraceniopus gibsoni*—together with that of *H. rosa*, was modelled with
14 two-level, hierarchical Bayesian models with varying intercept terms without interaction terms. The
15 presence of each species was modelled as a Bernoulli process with a logit link function and non-
16 informative priors for all parameters in all models. Each dependent variable (y), the presence of each
17 species at the pitcher level, was modelled as a function of pitcher-level predictor variables, x , and site-
18 level predictor variables, u . The pitcher-level model takes the form $y_i \sim \text{Bern}(\alpha_j + \beta x_i)$, for $i = 1, \dots, n_j$,
19 where y_i is the presence or absence of the species in the i^{th} pitcher, α_j is the regression intercept for the j^{th}

1 site, β is the matrix of coefficients for the pitcher-level predictors, and n is the total number of pitchers.
2 The second level of the hierarchical model was the same as that described above for species richness and
3 composition, as were the predictor variables.

4 **RESULTS**

5 **Species composition of all trophic levels**

6 Across all sites, we found a total of thirteen arthropod + rotifer species, forty-eight protozoan
7 morphospecies, and twenty-nine bacterial morphotypes (the most common are listed in Appendix S2).
8 Individual pitchers contained a mean of 3 ± 1.2 (SD) arthropod species (*Wyeomyia smithii* and
9 *Metriocnemus knabi* were most common), 2 ± 1.4 protozoan morphospecies (most abundant were
10 *Poterioochromonas malhamensis*, *Bodo* sp., and *Colpoda* near sp. *insula*), and 6 ± 2.1 bacterial
11 morphotypes. At the site level, we recorded 6 ± 1.4 arthropods, 9 ± 3.8 protozoan morphospecies, and
12 17 ± 2.6 bacterial morphotypes. Three of the four obligate pitcher-plant species (*W. smithii*, *M. knabi*,
13 and *S. gibsonii*) and the rotifer *H. rosa* were found at virtually all sites, whereas *F. fletcheri* was found at
14 only twenty-seven of the thirty-nine sites. The number of rare taxa was very large; of the ninety taxa
15 encountered, only fifty-six occurred in more than 1% of pitchers. Plots of the number of individuals
16 versus the number of occupied sites (Appendix S3) illustrate that most taxa were relatively rare and
17 occurred at <50% of the sampled sites.

18 Mean similarity in species composition among sites was 0.54 ± 0.04 . In other words, on average,
19 for any given site, just over half the species were the same as at any other given site. The similarity of

1 sites varied geographically; sites in western and central Canada had consistently higher among-site
2 similarity (and richness) than eastern sites (Fig. 1). Contrary to our initial prediction, the mean
3 similarity among pitchers within sites was much lower (0.36 ± 0.04) than the similarity among sites.

4 **Data reduction**

5 The first two axes of the PCoA of the fifty-six species occurring in at least 1% of pitchers sampled at the
6 thirty sites without missing data and for which pore water data were available accounted for 47% of the
7 variation in occurrence of arthropods + rotifers, 40% in occurrence of protozoans, and 21% in
8 occurrence of bacteria. The variation accounted for by these first two axes primarily reflected variation
9 in the presence of the more common species within pitchers. For example, for the arthropods + rotifers,
10 the loadings on the first PCoA axis were positively related to the presence of *W. smithii* and *M. knabi*
11 and negatively related to the presence of *S. gibsoni* and *H. rosa*. The loadings on the second axis were
12 negatively related only to the presence of *W. smithii*. For protozoans, the loadings on the first axis were
13 negatively related to the presence of *Bodo* sp and those on the second to the presence of
14 *Poterioochromonas* sp. For bacteria, the loadings on the first axis were strongly and positively related
15 to the presence of *Klebsiella pneumoniae*, a species of Cytophagales, and to the presence of unidentified
16 morphotype number 46. Loadings on this axis were strongly negatively related to presence of
17 *Flectobacillus* sp. Those on the second axis were strongly positively related to the presence of *K.*
18 *pneumoniae*, *Flectobacillus* sp., and morphotype number 46 and negatively to that of *Pseudomonas* sp.

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

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

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

1 values on the second axis had more basic pore water that contained more phosphorus but less
2 ammonium.

3 **Hierarchical modelling of food-web richness and composition at the thirty pore-water sites**

4 *Species richness*

5 Between 70% and 84% of the variation in richness of arthropods, rotifers, protozoans, and bacteria was
6 at the pitcher level rather than at the site level (Table 1). The hierarchical models revealed that richness
7 of arthropods+ rotifers was higher in larger, older pitchers (pitcher PC 1) that were not flattened (pitcher
8 PC 3), were surrounded by more *Sphagnum* (vegetation PC 1), and occurred at sites in the north-western
9 part of the host-plant range, where pH and PO₄ are lower (site PCs 1 and 2; Fig. 2a). Protozoan richness
10 was positively associated with midge abundance and pitcher age and negatively associated with older,
11 flatter pitchers (pitcher PC 3) that occurred at higher-latitude sites (Fig. 2b). Pitchers that contained
12 greater richness of bacterial morphotypes were older and larger (pitcher PC 1) and occurred at sites at
13 higher latitudes (site PC 1) (Fig. 2c). Despite these patterns, the predictor variables did not account for
14 much of the observed variation in species richness (maximum $R^2 = 0.32$; Table 1).

