



# DIGITAL ACCESS TO SCHOLARSHIP AT HARVARD

## Geographic Variation in Network Structure of a Nearctic Aquatic Food Web

The Harvard community has made this article openly available.  
[Please share](#) how this access benefits you. Your story matters.

<b>Citation</b>	Baiser, Benjamin, Nicholas J. Gotelli, Hannah L. Buckley, Thomas E. Miller, and Aaron M. Ellison. 2011. Geographic Variation in Network Structure of a Nearctic Aquatic Food Web. <i>Global Ecology and Biogeography</i> . doi: 10.1111/j.1466-8238.2011.00705.x.
<b>Published Version</b>	<a href="https://doi.org/10.1111/j.1466-8238.2011.00705.x">doi:10.1111/j.1466-8238.2011.00705.x</a>
<b>Accessed</b>	February 19, 2015 9:25:32 AM EST
<b>Citable Link</b>	<a href="http://nrs.harvard.edu/urn-3:HUL.InstRepos:8298848">http://nrs.harvard.edu/urn-3:HUL.InstRepos:8298848</a>
<b>Terms of Use</b>	This article was downloaded from Harvard University's DASH repository, and is made available under the terms and conditions applicable to Other Posted Material, as set forth at <a href="http://nrs.harvard.edu/urn-3:HUL.InstRepos:dash.current.terms-of-use#LAA">http://nrs.harvard.edu/urn-3:HUL.InstRepos:dash.current.terms-of-use#LAA</a>

*(Article begins on next page)*

1 **Geographic Variation in Network Structure of a Nearctic Aquatic**

2 **Food Web**

3  
4 **Benjamin Baiser<sup>1</sup>, Nicholas J. Gotelli<sup>2</sup>, Hannah L. Buckley<sup>3</sup>, Thomas E. Miller<sup>4</sup>**

5 **Aaron M. Ellison<sup>1</sup>**

6  
7 *<sup>1</sup>Harvard University, Harvard Forest, 324 N. Main St., Petersham, MA 01366, USA*

8 *<sup>2</sup>Department of Biology, University of Vermont, Burlington, VT 05405, USA*

9 *<sup>3</sup>Department of Ecology, P.O. Box 84, Lincoln University, Canterbury, New Zealand*

10 *<sup>4</sup>Department of Biological Science, Florida State University, Tallahassee, FL 32306-4295, USA*

11  
12 *\*Correspondence: Harvard University, Harvard Forest, 324 N. Main St., Petersham, MA 01366, USA*

13 *E-mail: bbaiser@fas.harvard.edu, Phone : 1-978-756-6155, Fax: 1-978-724-3595*

14  
15 **Article type:** Research Paper

16 **Running title:** Network structure in a cosmopolitan food web

21

22

23 **ABSTRACT**

24 **Aim** The network structure of food webs plays an important role in the maintenance of diversity and  
25 ecosystem functioning in ecological communities. Previous research has found that ecosystem size,  
26 resource availability, assembly history, and biotic interactions can potentially drive food web structure.  
27 However, the relative influence of climatic variables that drive broad-scale biogeographic patterns of  
28 species richness and composition has not been explored for food web structure. In this study, we assess  
29 the influence of broad-scale climatic variables in addition to known drivers of food web structure on  
30 replicate observations of a single aquatic food web, sampled from the leaves of the pitcher plant  
31 (*Sarracenia purpurea*), at different geographic sites across a broad latitudinal and climatic range.

32

33 **Location** Using standardized sampling methods, we conducted an extensive “snapshot” survey of 780  
34 replicated aquatic food webs collected from the leaves of the pitcher plant *Sarracenia purpurea* at 39 sites  
35 from northern Florida to Newfoundland and westward to eastern British Columbia.

36

37 **Methods** We tested for correlations of 15 measures of food web structure at the pitcher and site scales  
38 with geographic variation in temperature and precipitation, concentrations of nutrients from atmospheric  
39 nitrogen deposition, resource availability, ecosystem size, and the abundances of the pitcher plant  
40 mosquito (*Wyeomyia smithii*), a potential keystone species.

41

42 **Results** At the scale of a single pitcher plant leaf, linkage density, species richness, measures of chain  
43 length, and the proportion of omnivores in a web increased with pitcher volume. Linkage density and  
44 species richness were greater at high latitude sites which experience lower mean temperatures and

45 precipitation, and higher annual variation in both of these variables. At the site scale, variation in eight of  
46 the 15 food web metrics decreased at higher latitudes and variation in measures of chain length increased  
47 with the abundance of mosquitoes.

48 **Main Conclusions** Ecosystem size and climatic variables related to latitude were most highly correlated  
49 with network structure of the *Sarracenia* food web. However, even the best-fitting models explained less  
50 than 40% of the variation in food web structure, in spite of large sample sizes, thorough standardized  
51 sampling, and the large geographic extent of the survey. In contrast to biogeographic patterns of species  
52 richness, food web structure was largely independent broad-scale climatic variables. The large proportion  
53 of unexplained variance in our analyses suggests that stochastic assembly may be an important  
54 determinant of local food web structure.

55

56

57 **Key Words:** Biogeography, chain length, food web, keystone predation, network structure, *Sarracenia*  
58 *purpurea*

59

60

61

## 62 INTRODUCTION

63 Understanding the causes and consequences of food web structure is a central focus of community  
64 ecology (Hairston *et al.*, 1960; May, 1973; Pimm, 1982; Fretwell, 1987; Beckerman *et al.*, 2006; Schmitz,  
65 2010). Experimental studies have documented that food web structure is influenced by ecosystem size  
66 (Spencer & Warren, 1996; Post *et al.*, 2000; Takimoto *et al.*, 2008; McHugh *et al.*, 2010), the presence of  
67 keystone predators (Paine, 1969; Woodward *et al.*, 2008), disturbance (Power *et al.*, 1996; Marks *et al.*,  
68 2000; McHugh *et al.*, 2010), productivity (Townsend *et al.*, 1998; Arim *et al.*, 2007), and the availability  
69 of nutrients and resources (Jenkins *et al.*, 1992; Kaunzinger & Morin, 1998). Literature compilations and  
70 meta-analyses of studies of food web structure also have demonstrated that many food web metrics are  
71 scale dependent (Schoener, 1989; Martinez, 1993; Martinez & Lawton, 1995), that web connectance (the  
72 proportion of possible links realized) is constrained between 0.03 and 0.33 (Dunne, 2002a), and that food  
73 webs generally do not exhibit small-world network properties (Comacho *et al.*, 2002; Dunne *et al.*,  
74 2002b). However, it is difficult to infer general mechanisms from the results of single field experiments or  
75 meta-analyses because of differences in the spatial and temporal scale of the different studies, and  
76 differences in the collection, processing, and modeling of the raw data.

77 Here, we adopt a third strategy for understanding the control of food web structure. We test  
78 previously proposed correlations of food web structure with replicate observations of a single food web  
79 sampled at different geographic sites across a broad latitudinal and climatic range. We examine  
80 associations between metrics of food web structure, climatic variables related to precipitation and  
81 temperature that are strongly correlated to latitude, and potential causal variables such as nutrient inputs,  
82 ecosystem size, and the abundance of potential keystone species. Taking such an approach in North  
83 American lakes, Post *et al.* (2000) showed that food chain length is positively correlated with ecosystem  
84 size. Similarly, Schmitz (2006; 2010) used old-field food webs to show that trophic structure and adaptive  
85 foraging influence N mineralization rate, plant biomass production, and supply rate of solar radiation.  
86 Kitching (1987) found no relationship between tree-hole size and food web structure in Australian tree-

87 hole communities. However, this kind of replicated sampling of a single food web is uncommon because  
88 the composition of food webs normally varies extensively across sites, the large spatial extent of most  
89 food webs makes it difficult or even impossible to sample all the organisms and their feeding interactions  
90 in replicated food webs, and the spatial boundaries of most local food webs are often arbitrary and poorly  
91 defined.

92 We assessed variation in the structure of a single aquatic food web that can be effectively and  
93 thoroughly sampled over a large geographic scale: the invertebrate food web associated with the pitcher  
94 plant *Sarracenia purpurea* L. (Buckley *et al.*, 2003). Each of the cupped leaves of this plant holds up to  
95 ~50 ml of water and supports a small, but fully-functional detritus-based food web of insect larvae, other  
96 aquatic invertebrates (most commonly mites, rotifers, and copepods), protozoa, and microbes; captured  
97 insect prey is the resource base for this donor-controlled food web (Addicott, 1974; Butler *et al.*, 2008).  
98 The *Sarracenia* food web has been an ideal model system for experimental studies of the effects of prey  
99 resources (Kneitel & Miller, 2002; Miller *et al.*, 2002; Butler *et al.*, 2008; Hoekman, 2010a), predators  
100 (Addicott, 1974; Miller *et al.*, 2003; Kneitel, 2007), habitat structure (Ellison *et al.*, 2003), habitat volume  
101 (Gotelli & Ellison, 2006), and climate change (Hoekman, 2010b) on food web dynamics. Perhaps most  
102 importantly for the results presented here, the *Sarracenia* food web has remarkably high similarity in  
103 species composition of macroinvertebrates across the entire range of the host plant (Buckley *et al.*, 2003;  
104 2010). Finally, because this food web is spatially constrained within the small pools of rainwater that  
105 collects in *Sarracenia* pitchers, it is easy to thoroughly sample the organisms in replicated webs.

106 We analyze an extensive “snapshot” data set of 780 *Sarracenia* webs sampled in 2001 from 39  
107 sites throughout North America (western Canada to the Florida panhandle; Fig.1). Previous analyses of  
108 this data set have established geographic trends in species richness, composition, and abundance of  
109 individual taxa (Buckley *et al.*, 2003; 2010). Here, we turn our focus to network structure and metrics that  
110 summarize linkages and interactions among species within the *Sarracenia* food web. We calculated four  
111 categories of metrics: those related to complexity, food chain length, types of taxa, and variation in

112 trophic strategy (Table 1). We explore how the network structure of the *Sarracenia* food web varies  
113 systematically with broad-scale climate variables that are correlated with latitudinal patterns of species  
114 richness in this food web (e.g. mean temperature, annual precipitation), concentrations of nutrients from  
115 atmospheric nitrogen deposition that limit plant (= food web habitat) growth (Ellison, 2006), plant size  
116 and shape (Ellison & Gotelli, 2002; Ellison *et al.*, 2004), and three additional potential predictors of food  
117 web structure (resource availability, ecosystem size, and the abundances of a potential keystone species).