15 *Species composition*

16 The first PCoA axis describing variation in arthropod + rotifer species composition was positively
17 related to geographic location (site PC 1) and negatively to pitcher size (pitcher PC 1; Fig. 3a). The
18 second was related to geographic location (site PC 1), pitcher size (pitcher PC 1), and pitcher age and
19 was marginally related to the relative cover of *Sphagnum* (vegetation PC 1) (Fig. 3b). Composition of

1 protozoan taxa (PCoA 1) was related positively to pitcher age and negatively to midge density, mosquito
2 density, and *Sphagnum* cover (vegetation PC 1; Fig. 3c). Protozoan PCoA 2 was positively associated
3 with plants that had greater numbers of water-filled leaves (pitcher PC 2) and that occurred at sites in the
4 north-western part of the host-plant range, with lower PO₄ concentration in the pore water and lower pH
5 (site PC 1; Fig. 3d). Finally, variation in bacterial composition (PCoA 1) was positively related to the
6 density of midge larvae in pitchers, pitcher age, and plants that had greater numbers of water-filled
7 leaves (pitcher PC 2). This bacterial-composition axis was also marginally positively related to
8 *Sphagnum* cover surrounding pitchers (vegetation PC 1; Fig. 3e). Bacterial PCoA 2 was negatively
9 related to the density of midge larvae in pitchers and positively associated with pitchers that were
10 pitcher-like in morphology (pitcher PC 3) and greater tree cover surrounding the plant (vegetation PC 2).
11 This axis was also marginally negatively related to plant size (pitcher PC 1; Fig. 3). As with the species-
12 richness models, the variance explained by the hierarchical models was low and never exceeded 36%
13 (Table 1).

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

15 *Wyeomyia smithii* was more likely to occur in pitchers that were more pitcher-like in morphology
16 (pitcher PC 3) and on plants surrounded by higher tree cover (vegetation PC 2) and less likely to occur
17 in older, smaller pitchers (pitcher PC 1; Fig. 4a). *Fletcherimyia fletcheri* was more likely to occur in
18 younger pitchers from the current season and in pitchers on plants surrounded by greater *Sphagnum*
19 cover (vegetation PC 1) and was marginally associated with geographic location (site PC 1; Fig. 4b).

1 *Metriocnemus knabi* was more likely to occur in larger (pitcher PC 1), older pitchers from previous
2 seasons and was marginally associated with pitchers that were pitcher-like in morphology (pitcher PC 3)
3 on plants surrounded by higher tree cover (vegetation PC 2) and lower *Sphagnum* cover (vegetation PC
4 1; Fig. 4c). The mite *Sarraceniopus gibsoni* was more likely to occur in larger (pitcher PC 1), younger
5 pitchers that were more pitcher-like (pitcher PC 3; Fig. 4d). *Habrotrocha rosa* was more likely to occur
6 in older pitchers that were more pitcher-like (pitcher PC 3) on plants that were surrounded by lower
7 *Sphagnum* cover (vegetation PC 1) at higher-latitude sites (site PC 1; Fig. 4e).

8 **DISCUSSION**

9 We found significant variation in the composition of the food web among *Sarracenia* populations; our
10 ability to explain that variation, and the variation in species richness, using measured predictor variables,
11 was limited (Table 1). This result is not surprising because we were considering a community that is
12 highly variable at small spatial scales (Buckley *et al.*, 2004) and that spans such a large geographical
13 range, but contrary to our initial prediction, variation in food-web composition was greater (species
14 turnover was higher) at the among-pitcher than at the among-site scale. Among-site similarity values
15 were high (Fig. 1), and particular taxa—the obligate pitcher-plant residents and *Habrotrocha rosa*—
16 were consistently common across the range of the host plant, although *F. fletcheri* had a more north-
17 easterly distribution. These species therefore appear to have stronger associations with the host plant
18 itself than with large-scale variation in environmental conditions. The consistent and somewhat unusual
19 habitat provided by the pitcher itself may have resulted in a highly specialized suite of co-habiting

1 species that have all evolved to use the same habitat provided by the host plant. In fact, some studies
2 have suggested that the plant derives only minor benefits from carnivory (e.g., Chapin & Pastor, 1995;
3 Bott *et al.*, 2008). If the species that use the water-filled leaves of *S. purpurea* depend on their host plant
4 to a greater degree than each plant or leaf benefits from the presence of these associated species, then the
5 food-web composition may be structured by the consistent environment of the leaf itself and not by the
6 relatively large variation in seasonality, productivity, and abiotic factors across the plant's range.
7 Although we do not fully understand the exchanges of resources and other benefits between the host
8 plant and these species and among the species themselves (see, e.g., Bledzki & Ellison, 1998; Mouquet
9 *et al.*, 2008), they appear to represent a community-level mutualism, in which at least some species
10 benefit from the presence of other species in the community and their host plant.

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

1 Pitchers usually provide habitat for up to a year (Miller & Kneitel, 2005), but herbivory, especially by
2 noctuid larvae (Atwater *et al.*, 2006), eventually damages the leaf's ability to hold water.

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

15 The relative homogeneity at large spatial scales of these pitcher-plant inquiline communities, as
16 compared to tree-hole and other similar communities, may be due to the nature of the relationship with
17 their plant host. Many of the component species are obligate inhabitants of the relatively ephemeral
18 habitat provided by *S. purpurea* leaves, and their geographic distributions almost perfectly coincide with
19 that of the host plant. The exact nature of the relationship between the plant and its constituent

1 community is not well understood: it was originally thought to be an obligate mutualism (see, e.g.,
2 Bradshaw & Creelman, 1984), but more recent work has suggested that the plant receives no benefit
3 from the aquatic community in its leaves (Butler *et al.*, 2008) or even that some of the species parasitize
4 the host plant (Mouquet *et al.*, 2008). Regardless of the effects on the host plants, many inquiline
5 species appear to have evolved strong requirements for the host plant. This adaptation to the unique
6 habitat found inside the leaves may act to minimize any effects of large-scale variation in environmental
7 conditions.

8 Interestingly, processes acting at both large and small scales were important in determining the
9 variation in pitcher-level species richness and composition for all taxa and all taxon groups we analysed
10 (Figs 2-4). The among-pitcher variation was in many cases related to the geographic and spatially
11 structured environmental variables represented by 'site PC 1', which summarised a large set of
12 confounded variables (Appendix S4) that may represent a wide range of potential ecological drivers of
13 species' distribution and abundance, such as the effects of day length or temperature on behaviour or
14 metabolic rates. When determinants of richness and composition for local communities are considered
15 at small scales, much unexplained variation may be accounted for by processes traditionally seen to be
16 operating at much larger scales, such as the impact of landscape or climatic factors (Ricklefs & Schluter,
17 1993).

18 Our previous analysis of latitudinal gradients in species richness for this dataset (Buckley *et al.*,
19 2003) showed that the abundance of mosquito larvae (*W. smithii*) was correlated with species richness of

1 the lower trophic levels (protozoa and bacteria) and might have resulted in the reverse trend of
2 decreasing richness toward the equator. The analysis reported here used only the bog sites where pore
3 water was collected and, surprisingly, found no strong relationship between mosquito larval abundance
4 and the richness or composition of the lower trophic levels of the food web. The mean abundance of
5 mosquito larvae at the excluded, mostly southern, pine-savannah sites was 1.7 ± 1.1 individuals per mL
6 of pitcher fluid (± 1 S.D.), whereas the mean of the sites included in the current analysis was only $0.7 \pm$
7 0.5 , so habitat factors may drive mosquito abundance and, in turn, influence the lower trophic levels at
8 high densities.

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

1 Because they can be sampled on distinct spatial scales from pitchers to *Sarracenia* populations,
2 the food webs found in the leaves of pitcher plants provide important insight into the mechanisms
3 behind geographic variation in food-web species richness and composition. The wide range of the host
4 plant allows us to quantify the interacting effects of local and geographic abiotic and biotic variables on
5 species richness and composition at these multiple spatial scales. Future studies of the biogeography of
6 entire communities must address both the relationship between species and their habitat and the
7 relationships among species within the habitat, by investigating patterns and processes across a wide
8 range of spatial scales.
9

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8

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- 16

1 **Supplementary Material**

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

3 **Appendix S1** Diagram of the food web occurring within the pitchers of the North American purple
4 pitcher plant, *Sarracenia purpurea*.

5 **Appendix S2** The 56 taxa that occurred in >1% of 780 pitcher-plant (*Sarracenia purpurea*) leaves
6 sampled at thirty-nine sites throughout the plant's North American range.

7 **Appendix S3** Abundance-occupancy relationships for (a) arthropods + rotifers, (b) protozoans, and (c)
8 bacteria.

9 **Appendix S4** Results from the principal-components analysis of pitcher- and plant-morphology
10 variables (pitcher level), vegetation variables measured within a 1-m² quadrat centred on each plant
11 (pitcher level), and site-level environmental variables.

12

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15 corresponding author for the article.

16

1 **Biosketch**

2 Hannah Buckley is a Senior Lecturer in Ecology at Lincoln University. Her research interests include
3 community ecology and macroecology. She is particularly interested in understanding spatial patterns in
4 community structure.

5

6

1 **Table 1** Proportion of variance calculated from variance partitioning showing the relative amount of
2 variation in the data for each hierarchical Bayesian model at the pitcher and site levels. R^2 values give
3 the amount of variation explained by all predictors for each model.

Model	Proportion of variation		R^2
	Pitcher level	Site level	
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

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1 **Figure legends**

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

8 Figure 2 Plots showing the mean values (filled circles) and 95% posterior credibility intervals (lines) for
9 parameter estimates from hierarchical Bayesian models for the pitcher richness of (a) arthropods +
10 rotifers, (b) protozoans, and (c) bacteria. Intervals that do not overlap zero are considered to be
11 significantly different from zero. For protozoan and bacterial richness, the two additional predictors
12 were the number of mosquito larvae and the number of midge larvae present in pitchers. Models do not
13 include data from seven southern sites at which pore-water data were not collected or two sites with
14 missing environmental data. PC, principal component. PC site 1: Sites with high scores were at low
15 elevations in the southeast United States, had long growing seasons with high mean temperatures and
16 precipitation, and had low annual variation in both of these variables. Sites with high scores were more
17 acidic and had lower levels of calcium and ammonium in pore water. PC site 2: Sites with high values
18 on the second axis had more basic pore water that contained more phosphorus but less ammonium. PC
19 vegetation 1: High scores indicated habitats at which pitchers were surrounded by a higher percentage

1 cover of sphagnum and a lower percentage cover of forbs. PC vegetation 2: High scores indicated
2 habitats with a higher percentage cover of trees and a lower percentage cover of graminoids. PC pitcher
3 1 ('size'): High scores indicated high with rosette diameter, pitcher height, and pitcher volume. PC
4 pitcher 2 ('habitat area'): High scores indicated high pitcher volume. PC pitcher 3 ('pitcherness'):
5 indicated smaller keels and greater lip widths on pitchers.