118         We developed predictions of how food web structure would be related to known drivers (Post,  
119 2002). Although Post's (2002) framework specifically addresses measures of food chain length, we  
120 extended our analysis to several measures of food web complexity (Table 1). This is justified by the fact  
121 that many of the secondary consumers and top predators in the *Sarracenia* food web are omnivores (Fig.  
122 2) and as a result, measures of food chain length and complexity are highly correlated in this system  
123 (Table 2, Fig. 3). Furthermore, in an analysis of 14 well-studied webs (Vermatt *et al.* 2009), food chain  
124 length, the proportion of omnivores, and several measures of web complexity were positively correlated.  
125 Our first prediction is that food chain length and complexity of the *Sarracenia* food web will increase  
126 with potential resource availability (measured by microbial abundance, which is sensitive to prey inputs;  
127 Kneitel & Miller, 2002; Miller *et al.*, 2002; Hoekman, 2010a). Second, chain length and complexity will  
128 increase with habitat volume (measured as the volume of fluid in an individual pitcher plant leaf; Spencer  
129 & Warren, 1996; Post *et al.*, 2000; Gotelli & Ellison, 2006). Third, atmospheric nitrogen deposition,  
130 which alters leaf morphology such that pitchers have smaller openings and tubes (Ellison & Gotelli,  
131 2002), will decrease chain length and complexity. Fourth, we predict that chain length and complexity  
132 will increase with the presence of the larvae of the pitcher-plant mosquito, *Wyeomyia smithii* (Coq.), an  
133 important filter-feeding predator in this system (Cochran-Stafira & von Ende, 1998; Kneitel & Miller,  
134 2002; Gotelli & Ellison, 2006; Peterson *et al.*, 2008).

135         In addition to these predictors of food web structure, we also determined what percentage of the  
136 variance in food web structure could be accounted for by a suite of broad-scale climatic variables (List

137 and definitions of climate variables available in appendix S1) that are highly correlated with latitude  
138 across our study sites. In the *Sarracenia* food web, total species richness is greater at higher latitudes that  
139 generally experience lower and more variable temperatures along with lower and more variable amounts  
140 of precipitation (Buckley *et al.*, 2003; 2010). We predict that food chain length and complexity will  
141 increase with latitude due to the greater probability of omnivore and top predator presence in high latitude  
142 species-rich webs. Our final prediction is based on the previous finding that within-site compositional  
143 turnover shows an inverse relationship with latitude (Buckley *et al.*, 2010). We predict that within-site  
144 variability in web structure will track compositional turnover and increase at lower latitudes due to the  
145 lack of trophic redundancy in the low latitude species-poor pools (Baiser & Lockwood 2011).

## 146 **METHODS**

### 147 **The *Sarracenia* food web**

148 The food web inhabiting the aquatic microhabitat in the leaves of the northern pitcher plant is comprised  
149 of microbes, protozoa, the bdelloid rotifer *Habrotrocha rosa* Donner (Bledzki & Ellison, 2003), and a  
150 suite of obligate arthropods: the mite *Sarraceniopus gibsoni* (Nesbitt), and aquatic larvae of the pitcher-  
151 plant mosquito *Wyeomyia smithii*, the midge *Metriocnemus knabi* (Coq.) and the sarcophagid fly  
152 *Fletcherimyia fletcheri* (Aldrich) (Addicott, 1974). Less common members of this assemblage include  
153 loriculate rotifers, cladocerans, copepods, amphipods, nematodes, and multicellular algae (Addicott, 1974;  
154 Harvey & Miller, 1996; Hamilton *et al.*, 2000; Bledzki & Ellison, 2003).

155         Feeding interactions in the *Sarracenia* food web center on a detritus “processing chain”  
156 (Bradshaw and Creelman, 1984; Heard, 1994). Prey items that are captured by the plant are shredded by  
157 the midge and the sarcophagid fly into particulate organic matter (POM). Bacteria directly decompose  
158 prey items and also consume POM. Bacteria are preyed upon by a suite of intraguild predators including  
159 protozoa, rotifers, *Wyeomyia smithii*, and *Fletcherimyia fletcheri* (Fig. 2). *W. smithii*, and late instar *F.*  
160 *fletcheri* are the top predators in this 5-level food web (Fig. 2).



161 **Data collection**

162 We sampled 20 pitchers at each of 39 sites for a total of 780 pitchers across the range of *S. purpurea* (Fig.  
163 1). We determined the abundances of invertebrates, rotifers, protozoa, and bacteria in each pitcher. We  
164 counted and identified all invertebrates in each pitcher and rotifers and protozoa in 0.1-mL sub-samples  
165 using a phase-contrast scope at 100 $\times$ . Protozoa were identified to genus where possible and unidentified  
166 protozoa were not used in food web calculations (there were 16 unknown protozoa, 13 of which occurred  
167 in less than 2% of pitchers and three which occurred in 6-18 % of pitchers). Bacterial abundances were  
168 estimated using serial dilutions ( $10^{-5}$  and  $10^{-7}$ ) for each leaf and plating out samples on half-strength Luria  
169 broth agar. Thus, only plate culturable bacteria were included and identified by colony morphotypes. We  
170 calculated the density of the aforementioned taxonomic groups as abundance/mL in each pitcher. In total,  
171 75 taxa were included in web calculations (see food web metrics below). We determined latitude for each  
172 site using the satellite global positioning system and recorded the total volume of pitcher fluid for each  
173 pitcher (see Buckley *et al.*, 2003 and 2010 for details on site selection, leaf selection, sampling protocol,  
174 and a complete list of species found in all food webs).

175 **Food web metrics**

176 Feeding interactions (hereafter links) between the species of the *Sarracenia* food web were assigned  
177 based on previous studies (Addicott, 1974; Forsyth & Robertson, 1975; Heard, 1994; Cochran-Stafira &  
178 von Ende, 1998; Miller *et al.*, 2002; Butler *et al.*, 2008) and direct observation. We constructed an  $n \times 2$   
179 matrix for each of the 780 food webs, where the  $n$  rows are the number links; the first column of the  
180 matrix contains the predator species identity and the second column contains the prey species identity for  
181 each link. We used Network3D (Williams, 2010) to calculate a suite of 15 metrics that characterize  
182 complexity, chain length, type of taxa, and variation in trophic strategy for the *Sarracenia* food web  
183 (Table 1). Because metrics for most well studied food webs co-vary to some degree (Vermatt *et al.*,

184 2009), we used principal components analysis (prcomp in R version 2.11.1; R Development Core Team,  
185 2010) to account for covariance structure of the food web metrics.

## 186 **Nitrogen data**

187 Pitcher plants receive atmospheric N (in the form of  $\text{NH}_4$  and  $\text{NO}_3$ ) from rain and snowmelt that fill the  
188 pitchers. This atmospheric deposition can affect pitcher morphology and habitat structure for the food  
189 web (Ellison & Gotelli, 2002), and pitcher plant population dynamics (Gotelli & Ellison, 2002). We  
190 estimated deposition levels at each sampling site during the year of the survey to investigate these  
191 potential effects on food web structure. We used nitrogen deposition from National Atmospheric  
192 Deposition Data (NADP) monitoring stations that were closest to our sample sites in the United States  
193 (Fig. 1); deposition data for Canada are comparatively sparse and geographically distant from our sample  
194 sites. Therefore, for consistency, we estimated N deposition (total N =  $\text{NH}_4$  +  $\text{NO}_3$  as precipitation-  
195 weighted mean concentration in mg/L) at all our sites (i.e. United States + Canadian sites) in the summer  
196 quarter (July-September) using the AURAMS model (Moran *et al.*, 2008) and used this estimate as a  
197 predictor variable for all sites in our analyses of *Sarracenia* food webs. The estimates for United States  
198 sites were well-correlated with empirical NADP data ( $r = 0.66$ ,  $p < 0.0001$ ), and we assumed similar  
199 accuracy for Canadian sites. Further details on modeling N deposition are given in appendix S2.

## 200 **Climate Data**

201 Spatially referenced climate data for all sites were obtained using the program ANUSPLIN from the  
202 Landscape Analysis and Application Section of the Canadian Forest Service (McKenney *et al.*, 2006).  
203 Climate data for points nearest to the study site locations were queried in ArcGIS 9.0. We included 10  
204 climate variables that quantify precipitation and temperature across our 39 sites (Appendix S1). The 10  
205 climate variables and latitude were highly correlated (see appendix S3 for correlation matrix). To account  
206 for the interdependency of these measures, we conducted a principal components analysis (prcomp in R  
207 version 2.11.1; R Development Core Team, 2010) and used the first two principal components axis (PC1

208 and PC2) as predictor variables. Climate variables and latitude were transformed to standard deviation  
209 units for the principal components analysis. To insure that any one climate variable did not account for  
210 the majority of the variation in a given food web metric, we ran a set of preliminary univariate regressions  
211 with each climate variable, latitude, PC1, and PC 2 as predictor variables and food web metrics as  
212 response variables. We ranked models using the Akaike Information Criterion (AIC), and used the AIC  
213 score to select the best fitting model(s) among the candidate set (Burnham & Anderson, 2002). If any  
214 single climate variable had a  $\Delta AIC < 2$  when compared to the first primary component axis (PC1), we  
215 selected that climate variable for further consideration in the regression models described below. If no  
216 single variable distinguished itself as a better fit ( $\Delta AIC < 2$ ) than PC1, PC1 was selected for further  
217 consideration in the regression models described below. PC1 was the climate variable used in regression  
218 models for all but one case.

219

## 220 **Data analyses**

### 221 *Pitcher scale*

222 We used linear mixed effects models (function 'lme' in package 'nlme' in R v.2.11.1) to assess the  
223 influence of predictor variables on food web structure for the 780 individual pitchers (the pitcher scale of  
224 analysis). We used food web metrics as response variables, site as a random effect, and PC1, pitcher  
225 volume, nitrogen deposition, mosquito abundance, and bacterial abundance as fixed effects for the  
226 pitcher-scale analyses.

227 We built a set of candidate models for each response variable that included a null model (i.e.  
228 random intercept only), global model (with random intercept and all predictor variables entered),  
229 univariate models for each predictor variable, and all subsets of variables that had a  $P$ -value  $< 0.1$  for the  
230 slope coefficient in both the global and univariate models (model structure is given in appendix S4). We  
231 ranked models using the Akaike Information Criterion (AIC), and used the AIC score to select the best

232 fitting model(s) among the candidate set (Burnham & Anderson, 2002). We calculated the variance  
233 explained ( $R^2$ ) by the fixed effects in this mixed-effects model using Xu's (2003) method (see appendix  
234 S5 for calculation).