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

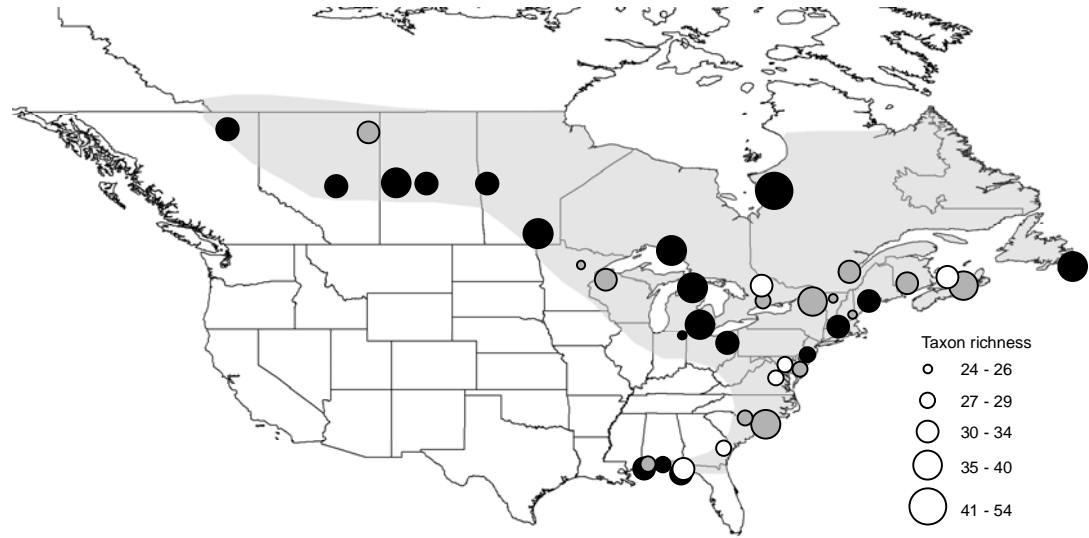
15 Figure 4 Maps showing the proportion of pitchers occupied (above) and plots (below) showing the
16 mean values (filled circles) and 95% posterior credibility intervals (lines) for parameter estimates from
17 hierarchical Bayesian models for the presence in pitchers of (a) the mosquito *Wyeomyia smithii*, (b) the
18 sarcophagid *Fletcherimyia fletcheri*, (c) the midge *Metriocnemus knabi*, (d) the histiostomatid mite
19 *Sarraceniopus gibsoni*, and (e) the bdelloid rotifer *Habrotrocha rosa*. Intervals that do not overlap zero

1 are considered to be significantly different from zero. Note that the models do not include data from
2 seven southern sites at which pore-water data were not collected or two sites with missing environmental
3 data. PC, principal component; see caption of Figure 2 for further explanation.

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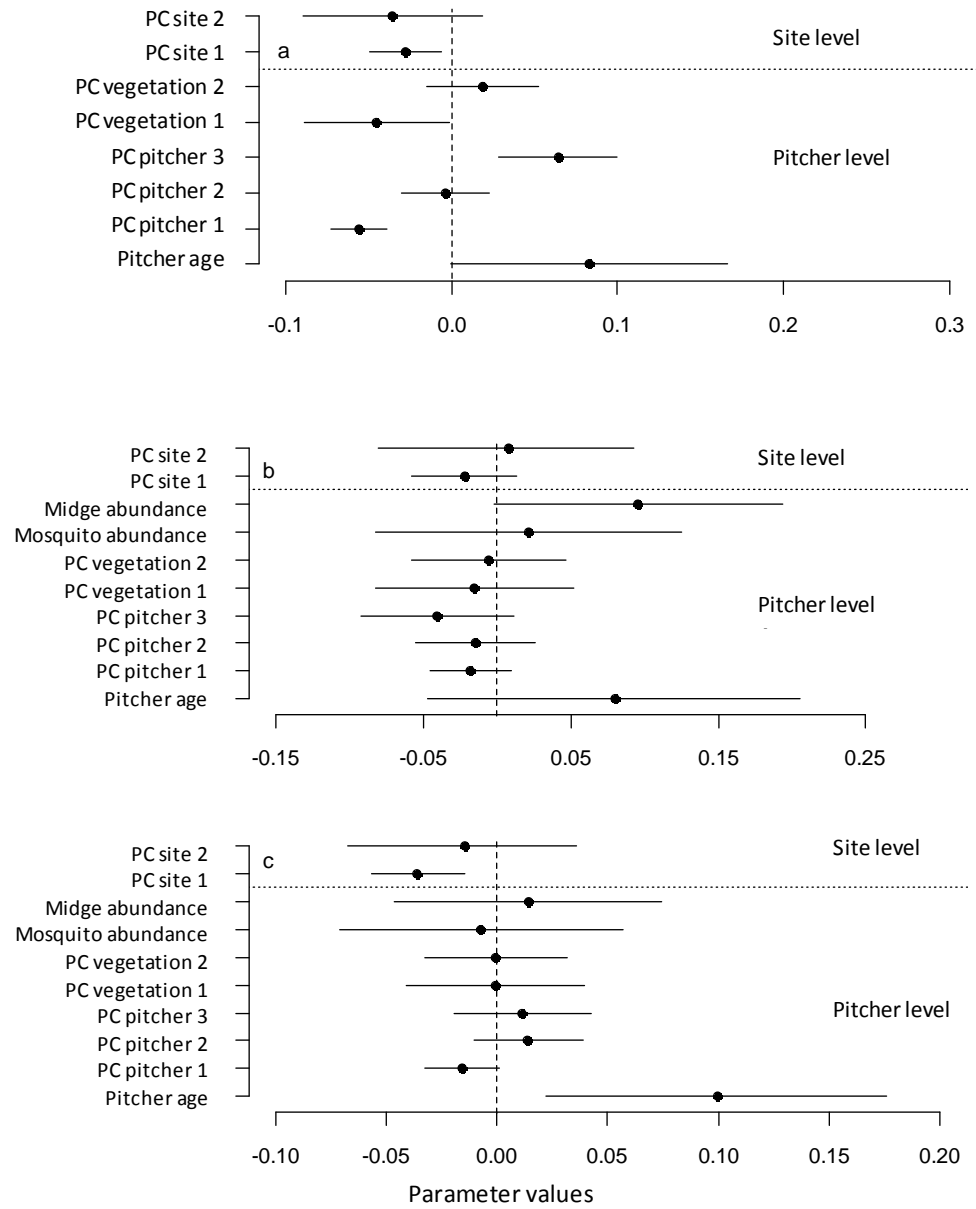
1 Figure 1



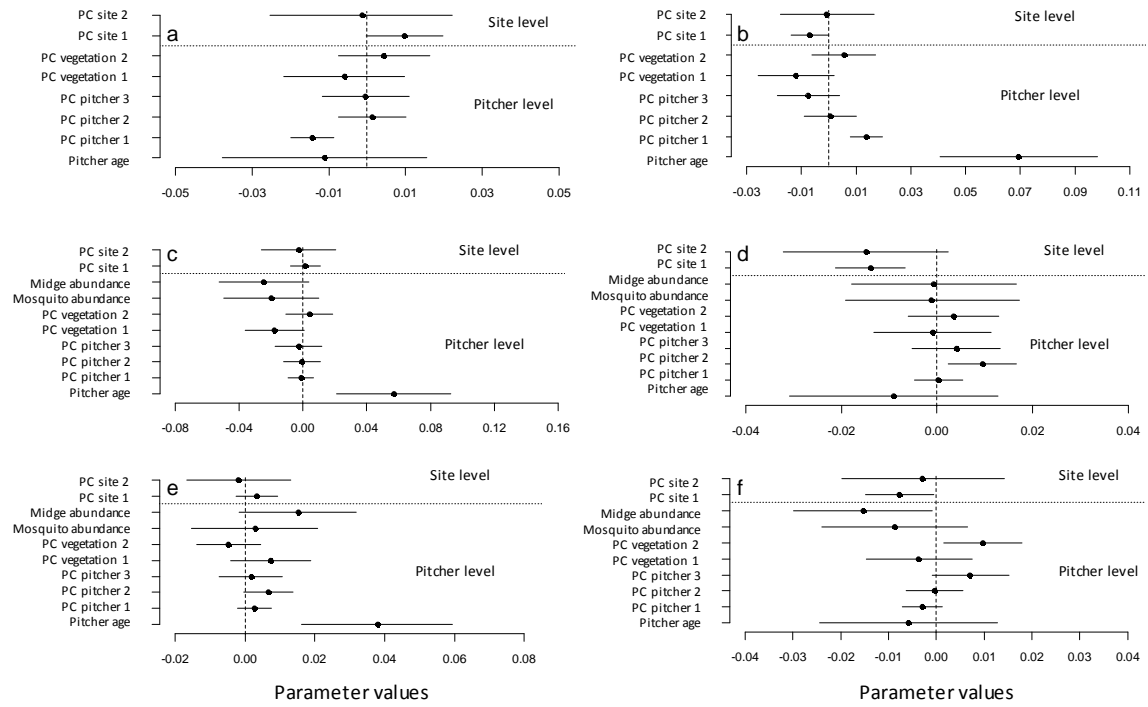
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1 Figure 2