### 235 *Site scale*

236 Variation in species richness and compositional turnover are greater within sites than across sites in the  
237 *Sarracenia* food web (Buckley *et al.*, 2010). Therefore, to measure variation in food web structure within  
238 sites, we calculated the coefficient of variation (CV) of each web metric in the 20 webs at each of our 39  
239 sites (site scale). We term this measure *structural turnover* and use it in the same sense as compositional  
240 turnover (i.e.  $\beta$ -diversity). High structural turnover means that when moving from one web to the next we  
241 are likely to encounter different network structure; high structural turnover results in a high CV at that  
242 site. Low structural turnover (measured as a low CV) means that web structure is similar from pitcher to  
243 pitcher within a single site.

244 We used linear models (lm in R v.2.11.1) to assess the influence of predictor variables on  
245 structural turnover at each of our 39 sites. We regressed structural turnover (the CV of each food web  
246 metric for the 20 pitchers at each of the 39 sites) on PC1, and the CVs of pitcher volume, mosquito  
247 abundance, and bacterial abundance. The model for the food web metric Top included the climate  
248 variable CV of precipitation instead of PC1 based on the climate variable model selection (See Climate  
249 Data). We used the CV of pitcher volume, mosquito abundance, and bacterial abundance for this analysis  
250 because we were interested in how pitcher-to-pitcher variation of predictor variables within each site was  
251 correlated with pitcher-to-pitcher variation in food web metrics across all pitchers within each site.

252 We built a set of candidate models for each response variable that included a global model,  
253 univariate models for each predictor variable, and all subsets of variables that had a  $P$ -value  $< 0.1$  for the  
254 slope coefficient in both the global and univariate models. We ranked models using the Akaike  
255 Information Criterion (AIC), and used this score to select the best fitting model(s) among the candidate

256 set (Burnham & Anderson, 2002). We calculated the adjusted  $R^2$  to determine the proportion of variance  
257 explained by each model.

### 258 *Predictor variables*

259 The correlations among predictor variables had correlation coefficients  $< 0.4$ . All variables were  
260 transformed into standard deviation units (positive values indicate observations that were greater than the  
261 mean and negative values were less than the mean) for the pitcher-scale analyses except for PC1. N  
262 deposition was also transformed to standard deviation units for the site-scale analyses.

263

## 264 **RESULTS**

### 265 **Principal components analysis of pitcher-scale variation in food web metrics**

266 The first two principal components explained 70% of the variation in network structure for the set of 780  
267 *Sarracenia* food webs. The first principal axis (PC1) explained 45% of the variation and was related to  
268 complexity and chain length. This axis was negatively correlated with metrics related to complexity (e.g.  
269 connectance, species richness, links per species) and chain length (e.g. mean trophic level, chain length)  
270 (Table 2). Percentage of omnivores and intermediate species were also negatively correlated with PC1  
271 (Table 2). Webs with negative scores on PC1 were species-rich and contained many omnivores, which  
272 increased chain length, linkage density, and connectance (Fig 3a). PC1 was positively correlated with the  
273 percentage of top species in a web, the percentage of detritivores in the web, variation in the number of  
274 consumers and links per taxon, and the mean path length across the network (Table 2). An example of a  
275 web with a high positive PC1 score contains only detritivores (e.g. bacteria), which are all top species in  
276 this context (Fig. 3b). The second principal axis (PC2) explained 25% of the variation and was related to  
277 trophic redundancy and variation in prey and predator strategies. Webs with a positive score for PC2 (Fig.  
278 3c) tended to have more species, and these species were intermediate detritivore species (i.e. bacteria) and

279 had higher trophic similarity and greater variation in the number of prey per taxon (Table 2). Webs on the  
280 negative side of this axis (Fig. 3d) had fewer species and the species that dropped out were bacteria.

### 281 **Principal components analysis of climate variables and latitude**

282 The first two principal components explained 92% of the climatic variation across our 39 sites. The first  
283 principal axis (PC1) explained 78% of the variation. Sites with high scores on this axis were at high  
284 latitudes, had short growing seasons with low mean temperatures and precipitation, and had high annual  
285 variation in both of these variables (Table 3). Sites representative of these conditions were located in the  
286 northern US and Canada (Fig. 1). Sites with low scores are located at low latitudes and experience higher  
287 mean temperatures and precipitation, but lower variability in both variables (Table 3). These sites are  
288 located in the south-eastern US. PC2 explained 14% the climatic variation across our 39 sites. Sites with  
289 positive scores had a high mean diurnal temperature range.

290

### 291 **Resource availability, food chain length, and food web complexity**

292 The hypothesized positive relationships between resource availability measured as bacterial abundance  
293 and measures of complexity and chain length were not observed. Bacterial abundance showed no  
294 relationship with any of the food web metrics at either the pitcher or site scale and was absent from all  
295 best-fit models (Tables 4 and 5).

### 296 **Habitat size, food chain length, and food web complexity**

297 Pitcher volume, which is a measure of ecosystem size, was positively correlated with the number of links  
298 per species, species richness, mean trophic level, chain length, and the percent of omnivores, and was  
299 negatively correlated with variation in links per species at the pitcher scale (Table 4). At the site scale,  
300 variation in pitcher volume was positively correlated with structural turnover in the clustering coefficient  
301 (Table 5; Fig. 4d). As predicted, we observed increases in several measures of web complexity with  
302 ecosystem size at the pitcher scale and increases in structural turnover with the CV of ecosystem size at

303 the site scale. However, chain length increased with ecosystem size only at the pitcher scale and showed  
304 no relationship with variation in pitcher volume at the site scale.

### 305 **Nitrogen deposition, food chain length, and food web complexity**

306 Nitrogen deposition, which was predicted to have a negative effect on complexity and chain length  
307 metrics, showed no relationship with food web metrics and was not a significant predictor in any of the  
308 best-fitting models.

### 309 **Predator-prey interactions, food chain length, and food web complexity**

310 Mosquito abundance was not correlated with food web structure at the pitcher scale. However, variation  
311 in mosquito abundance at the site scale was positively correlated with structural turnover in two measures  
312 of chain length – mean trophic level and mean chain length (Table 4; Fig 4 a, b). Although the  
313 hypothesized relationship between mosquito abundance and chain length was observed at the site scale,  
314 food web complexity did not increase with mosquito abundance at the pitcher scale and variation in  
315 mosquito abundance within site did not increase structural turnover in complexity metrics.

### 316 **Biogeographic correlates of food chain length, and food web complexity**

317 PC1, which is positively correlated with latitude (Table 3) was present in all of the best-fitting models  
318 that explained more than 5% of the variation in food web structure (Tables 4, 5). At the pitcher scale, PC1  
319 was positively correlated with two measures of food web complexity – linkage density and species  
320 richness. Species richness was shown to follow the same patterns and increase with latitude in previous  
321 analyses of these data (Buckley *et al.*, 2003; 2010). Structural turnover at the site scale showed a  
322 consistent negative relationship with PC1 for more than half of the food web metrics measured (Table 5;  
323 Fig. 5). Thus, variation in food web structure within sites was greater at lower latitudes.

324 Overall, network structure of the *Sarracenia* food web was only weakly influenced by all  
325 predictor variables at the pitcher scale across 780 webs. The best-fit models left a large portion (> 95%)

326 of the variance in food web structure unexplained at the pitcher scale (Table 4). At the site scale, predictor  
327 variables explained more (8% –35%) variance in structural turnover in food webs (Table 5).

## 328 **DISCUSSION**

329 Ecosystem size has been associated with increased chain length in both aquatic (Spencer &  
330 Warren, 1996; Post, 2000; McHugh *et al.*, 2010) and terrestrial (Takimoto *et al.*, 2008) ecosystems. Our  
331 measure of ecosystems size, pitcher volume had a positive effect on both measures of chain length and  
332 measures of food web complexity, linkage density, species richness, and the percentage of omnivores in  
333 the web. Previous research on this data set has shown that species richness of arthropods, rotifers, and  
334 bacteria all increase with pitcher volume (Buckley *et al.*, 2010). Our results suggest that as species  
335 richness increases with pitcher volume, an increasing number of omnivores are added to the web.  
336 Omnivores feed on more than one trophic level resulting in a wider diet breadth which increases linkage  
337 density. Omnivore presence increases measures of chain length because the majority of omnivores in the  
338 *Sarracenia* food web feed at high trophic levels.

339 Resource availability showed no relationship with food web structure at the pitcher or site scales.  
340 One possibility why the predicted relationship was not observed is that bacterial abundance is not an  
341 appropriate measure for resource availability. The true resources are prey items that are captured by the  
342 plant. Although a bottom-up effect of prey abundance on bacterial abundance has been demonstrated  
343 repeatedly in the *Sarracenia* system (Kneitel & Miller, 2002; Miller *et al.*, 2002; Hoekman, 2010a), it is  
344 possible that bacterial abundance is a poor surrogate for resource availability due to sampling effects (i.e.  
345 only a fraction of the bacterial species can be cultured) or because abundance may not reflect productivity  
346 because of ongoing consumption of bacteria by higher trophic levels.

347 Although mosquito abundance had no effect on food web structure at the pitcher scale, increased  
348 variation in mosquito abundance between pitchers was positively correlated with structural turnover in  
349 chain length and mean trophic level within sites. Mosquito larval density varied from 0 to over 11 larvae



350 per ml. The simple presence of *W. smithii* can increase metrics related to chain length (Kitching, 2001;  
351 Post & Takimoto, 2007), or at high densities, extirpate intermediate consumers through predation  
352 (Addicott, 1974; Kneitel, 2007), concomitantly decreasing chain length. Mosquito abundance was not  
353 related to any measures of food web complexity, suggesting that the observed keystone effects of  
354 increased bacterial and protozoan diversity (Cochran-Stafira & von Ende, 1998; Peterson *et al.*, 2008)  
355 were not manifested in food web metrics related to complexity (consistent with Kneitel and Miller, 2002).

356         The ability to assess the influence of broad-scale climatic variables on food web structure was a  
357 novel aspect of this study. No single climate variable explained variation in food web structure due to  
358 colinearity among climate variables. Instead, PC1, which was derived from a suite of climate variables,  
359 captured latitudinal variation in temperature and precipitation across our sites and allowed us to  
360 specifically test predictions related to the biogeographic patterns of species richness and compositional  
361 turnover in the *Sarracenia* food web (Buckley *et al.*, 2003; 2010). Our original prediction was that  
362 metrics related to chain length and complexity would increase with latitude. Specifically, we found that  
363 the complexity metric linkage density increased with latitude and this was most likely due to higher  
364 species richness of arthropods and rotifers (which represent 75% of the omnivores in the species pool) at  
365 higher latitudes (Buckley *et al.*, 2003; 2010). We also confirmed the prediction that structural turnover  
366 would follow the same pattern as compositional turnover and have an inverse relationship with latitude  
367 (Buckley *et al.*, 2010). Increased compositional and structural turnover at lower latitudes implies that  
368 when certain species drop out of the web they are either replaced by a trophically different species, or not  
369 replaced at all. A positive correlation between compositional turnover and structural turnover is likely  
370 when communities are assembled from a species pool with low functional or trophic redundancy (Baiser  
371 & Lockwood, 2011). As a result, when a new species is added to a web it likely represents a new trophic  
372 strategy and hence an alteration in network structure.