1 Figure 3

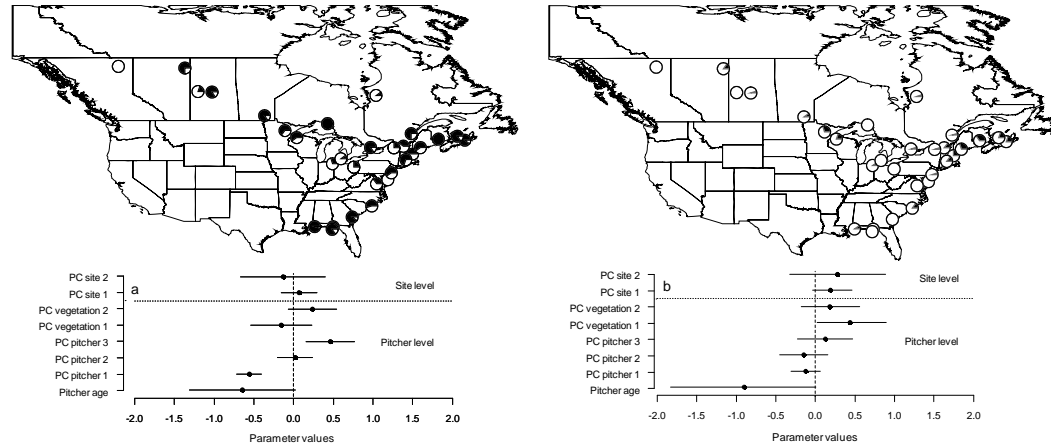


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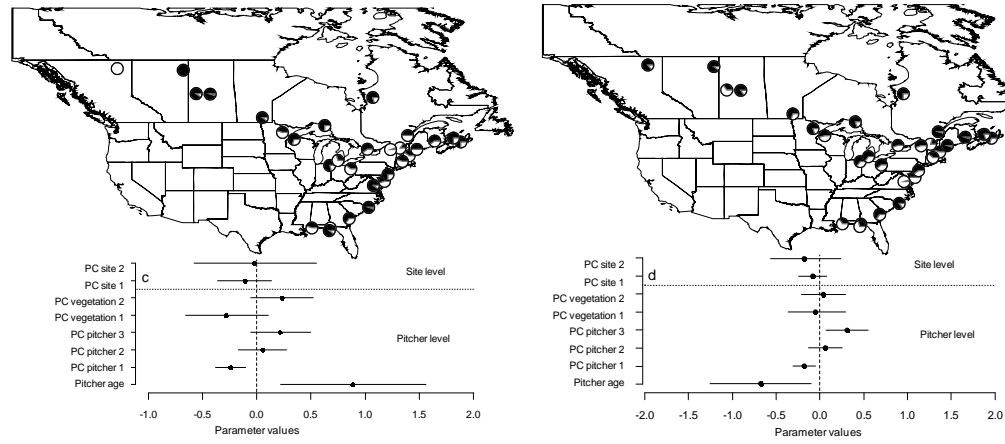
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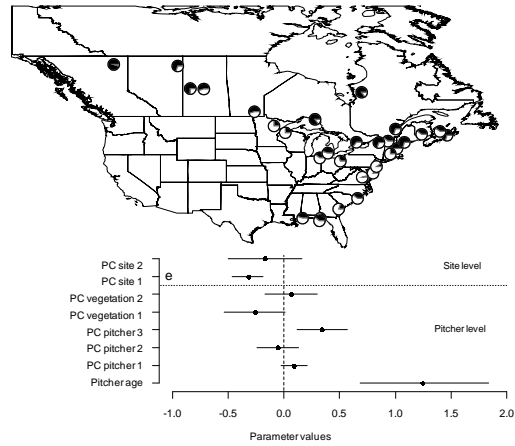
1 Figure 4



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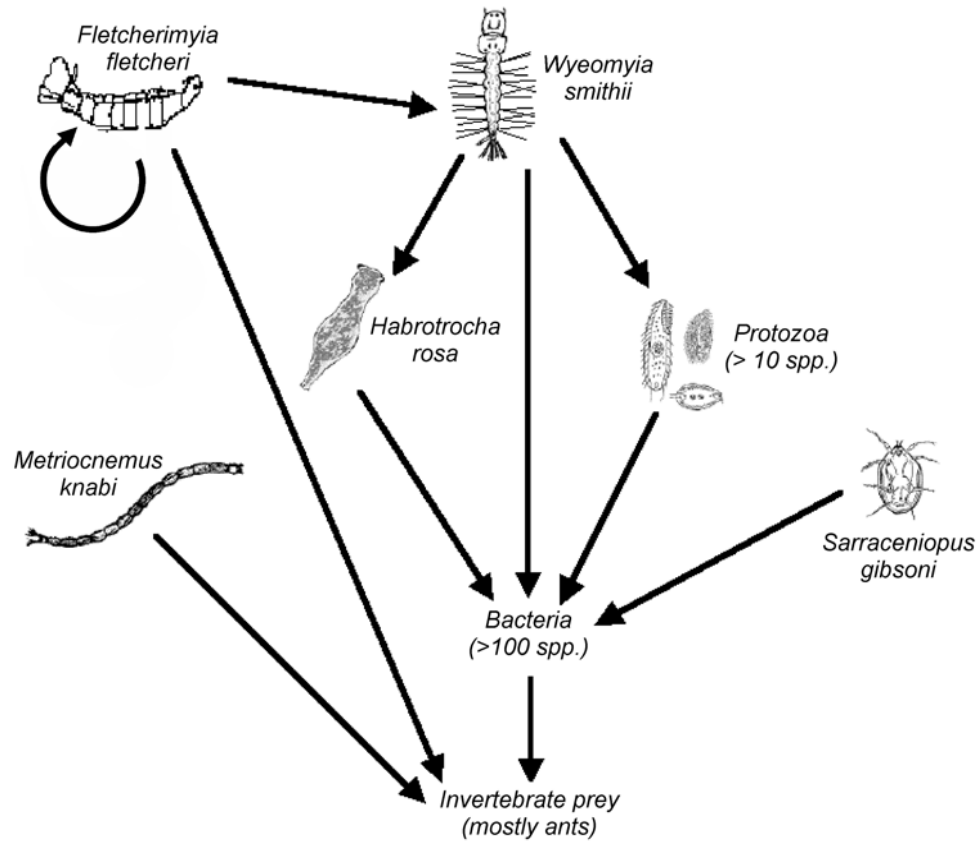


4

1 **Appendix S1** Diagram of the food web occurring within the pitchers of the North American purple
2 pitcher plant, *Sarracenia purpurea*. Note that *Fletcherimyia* is uncommon in the southern part of the
3 host plant's range.

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- 1 **Appendix S2** The 56 taxa that occurred in >1% of 780 pitcher-plant leaves sampled at thirty-nine sites
- 2 throughout the plant's North American range.

Group	Species name	Proportion of pitchers	Number of sites
Arthropods and rotifers	<i>Metriocnemus knabi</i>	0.66	38
	<i>Sarraceniopus gibsoni</i>	0.65	38
	<i>Wyeomyia smithii</i>	0.64	37
	<i>Habrotrocha rosa</i>	0.51	38
	rotifer sp. 'a'	0.38	10
	unknown gastrotrich	0.37	9
	unknown amphipod	0.36	8
	unknown tardigrade	0.36	8
	loricate rotifer	0.33	13
	unknown cladoceran	0.32	13
	<i>Fletcherimyia fletcheri</i>	0.29	27
	unknown nematode	0.27	13
	unknown copepod	0.25	20
Protozoan morphospecies	<i>Bodo</i> sp.	0.52	39
	<i>Tachysoma</i> sp.	0.42	10

	<i>Menoidium</i> sp.	0.41	8
	unknown sp. a	0.38	5
	<i>Peranema</i> sp.	0.33	17
	chryomonads	0.32	32
	<i>Cryptomonas</i> spp.	0.31	14
	<i>Petalomonas</i> sp.	0.31	9
	<i>Anisonema</i> sp.	0.29	13
	<i>Colpidium</i> sp.	0.29	34
	unknown sp. 'b'	0.29	15
	<i>Cyclidium</i> sp.	0.28	32
	<i>Vorticella</i> sp.	0.28	5
	<i>Euglena</i> sp.	0.26	8
	<i>Paramecium</i> sp.	0.25	9
	<i>Colpoda</i> sp. 'big'	0.24	37
	<i>Notoselenus</i> sp.	0.23	6
	unknown sp. 'c'	0.22	16
Bacterial morphotypes	<i>Sphingomonas</i> sp. 'a'	0.89	39
	<i>Sphingomonas</i> sp. 'b'	0.69	39
	Cytophagales	0.57	39

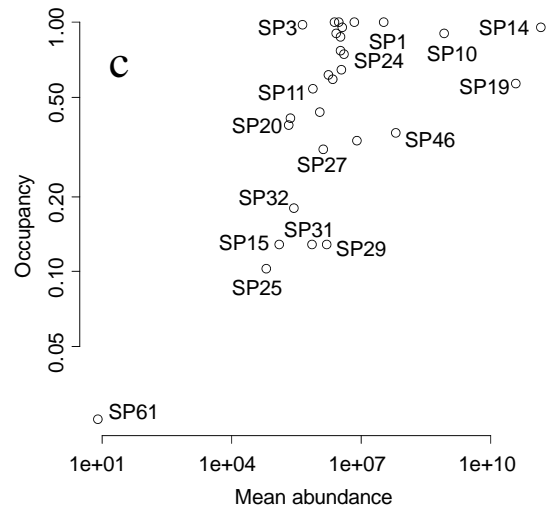
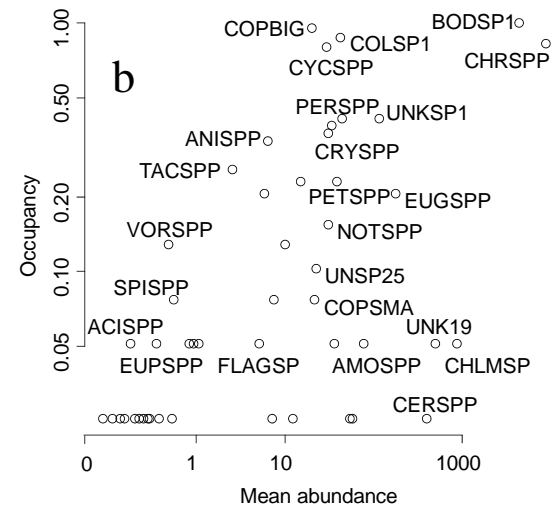
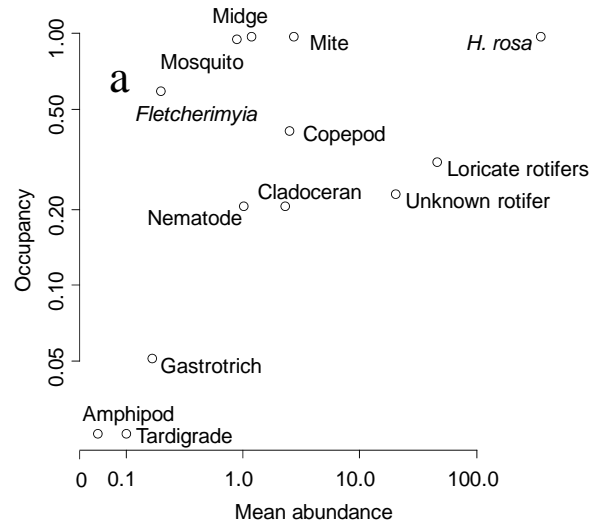
<i>Pseudomonas</i> sp.	0.50	37
<i>Klebsiella pneumoniae</i>	0.49	38
morphotype number 46	0.46	14
<i>Chromobacterium violaceum</i>	0.42	17
morphotype number 32	0.40	8
<i>Flectobacillus</i> sp. 'a'	0.38	37
morphotype number 30	0.38	30
morphotype number 29	0.37	5
unknown yeast	0.36	35
<i>Microbacterium</i> sp.	0.36	39
<i>Agrobacterium rhizogenes</i>	0.36	34
<i>Chromobacterium</i> sp.	0.36	15
morphotype number 27	0.35	12
<i>Rhodoferax</i> sp.	0.34	24
<i>Sphingomonas</i> sp. 'c'	0.33	13
morphotype number 28	0.33	25
<i>Chromobacterium</i> sp.	0.32	16
morphotype number 37	0.32	23
<i>Flectobacillus</i> sp. 'b'	0.31	35