373         Few other studies have examined broad-scale correlates of food web structure over such a large  
374 spatial scale. The *Sarracenia* web may be exceptional because the species pool of macroinvertebrates is

375 invariant over a large geographic area (Buckley et al., 2010). However, our results provide a general  
376 framework for understanding how patterns of compositional turnover and species richness influence  
377 variation in food web. If species are replaced by trophically unique species or not at all, as in the case of  
378 the low latitude *Sarracenia* food webs, compositional and structural turnover may be tightly linked. If a  
379 species pool has high trophic redundancy, species replacements will be trophically similar and food web  
380 structure may be conserved independent of compositional turnover. The degree to which both trophic  
381 redundancy is related to the richness of a species pool and patterns of species richness are correlated with  
382 broad-scale variables, are important factors in understanding the relationship between food web structure  
383 and biogeography. Trophic or functional redundancy within a given web mitigates against secondary  
384 extinctions (Borvall et al. 2000) and trophically redundant species are less vulnerable to cascading  
385 extinctions (Petchey et al. 2009). Trophic redundancy in the regional species pool may have a similarly  
386 stabilizing effect on food web structure as species composition turns over.

387 Overall, our results show that the commonly observed relationship between ecosystem size and  
388 food chain length (Spencer & Warren, 1996; Post, 2000; Takimoto *et al.*, 2008; McHugh *et al.*, 2010) is  
389 extended to several measures of network structure in the *Sarracenia* food web and that biogeographic  
390 patterns of species richness and compositional turnover influence food web structure. However, our  
391 predictor variables leave a large portion of variability in food web structure unexplained. We suggest that  
392 stochastic assembly processes related to dispersal and arrival order and timing of propagules (Knietal and  
393 Miller, 2003; Chase, 2010) that are not captured in our snapshot data set may be the driving influence of  
394 food web structure in the *Sarracenia* system. A study assessing assembly trajectory is necessary to  
395 explicitly test the hypothesis that stochastic assembly processes are the main determinant of network  
396 structure in the *Sarracenia* food web.

397

398

399 **ACKNOWLEDGEMENTS**

400 We thank Mike Moran and Junhua Zhang (Environment Canada, Air Quality Research Division) for  
401 providing nitrogen deposition estimates for our sites using their AURAMS model. Support for this  
402 research was provided by NSF grants 0083617 to TEM, AME, and NJG, and 0541680 to AME.

403

404 **REFERENCES**

- 405 Addicott, J.F. (1974) Predation and prey community structure: an experimental study of the effect of  
406 mosquito larvae on the protozoan communities of pitcher plants. *Ecology*, **55**, 475–492.
- 407 Arim, M., Bozinovic, F. & Marquet, P.A. (2007) On the relationship between trophic position, body mass  
408 and temperature: reformulating the energy limitation hypothesis. *Oikos*, **116**, 1524–1530.
- 409 Baiser, B. & Lockwood, J. L. (2011) The relationship between functional and taxonomic homogenization.  
410 *Global Ecology and Biogeography*, **20**, 134–144.
- 411 Beckerman, A.P., Petchey, O.L. & Warren, P.H. (2006) Foraging biology predicts food web complexity.  
412 *Proceedings of the National Academy of Sciences USA*, **103**, 13745–13749.
- 413 Bledzki, L.A. & Ellison, A.M. (2003) Diversity of rotifers from northeastern USA bogs with new species  
414 records for North America and New England. *Hydrobiologia*, **385**, 193–200.
- 415 Bradshaw, W.E. & Creelman, R.A. (1984) Mutualism between the carnivorous purple pitcher plant  
416 *Sarracenia purpurea* and its inhabitants. *American Midland Naturalist*, **112**, 294–304.
- 417 Bradshaw, W.E., Holzapfel, C.M., Kleckner, C.A. & Hard, J.J. (1997) Heritability of development time  
418 and protandry in the pitcher-plant mosquito, *Wyeomia smithii*. *Ecology*, **78**, 969–976.
- 419 Buckley, H. L., Miller, T., Ellison, A. M. & Gotelli, N. J. (2003) Reverse latitudinal trends in species  
420 richness of pitcher-plant food webs. *Ecology Letters*, **6**, 825–829.
- 421 Buckley, H. L., Miller, T. E., Ellison, A. M. and Gotelli, N. J. (2010) Local- to continental-scale variation  
422 in the richness and composition of an aquatic food web. *Global Ecology and Biogeography*,  
423 **19**, 711–723.
- 424 Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference: a Practical*  
425 *Information Theoretic Approach*, 2nd edn. Springer-Verlag, New York.
- 426 Butler, J. L., & Ellison, A. M. (2007) Nitrogen cycling dynamics in the carnivorous northern pitcher  
427 plant, *Sarracenia purpurea*. *Functional Ecology*, **21**, 835–843.

428 Butler, J.L., Gotelli, N.J. & Ellison, A.M. (2008) Linking the brown and green: nutrient transformation  
429 and fate in the *Sarracenia* microecosystem. *Ecology*, **89**, 898–904.

430 Camacho, J., Guimer`a, R. & Amaral, L.A.N. (2002) Robust patterns in food web structure. *Physical*  
431 *Review Letters*, **88**, 228102.

432 Chase, J.M. (2010). Stochastic community assembly causes higher biodiversity in more productive  
433 environments. *Science*, 328, 1388–1391.

434 Cochran-Stafira, D.L. & von Ende, C.N. (1998) Integrating bacteria into food webs: studies with  
435 *Sarracenia purpurea* inquilines. *Ecology*, **79**, 880–898.

436 Dunne, J.A. 2009. *Food webs. in the Complex Networks and Graph Theory section of the Encyclopedia of*  
437 *Complexity and Systems Science*, (ed. Meyers, R.A.) Springer, NewYork. Pages 3661-3682.

438 Dunne, J. A., Williams, R. J. & Martinez, N. D. (2002a) Network structure and biodiversity loss in food  
439 webs: robustness increases with connectance. *Ecology Letters*, **5**, 558–567

440 Dunne, J. A., Williams, R. J. & Martinez, N. D. (2002b) Food-web structure and network theory: the role  
441 of connectance and size. *Proceedings of the National Academy of Sciences USA*, **99**, 12917–  
442 12922.

443 Ellison, A.M. (2006) Nutrient limitation and stoichiometry of carnivorous plants. *Plant Biology*, **8**, 740–  
444 747.

445 Ellison, A.M. & Gotelli, N.J. (2002) Nitrogen availability alters the expression of carnivory in the  
446 northern pitcher plant, *Sarracenia purpurea*. *Proceedings of the National Academy of Sciences*  
447 *USA*, **99**, 4409–4412.

448 Ellison, A.M., Gotelli, N.J., Brewer, J.S., Cochran-Stafira, L., Kneitel, J., Miller, T.E., Worley, A.S. &  
449 Zamora, R. (2003) The evolutionary ecology of carnivorous plants. *Advances in Ecological*  
450 *Research*, **33**, 1–74.

451 Ellison, A.M., Buckley, H.L., Miller, T.E. & Gotelli, N.J. (2004). Morphological variation in *Sarracenia*  
452 *purpurea* (Sarraceniaceae): geographic, environmental, and taxonomic correlates. *American*  
453 *Journal of Botany*, **91**, 1930–1935.

454 Forsyth, A.B. & Robertson, R.J. (1975) *K* reproductive strategy and larval behaviour of the pitcher plant  
455 sarcopagid fly, *Blaesoxipha fletcheri*. *Canadian Journal of Zoology.*, **53**, 174–179.

456 Fretwell, S.D. (1987) Food-chain dynamics: the central theory of ecology. *Oikos*, **50**, 291–301.

457 Gotelli, N.J. & Ellison, A.M. (2002) Nitrogen deposition and extinction risk in the northern pitcher plant,  
458 *Sarracenia purpurea*. *Ecology*, **83**, 2758–2765.

459 Gotelli, N.J. & Ellison, A.M. (2006) Food-web models predict species abundance in response to habitat  
460 change. *PLoS Biology*, **44**, e324.

461 Hairston, N. G., Smith, F. E. & Slobodkin, L. B. (1960) Community structure, population control, and  
462 competition. *American Naturalist*, **94**, 421–425.

463 Hamilton, R., Reid, J. W. & Duffield, R. M. (2000) Rare copepod, *Paracyclops canadensis* (Willey),  
464 common in leaves of *Sarracenia purpurea* L. *Northeastern Naturalist*, **7**, 17–25.

465 Harvey, E. & Miller, T. E. (1996) Variance in composition of inquiline communities in leaves of  
466 *Sarracenia purpurea* L on multiple spatial scales. *Oecologia*, **108**, 562–566.

467 Heard, S. B. (1994) Pitcher plant midges and mosquitoes: a processing chain commensalism. *Ecology*, **75**,  
468 1647–1660.

469 Hoekman, D. (2010a) Relative importance of top-down and bottom-up forces in food webs of *Sarracenia*  
470 pitcher communities at a northern and a southern site. *Oecologia*, DOI: 10.1007/s00442-010-  
471 1802-2.

472 Hoekman, D. (2010b) Turning up the heat: Temperature influences the relative importance of top-down  
473 and bottom-up effects. *Ecology*, **91**, 2819–2825.

474 Jenkins, B., Kitching, R.L. & Pimm S.L. (1992) Productivity, disturbance and food web structure at a  
475 local spatial scale in experimental container habitats. *Oikos*, **65**, 249–255

476 Kaunzinger, C.M.K. & Morin, P.J. (1998) Productivity controls food-chain properties in microbial  
477 communities. *Nature*, **395**, 495–497.

478 Kitching, R.L. (2000) Food webs and container habitats: the natural history and ecology of phytotelmata,  
479 Cambridge University Press, Cambridge.

480 Kitching, R.L. (2001) Food webs in phytotelmata: ‘bottom-up’ and ‘top-down’ explanations for  
481 community structure. *Annual Review of Entomology*, **46**, 729–760.

482 Kneitel J.M. (2007) Intermediate-consumer identity and resources alter a food web with omnivory.  
483 *Journal of Animal Ecology*, **76**, 651–659.

484 Kneitel J.M. & Miller, T.E. (2002) Resource and top-predator regulation in the pitcher plant (*Sarracenia*  
485 *purpurea*) inquiline community. *Ecology*, **83**, 680–688.

486 Kneitel J.M. & Miller, T.E. (2003) Dispersal rates affect species composition in metacommunities of  
487 *Sarracenia purpurea* inquilines. *American Naturalist*, **162**, 165–171.

488 Koopman, M.M., Fuselier, D.M., Hird, S. & Carstens, B.C. (2010) The carnivorous pale pitcher plant  
489 harbors diverse, distinct, and time-dependent bacterial communities. *Applied and Environmental*  
490 *Microbiology*, **76**, 1851-1860.

491 Marks, J.C., Power, M.E. & Parker, M.S. (2000) Flood disturbance, algal productivity, and interannual  
492 variation in food chain length. *Oikos*, **90**, 20–27.

493 Martinez, N.D. (1994) Scale-dependent constraints on food-web structure. *American Naturlist*, **144**, 935–  
494 953.

495 Martinez, N. D. & Lawton, J. H. (1995) Scale and food-web Structure—from local to global. *Oikos*, **73**,  
496 148–154.

497 May, R.M. (1973) *Stability and Complexity in Model Ecosystems*. Princeton University Press, Princeton  
498 NJ.

499 McHugh, P.A., McIntosh, A.R. & Jellyman, P.G. (2010) Dual influences of ecosystem size and  
500 disturbance on food chain length in streams. *Ecology Letters*, **13**, 881–890.

501 McKenney, D., Papadopol, P., Campbell, K., Lawrence, K. & Hutchinson, M. (2006) *Spatial models of*  
502 *Canada– and North America–wide 1971/2000 minimum and maximum temperature, total*  
503 *precipitation and derived bioclimatic variables*. Forestry Research Applications Technical Note  
504 No. 106. Canadian Forest Service, Great Lakes Forestry Centre, Sault Ste. Marie, Canada.

505 Miller, T.E., Horth, L., & Reeves, R.H. (2002) Trophic interactions in the phytotelmata communities of  
506 the pitcher plant, *Sarracenia purpurea*. *Community Ecology*, **3**, 109–116.

507 Miller, T. E. & Kneitel, J. M. (2005) *Inquiline communities in pitcher plants as a prototypical*  
508 *metacommunity*. In *Metacommunities: Spatial Dynamics and Ecological Communities*. (eds.  
509 Holyoak, M., Leibold, M. A. & Holt, R. D) University of Chicago Press, Chicago, pp. 122–145.

510 Moran, M. D., Zheng, Q., Pavlovic, R., Cousineau, S., Bouchet, V. S., Sassi, M., Makar, P. A., Gong, W.  
511 & Stroud, C. (2008) Predicted acid deposition critical-load exceedances across Canada from a  
512 one-year simulation with a regional particulate-matter model. Proc. 15th Joint AMS/A&WMA  
513 Conf. on Applications of Air Pollution Meteorology, 21–24 January, New Orleans, American  
514 Meteorological Society, Boston, 20 pp., online available at: [http://ams.confex.com/  
515 ams/pdfpapers/132916.pdf](http://ams.confex.com/ams/pdfpapers/132916.pdf).

516 Paine, R. T. (1969) The *Pisaster-Tegula* interaction: prey patches, predator food preferences and intertidal  
517 community structure. *Ecology*, **50**, 950–61.

518 Peterson, C.N., Day S., Wolfe, B.E., Ellison, A.M., Kolter R. & Pringle A. (2008) A keystone predator  
519 controls bacterial diversity in the pitcher-plant (*Sarracenia purpurea*) microecosystem.  
520 *Environmental Microbiology*, **10**, 2257–2266.

521 Pimm, S.L. (1982) *Food Webs*. Chapman & Hall, London.

522 Post, D.M. (2002) The long and short of food-chain length. *Trends in Ecology and Evolution*, **17**, 269–  
523 277.

524 Post, D.M. & Takimoto, G. (2007) Proximate structural mechanisms for variation in food-chain length.  
525 *Oikos*, **116**, 775–782.

526 Post, D.M., Pace, M.L. & Hairston, N.G. (2000) Ecosystem size determines food-chain length in lakes.  
527 *Nature*, **405**, 1047–1049.

528 Power, M.E., Parker, M.S. & Wootton, J.T. (1996) *Food webs in space: an island biogeographic*  
529 *perspective*. In: *Food Webs* (eds Polis, G.A. & Winemiller, K.O.). Chapman & Hall, New York,  
530 pp. 286–297.



531 Schmitz, O.J. (2006) Predators have large effects on ecosystem properties by changing plant diversity, not  
532 plant biomass. *Ecology*, **87**, 1432–1437.

533 Schmitz, O.J. (2010) *Resolving Ecosystem Complexity*. Princeton University Press, Princeton.

534 Schoener, T.W. (1989) Food webs from the small to the large. *Ecology*, **70**, 1559–1589.

535 Spencer, M. & Warren, P.H. (1996) The effects of habitat size and productivity on food web structure in  
536 small aquatic microcosms. *Oikos*, **75**, 419–430.

537 Srivastava, D.S., Kolasa, J., Bengtsson, J., Gonzalez, A., Lawler, S.P., Miller, T.E., Munguia, P.,  
538 Romanuk, T., Schneider, D.C. & Trzcinski, M.K. (2004) Are natural microcosms useful model  
539 systems for ecology? *Trends in Ecology and Evolution*, **19**, 379–384.

540 Takimoto, G., Spiller, D.A. & Post, D.M. (2008) Ecosystem size, but not disturbance, determines food-  
541 chain length on islands of the Bahamas. *Ecology*, **89**, 3001–3007.

542 Townsend, C.R., Thompson, R.M., McIntosh, A.R., Kilroy, C., Edwards, E. & Scarsbrook, M.R. (1998)  
543 Disturbance, resource supply, and food-web architecture in streams. *Ecology Letters*, **1**, 200–209.

544 Vermaat, J.E., Dunne, J.A. & Gilbert, A.J. (2009) Major dimensions in foodwebstructure properties.  
545 *Ecology*, **90**, 278–282.

546 Williams, R. J. (2010) Network 3D Software. Microsoft Research, Cambridge, UK.

547 Woodward, G., Papantoniou, G., Edwards, F. & Lauridsen, R. B. (2008) Trophic trickles and cascades in  
548 a complex food web: impacts of a keystone predator on stream community structure and  
549 ecosystem processes. *Oikos*, **117**, 683–692.

550 Xu, R. (2003) Measuring explained variation in linear mixed effects models. *Statistics in Medicine*, **22**,  
551 3527–3541.

552

553

554

555

556

557

558

559

560

561 **BIOSKETCH**

562 **Ben Baiser** is a Postdoctoral Research Associate at Harvard Forest. He has interests in community  
563 ecology, conservation biology, invasion ecology, and understanding the impact of global change on  
564 biodiversity.

565

566

567 **TABLES**

568 Table 1. Definitions of food web metrics. Each metric is assigned a metric “type”. Complexity metrics  
 569 relate to the number of nodes (i.e. species) and links. Chain length metrics relate to the number of trophic  
 570 levels in a web. Type of taxa describes the proportions of taxa found in a given trophic role. Trophic  
 571 strategy relates to variation in the number and similarity of predators and prey among species in a web.

<b>Metric</b>	<b>Type</b>	<b>Definition*</b>
C	Complexity	connectance, or the proportion of possible links realized. $C = L/S^2$ , where L is number of links and S is the number of species
S	Complexity	species richness
LS	Complexity	linkage density = L/S, number of links per species
Clust	Complexity	clustering coefficient, probability that two taxa linked to the same taxon are also linked
Path	Complexity <sup>§</sup>	characteristic path length, the mean shortest set of links (where links are treated as undirected) between species pairs
ChLen	Chain length	mean food chain length, averaged over all species
TL	Chain length	short-weighted trophic level averaged across taxa
Top	Type of taxa	percentage of top species in a web (taxa have no predators)
Int	Type of taxa	percentage of intermediate species in a web (taxa with both predators and prey)
Omn	Type of taxa	percentage of omnivores in a web (taxa that feed on more than one trophic level)
Det	Type of taxa	percentage of detritivores in a web (taxa that feed on Basal resources)
GenSD	Strategy	normalized standard deviation of generality (# resources per taxon)
VulSD	Strategy	normalized standard deviation of vulnerability (# consumers per taxon)
LinkSD	Strategy	normalized standard deviation of links (# links per taxon)
MaxSim	Strategy	mean across taxa of the maximum trophic similarity of each taxon to other taxa

572

573 \*Definitions are taken from Dunn *et al.* (2009) and Vermatt *et al.* (2009). For further information on food  
 574 web metrics, see Dunn *et al.* (2009) and sources therein.

575 <sup>§</sup>Path is negatively correlated with complexity.

576

577

578

579

580 Table 2. Factor loadings for the first two principal components axis (PC1 and PC2) describing variation in  
581 food web structure. PC1 explained 45% of the variation and PC2 explained 25%. See Table 1 for web  
582 metric definitions.

<b>Web Metric</b>	<b>PC1</b>	<b>PC2</b>
S	-0.21	0.31
LS	-0.30	0.20
C	-0.33	-0.18
Top	0.20	-0.32
Int	-0.23	0.36
Det	0.27	0.33
Omn	-0.29	-0.02
GenSD	0.06	0.45
VulSD	0.32	-0.10
LinkSD	0.29	0.24
TL	-0.33	-0.03
MaxSim	-0.10	0.36
Path	0.25	0.30
Clust	-0.25	0.01
ChLen	-0.28	0.001

583

584 Table 3. Factor loadings for the first two principal components axis (PC1 and PC2) describing climatic  
 585 variation across our 39 sites. PC1 explained 78% of the variation and PC2 explained 14%. PC1 describes  
 586 latitudinal variation in temperature and precipitation. Sites with high scores on this axis were at high  
 587 latitudes, had short growing seasons with low mean temperatures and precipitation, and had high annual  
 588 variation in both of these variables. Sites representative of these conditions were located in the northern  
 589 US and Canada (Fig. 1). Sites with low scores are located at low latitudes and experience higher mean  
 590 temperatures and precipitation, but lower variability in both variables. Climate variables are defined in  
 591 Appendix S1.