morphotype number 24	0.29	29
<i>Flectobacillus</i> sp. 'c'	0.27	21
<i>Bacillus</i> sp.	0.27	22

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1 **Appendix S3** Abundance-occupancy relationships for (a) arthropods + rotifers, (b) protozoans, and (c)
2 bacteria. Abundance was calculated as the mean number of individuals per pitcher where present.
3 Occupancy is the proportion of sites occupied out of thirty-nine. Abbreviations are as follows:
4 Mosquito = *Wyeomyia smithii*, Chironomid = *Metriocnemus knabi*, Mite = *Saraceniopus* spp., Copepod
5 = unidentified copepod, Cladoceran = unidentified cladoceran, *Fletcherimyia* = *Fletcherimyia fletcheri*,
6 Nematode = unidentified nematodes, Amphipod = unidentified amphipods, Gastrotrich = unidentified
7 gastrotrichs, Tardigrade = unidentified tardigrades, *H. rosa* = *Habrotrocha rosa*, Loricata rotifers =
8 Loricata rotifers, Unknown rotifer = unidentified rotifer, ACISPP = *Acineta*, AMOSPP = unidentified
9 *Amoeba*, ANISPP = *Anisonema*, BODSP1 = *Bodo* sp1, CERSPP = *Cercomonas*, CHLSPP =
10 *Chlamydodon*, CHRSP1 = *Chrysomonads*, COLSP1 = unidentified *Colpidium* sp., COPBIG =
11 unidentified *Colpoda* sp., COPSMA = *Colpoda* sp. small, CRYSP1 = *Cryptomonas*, CYCSPP =
12 *Cyclidium*, EUGSP1 = *Euglena*, EUPSP1 = *Euplotes*, FLAGSP = unidentified flagellate, NOTSP1 =
13 *Notoselenus*, PERSPP = *Peranema*, PETSPP = *Petalomonas*, SPISPP = *Spirostomum*, TACSPP =
14 *Tachysoma*, UNK19 = unidentified protozoan, UNKSP1 = unidentified protozoan, UNSP25 =
15 unidentified protozoan, VORSPP = *Vorticella*, SP1 = *Sphingomonas*, SP3 = *Klebsiella (K. pneumoniae)*,
16 SP10 = *Flectobacillus*, SP11 = *Flectobacillus*, SP14 = *Flectobacillus*, SP19 = *Bacillus/soil bacterium*,
17 SP20 = *Chromobacterium*, SP15, 24, 25, 27, 29, 31, 32, and 46 = unknown bacterium.



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1 **Appendix S4** Results from the principal-components analysis of pitcher- and plant-morphology
2 variables (pitcher level), vegetation variables measured within a 1-m² quadrat centred on each plant
3 (pitcher level), and site-level environmental variables. Values shown are the cumulative percentages of
4 variance accounted for by the axes shown and the loadings of each variable on each axis. Analyses
5 included data from seven southern sites at which soil pore-water data were not collected and two sites
6 with missing environmental data.

Variable	Axis 1	Axis 2	Axis 3
Pitcher- and plant-morphology variables			
<i>Cumulative percent variation</i>	40.2	59.5	74.7
Pitcher width at base	-0.44	-0.14	0.19
Aperture diameter	-0.42	-0.19	0.29
Pitcher length from base to neck	-0.40	-0.15	-0.39
Fluid volume	-0.37	-0.11	0.06
Rosette diameter	-0.36	0.14	-0.40
Lip thickness	-0.31	-0.04	0.52
Width of keel	-0.23	-0.02	-0.51
Number of water-filled leaves	-0.17	0.64	0.17
Vegetation variables			
<i>Cumulative percent variation</i>	37.1	63.8	

Sphagnum	0.89	-0.10
Shrubs	0.48	0.50
Trees	-0.23	0.84
Graminoids	-0.34	-0.57
Forbs	-0.81	0.19
Site-level environmental variables		
<i>Cumulative percent variation</i>	60.2	73.6
Mean monthly precipitation	0.93	-0.07
Mean monthly temperature	0.90	0.14
Number of growing-season days	0.89	0.13
Longitude	0.80	-0.12
Pore water PO ₄	0.16	0.79
Pore water NH ₄	-0.43	-0.50
Pore water pH	-0.56	0.73
Pore water Ca ⁺²	-0.71	-0.04
Elevation	-0.72	0.29
Coefficient of variation in mean monthly precipitation	-0.90	0.09
Latitude	-0.94	-0.12

Coefficient of variation in mean	-0.95	-0.14
monthly temperature		