<b>Variable</b>	<b>PC1</b>	<b>PC2</b>
MDT	-0.04304	0.722233
CVMT	0.334351	0.06211
ATR	0.32642	0.141781
Ap	-0.30974	-0.24194
CVp	0.219126	0.425786
GR	-0.32155	0.209303
MT	-0.33032	0.176812
MMINT	-0.33329	0.118973
MMXT	-0.32543	0.230974
MMONP	-0.30975	-0.2419
Lat	0.332285	-0.11618

592  
 593  
 594  
 595  
 596  
 597  
 598

599

600 Table 4. Top ranked mixed models with site as a random effect describing network structure for the  
 601 *Sarracenia* food web. Metrics for which the top model was the null model (intercept only) or where the  
 602  $\Delta AIC < 2$  between the null model and the top model are not included. See Table 1 for web metric  
 603 definitions.

<b>Web Metric</b>	<b>Variable</b>	<b>Estimate (SE)</b>	<b>t-value</b>	<b>p-value</b>	<b>R<sup>2</sup>*</b>
<b>LS</b>	Intercept	2.95 (0.05)	55.19	<0.001	0.05
	PC1	0.07 (0.02)	3.57	<0.01	
	Vol	0.26 (0.04)	7.26	<0.001	
<b>S</b>	Intercept	10.76 (0.18)	59.19	<0.001	0.05
	PC1	0.24 (0.06)	3.85	<0.001	
	Vol	0.82 (0.12)	7.01	<0.001	
<b>TL</b>	Intercept	2.12 (0.008)	256.07	<0.001	0.04
	Vol	0.03 (0.005)	6.02	<0.001	
<b>ChLen</b>	Intercept	2.08 (0.007)	277.73	<0.001	0.04
	Vol	0.03 (0.005)	5.93	<0.001	
<b>Omn</b>	Intercept	0.27 (0.007)	35.96	<0.001	0.04
	Vol	0.03 (0.005)	5.78	<0.001	
<b>LinkSD</b>	Intercept	0.29 (0.01)	32.02	<0.001	0.02
	Vol	-0.03 (0.007)	3.82	<0.001	

604

605 \* R<sup>2</sup> calculated using the methods of Xu (2003) for assessing the fit of mixed models.

606

607 Table 5. Top ranked linear models describing structural turnover (CV of food web metrics) for the  
 608 *Sarracenia* food web. Only models significant at a P-value of 0.05 with an adjusted  $R^2 \geq 0.05$  are shown.  
 609 See Table 1 for web metric definitions.

610

<b>Web Metric</b>	<b>Variable</b>	<b>Estimate (SE)</b>	<b>t-value</b>	<b>p-value</b>	<b>adj-R<sup>2</sup></b>
<b>ChLen</b>	Intercept	0.04 (0.004)	10.0	<0.001	0.35
	PC1	-0.003 (0.004)	-3.86	<0.001	
	Mosq	0.008 (0.002)	3.43	<0.01	
<b>TL</b>	Intercept	0.05 (0.005)	10.15	<0.001	0.33
	PC1	-0.003 (0.001)	-3.98	<0.001	
	Mosq	0.008 (0.003)	2.93	<0.01	
<b>Clust</b>	Intercept	0.18 (0.09)	2.07	<0.05	0.33
	PC1	-0.03 (0.008)	-3.24	<0.01	
	Vol	0.34 (0.14)	2.40	<0.05	
<b>Omn</b>	Intercept	0.44 (0.02)	18.17	<0.001	0.18
	PC1	-0.03 (0.008)	-3.03	<0.01	
<b>LS</b>	Intercept	0.31 (0.01)	24.63	<0.001	0.15
	PC1	-0.01 (0.004)	-2.75	<0.01	
<b>Int</b>	Intercept	0.20 (0.01)	14.58	<0.001	0.12
	PC1	-0.01 (0.005)	2.47	<0.05	
<b>Det</b>	Intercept	0.20 (0.007)	29.89	<0.001	0.11
	PC1	-0.006 (0.002)	-2.40	<0.05	
<b>S</b>	Intercept	0.27 (0.01)	26.82	<0.001	0.09
	PC1	-0.008 (0.004)	2.19	<0.05	
<b>MaxSim</b>	Intercept	0.06(0.004)	13.68	<0.001	0.08
	PC1	-0.003(0.001)	-2.05	<0.05	

611

612

613

614 **FIGURE LEDGENDS**

615 Figure 1. Map showing the 39 sites where *Sarracenia* food webs were sampled (solid circles) and  
616 National Atmospheric Deposition (NADP) sites (open circles) used for modeling nitrogen deposition.

617 Figure 2. Main components of the *Sarracenia* food web. Captured prey is shredded by both midge  
618 (*Metriocnemus knabi*) and flesh fly (*Fletcherimyia fletcheri*) larvae into particulate organic matter (POM)  
619 and directly decomposed by Bacteria. Bacteria also feed on POM along with mites (*Sarraceniopus*  
620 *gibsoni*) and rotifers (*Habrotrocha rosa*). Bacteria is consumed by protozoa, rotifers (which also prey on  
621 protozoa), all of which are preyed upon by the top predators the larvae of the mosquito *Wyeomyia smithii*  
622 and the sarcophagid fly *F. fletcheri*. *Fletcherimyia larvae* are cannibalistic and also prey upon on first-  
623 and second-instar *W. smithii* larvae. This is an aggregated general version of the pitcher plant web. For  
624 topological representation of actual webs see the inlay of Fig. 3.

625 Figure 3. Principal components analysis of food web metrics (See Table 1 for web metric definitions.)  
626 calculated for 780 *Sarracenia* food webs. Component 1 is related to complexity and chain length and  
627 component 2 is related to trophic redundancy and variation in prey and predator strategies. These two  
628 components explain 70% of the variation in *Sarracenia* food web structure. Inlay, four networks (a,b,c,d)  
629 representing the extremes of each axis. For these four food webs, arrows are drawn from their position in  
630 the PCA plot to the food web. White nodes represent the resource (dead prey items), grey nodes represent  
631 bacteria, and black nodes represent consumers.

632 Figure 4. Univariate models showing the relationship between variables (other than latitude) and  
633 structural turnover (CV of food web metrics) for the *Sarracenia* food web at the site-scale ( $P < 0.05$  for all  
634 models). See Table 1 for web metric definitions.



635 Figure 5. Univariate models showing the relationship between PC1 and structural turnover (i.e. variation  
636 in network structure between webs within each site as measured by the CV of each food web metric) for  
637 the *Sarracenia* food web at the site-scale. Structural turnover significantly decreased ( $P < 0.05$ ) with PC1  
638 and thus latitude for a) Chain Length, b) Mean Trophic Level, c) Clustering Coefficient, d) % Omnivores,  
639 e) Linkage Density, f) % Intermediate species, g) % Detritivores, h) Species Richness, and i) Maximum  
640 Trophic Similarity.

641

642

643

644

645

646

647

648

649

650

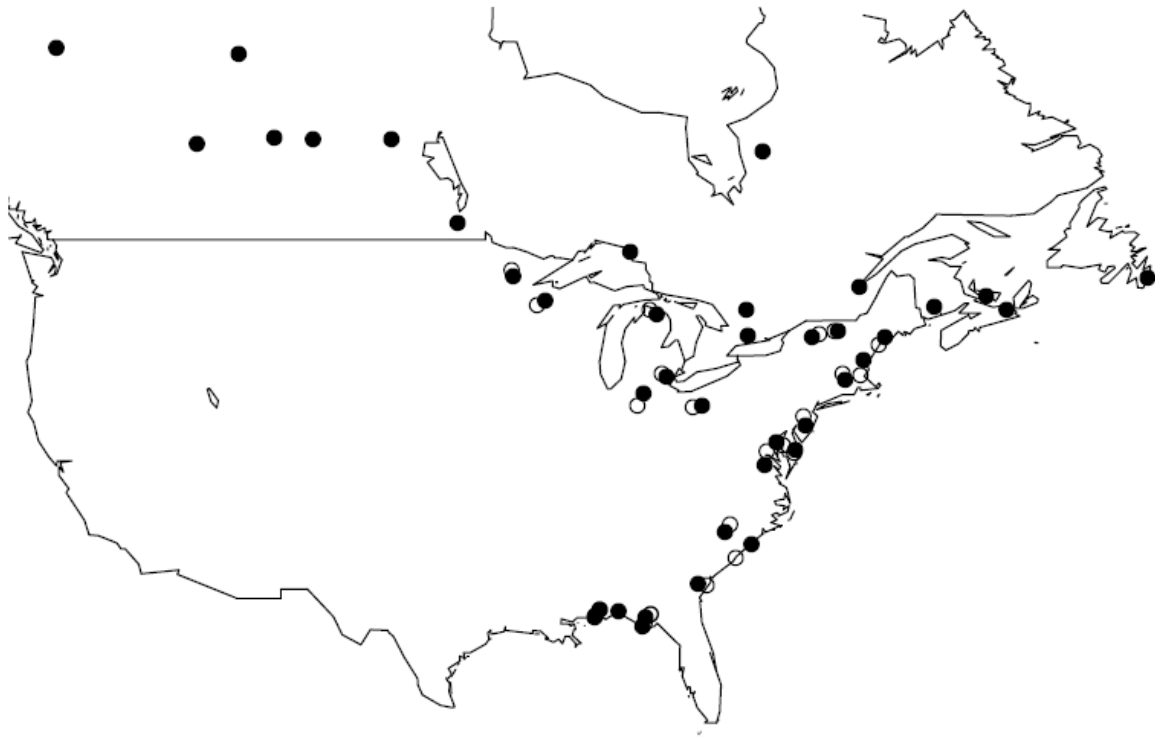
651

652

653

654

655 Figure 1.



656

657

658

659

660

661

662

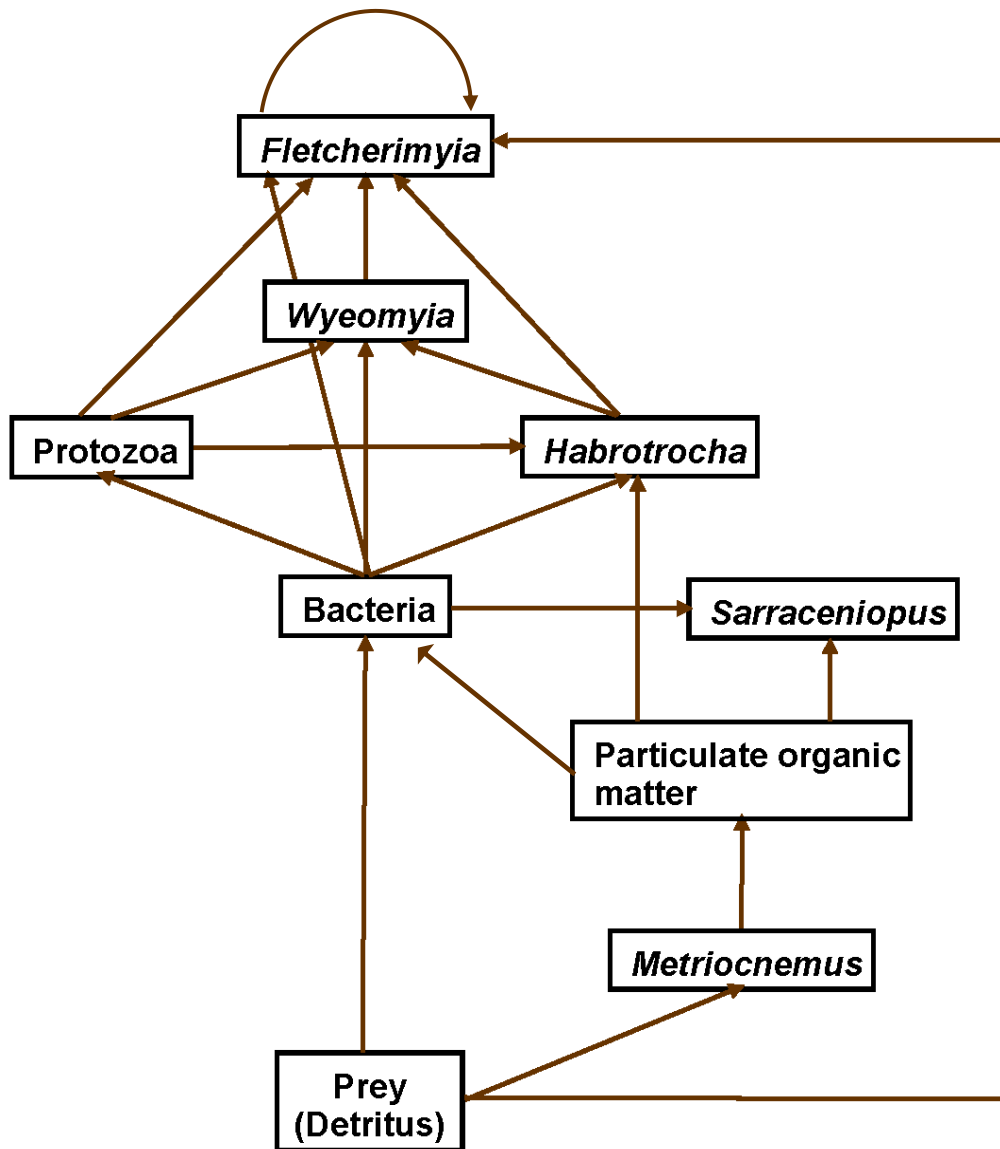
663

664

665

666

667 Figure 2.



668

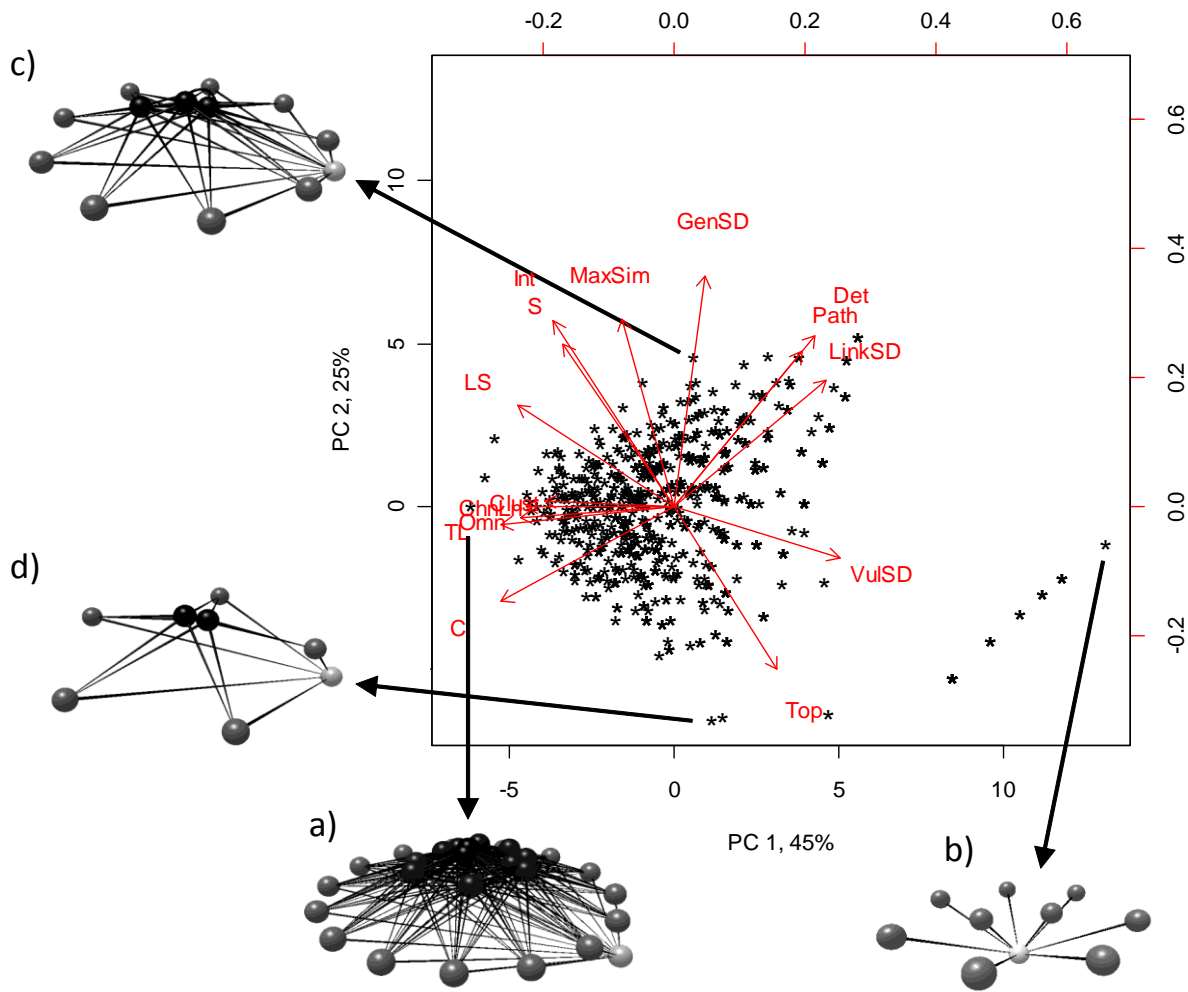
669

670

671

672

673 Figure 3.



674

675

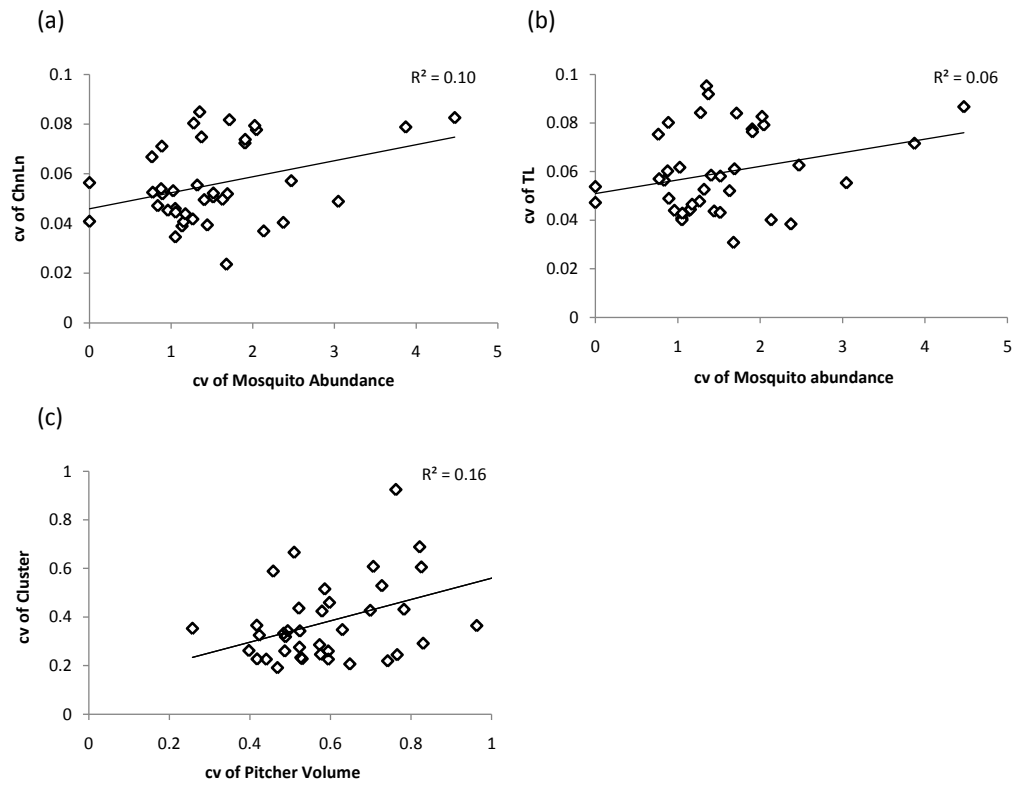
676

677

678

679

680 Figure 4.



681

682

683

684

685

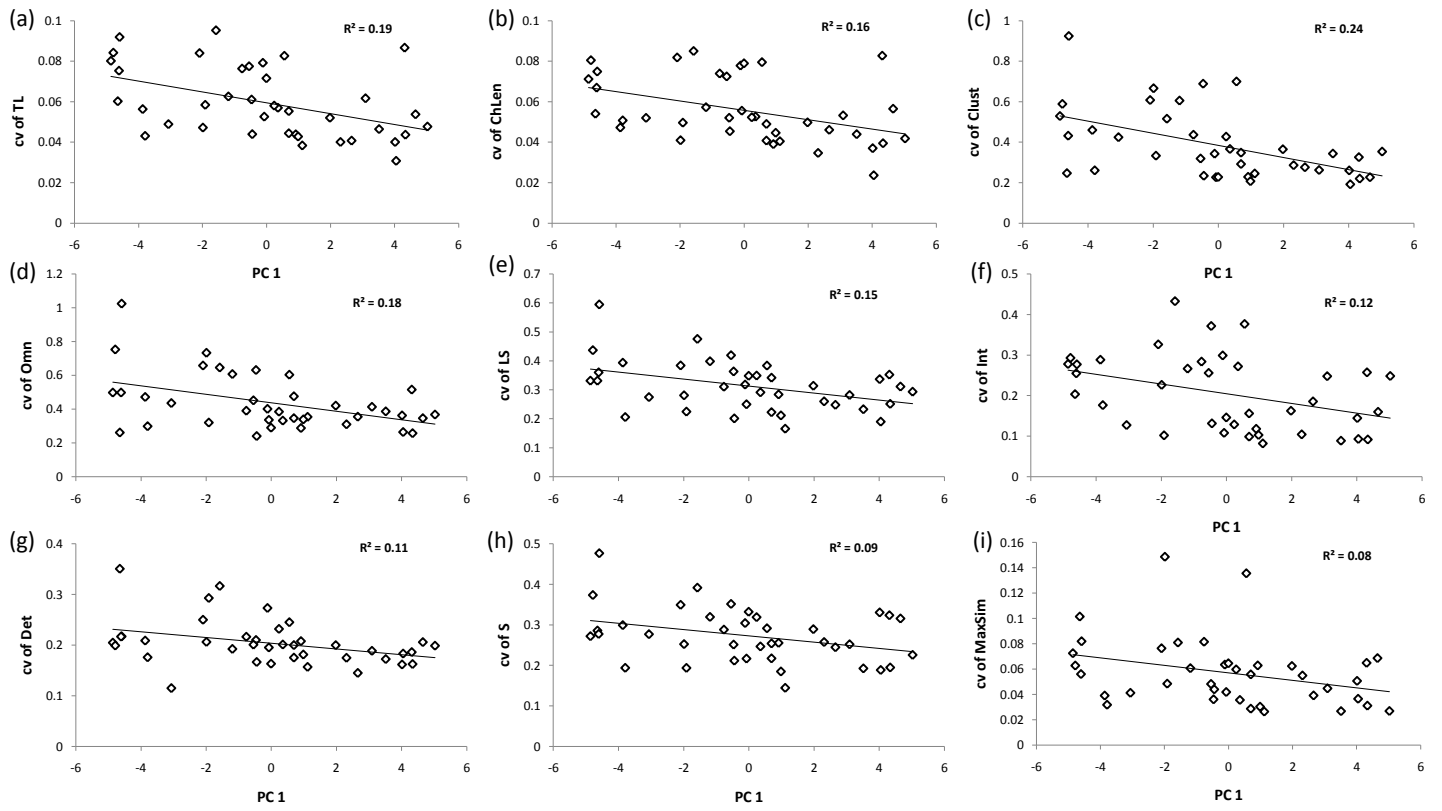
686

687

688

689

690 Figure 5



691

692

693 **Appendix S1**

694 **Climate variables (and latitude) used in climate variable principal components analysis and**  
695 **regressions. See <http://cres.anu.edu.au/outputs/anuclim.php> for further information about climate**  
696 **variables.**

697 MT = Annual Mean Temperature

698 MDTR = Mean Diurnal Range (Mean of monthly (max temp - min temp))

699 CVMT = Temperature Seasonality (Coefficient of Variation)

700 MMXT = Mean Max Temperature

701 MMINT = Mean Min Temperature

702 ATR = Temperature Annual Range

703 GR- Growing Season Days

704 AP = Annual Precipitation

705 MMONP= Mean Monthly Precipitation

706 CVP = Precipitation Seasonality (Coefficient of Variation)

707 Lat= Latitude

708

709

710

711

712

713

714

715

716

717

718

719 **Appendix S2**

720 **Methods for modeling nitrogen deposition.**

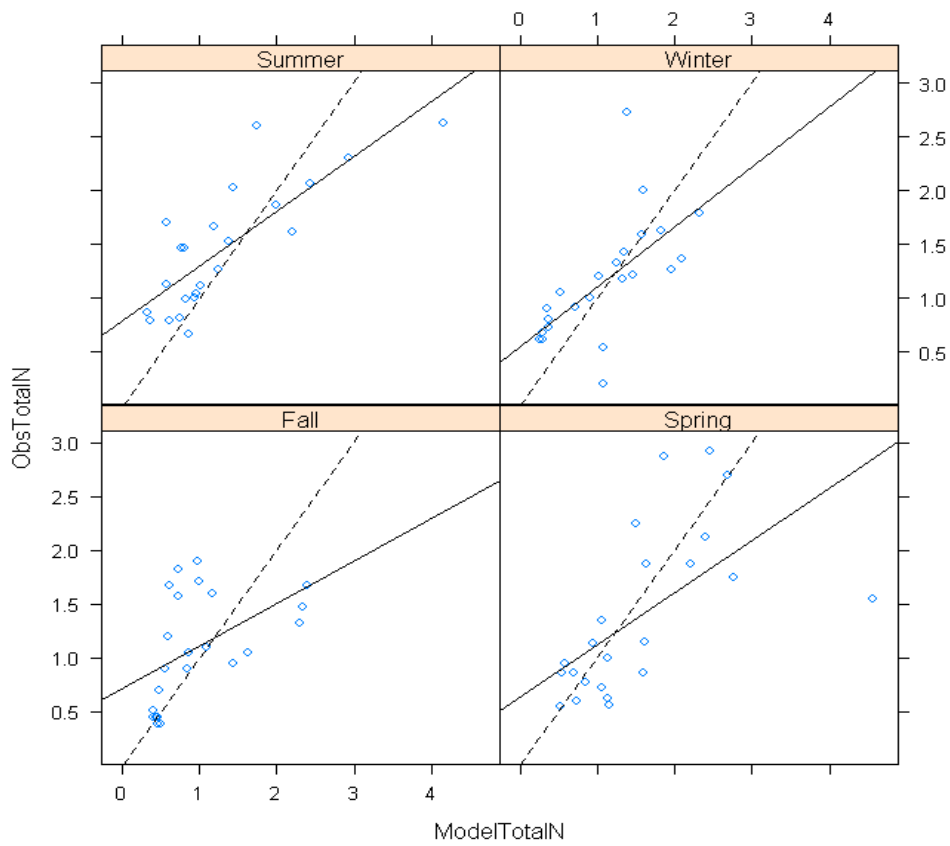
721 Data on nitrogen deposition were available through National Atmospheric Deposition Data (NADP)  
722 network only for sites in the United States (Fig. 1). Therefore, we used modeled depositional data for all  
723 sites (i.e. including Canadian sites) provided by the AURAMS model (Moran *et al.* 2008). To estimate  
724 the accuracy of the modeled data, we used linear regression to compare available empirical data from the  
725 NADP sites with the modeled data. Where possible, NADP data were from 2001, the year in which  
726 sampling occurred. When stations were not active during 2001, we used the closest full calendar year  
727 data. Modeled data are for 2002 since NADP data ranged from 2001-2004. NADP and modeled  
728 depositional data are quarterly totals of  $\text{NH}_4$  and  $\text{NO}_3$  in mg/L (precipitation-weighted mean  
729 concentration). We used the total nitrogen deposition ( $\text{N} = \text{NH}_4 + \text{NO}_3$ ) for the summer quarter (July-  
730 September) as a predictor variable in our analyses of *S. purpurea* food webs. The modeled data was a  
731 good fit to the NADP data ( $R^2=0.43$ , p-value  $<0.0001$ ).

732

733

734





735

736

737 Figure 1. Quarterly/seasonal comparison of observed NAPD data for pitcher plant sites in the US with  
 738 modeled data from the AURAMS model (Moran *et al.* 2008). The observed regression line is solid and  
 739 the dotted line is a 1:1 relationship.

740

741

742

743

744

745 **Appendix S3**

746 **Correlations among climate variables and latitude.** Analysis conducted using function ‘r.corr.test’ in  
 747 package ‘ltm’ in R v.2.11.1. The upper diagonal part contains correlation coefficient estimates and the  
 748 lower diagonal part contains corresponding p-values. Climate variables are defined in Appendix S1.

749

	<b>MT</b>	<b>MDT</b>	<b>CVMT</b>	<b>MMINT</b>	<b>MMXT</b>	<b>GR</b>	<b>ATR</b>	<b>Ap</b>	<b>CVp</b>	<b>MMONP</b>	<b>Lat</b>
<b>MT</b>	*****	0.274	-0.926	0.997	0.997	0.987	-0.891	0.783	-0.488	0.783	-0.974
<b>MDT</b>	0.091	*****	-0.051	0.195	0.348	0.28	0.082	-0.093	0.231	-0.092	-0.255
<b>CVMT</b>	<0.001	0.759	*****	-0.94	-0.907	-0.892	0.987	-0.9	0.644	-0.9	0.927
<b>MMINT</b>	<0.001	0.234	<0.001	*****	0.987	0.982	-0.916	0.807	-0.518	0.807	-0.972
<b>MMXT</b>	<0.001	0.03	<0.001	<0.001	*****	0.985	-0.862	0.755	-0.457	0.755	-0.97
<b>GR</b>	<0.001	0.084	<0.001	<0.001	<0.001	*****	-0.863	0.748	-0.418	0.748	-0.946
<b>ATR</b>	<0.001	0.619	<0.001	<0.001	<0.001	<0.001	*****	-0.898	0.634	-0.898	0.881
<b>Ap</b>	<0.001	0.575	<0.001	<0.001	<0.001	<0.001	<0.001	*****	-0.708	1	-0.833
<b>CVp</b>	0.002	0.158	<0.001	0.001	0.003	0.008	<0.001	<0.001	*****	-0.708	0.577
<b>MMONP</b>	<0.001	0.576	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	*****	-0.833
<b>Lat</b>	<0.001	0.117	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	*****

750

751

752

753

754

755

756

757

758

759

760

761

762 **Appendix S4**

763 **Mixed effect models for the pitcher-scale analysis using function ‘lme’ in package ‘nlme’ in R**

764 **v.2.11.1.**

765 Random intercept only model (null model):

- 766 • `summary(NULL <- lme(webmetric~1 , random = ~1|Site, data = web))`

767 Global Model:

- 768 • `summary(Global <- lme(webmetric~ Lat + Long + Elev + Vol + N + Mosq + Bact, random =`  
769 `~1|Site,data = web))`

770 Univariate Model:

- 771 • `summary(Univariate <- lme(webmetric~ Vol, random = ~1|Site,data = web))`

772

773

774

775

776

777

778

779

780

781

782

783 **Appendix S5**

784 Xu's (2003) method for calculating the variance explained ( $R^2$ ) by the fixed effects in a mixed-effects

785 model. The residual variance from the model with fixed effects ( $Var_{fixed}$ ) is divided by residual variance of

786 a model containing only the random effect (i.e. null model) ( $Var_{null}$ ). This quotient is subtracted from one.

787

$$R^2 = 1 - \left( \frac{Var_{fixed}}{Var_{null}} \right)$$