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RESEARCH PAPER

Geographic variation in network structure of a nearctic aquatic food web

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ABSTRACT

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

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

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

Results At the scale of a single pitcher plant leaf, linkage density, species richness, measures of chain length and the proportion of omnivores in a web all increased with pitcher volume. Linkage density and species richness were greater at high-latitude sites, which experience low mean temperatures and precipitation and high annual variation in both of these variables. At the site scale, variation in 8 of the 15 food web metrics decreased at higher latitudes, and variation in measures of chain length increased with the abundance of mosquitoes.

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

Keywords

Chain length, climate, food web, keystone predation, network structure, North America, pitcher plant, *Sarracenia purpurea*.

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INTRODUCTION

Understanding the causes and consequences of food web structure is a central focus of community ecology (Hairston *et al.*, 1960; May, 1973; Pimm, 1982; Fretwell, 1987; Beckerman *et al.*, 2006; Schmitz, 2010). Experimental studies have documented that food web structure is influenced by ecosystem size (Spencer & Warren, 1996; Post *et al.*, 2000; Takimoto *et al.*, 2008; McHugh *et al.*, 2010), the presence of keystone predators (Paine, 1969; Woodward *et al.*, 2008), disturbance (Power *et al.*, 1996; Marks *et al.*, 2000; McHugh *et al.*, 2010), productivity (Townsend *et al.*, 1998; Arim *et al.*, 2007) and the availability of nutrients and resources (Jenkins *et al.*, 1992; Kaunzinger & Morin, 1998). Literature compilations and meta-analyses of studies of food web structure have also demonstrated that many food web metrics are scale-dependent (Schoener, 1989; Martinez, 1994; Martinez & Lawton, 1995), that web connectance (the proportion of possible links realized) is constrained between 0.03 and 0.33 (Dunne *et al.*, 2002a) and that food webs generally do not exhibit small-world network properties (Camacho *et al.* 2002; Dunne *et al.*, 2002b). However, it is difficult to infer general mechanisms from the results of single field experiments or meta-analyses because of differences in the spatial and temporal scale of the different studies, and differences in the collection, processing and modelling of the raw data.

Here, we adopt a third strategy for understanding the control of food web structure. We test previously proposed correlations of food web structure with replicate observations of a single food web sampled at different geographic sites in North America spanning a broad latitudinal and climatic range. We examine associations between metrics of food web structure, climatic variables related to precipitation and temperature, and potential causal variables such as nutrient inputs, ecosystem size and the abundance of potential keystone species. Taking such an approach in North American lakes, Post *et al.* (2000) showed that the length of the food chain is positively correlated with ecosystem size. Similarly, Schmitz (2006, 2010) used old-field food webs to show that trophic structure and adaptive foraging influence the nitrogen mineralization rate, plant biomass production and the supply rate of solar radiation. On the other hand, Kitching (2000) found no relationship between tree-hole size and food web structure in Australian tree-hole communities. However, this kind of replicated sampling of a single food web is uncommon because the composition of food webs normally varies extensively across sites, the large spatial extent of most food webs makes it difficult or even impossible to sample all the organisms and their feeding interactions in replicated food webs, and the spatial boundaries of most local food webs are often arbitrary and poorly defined.

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

We analyse an extensive ‘snapshot’ data set of 780 *Sarracenia* webs sampled in 2001 from 39 sites throughout North America (western Canada to the Florida panhandle; Fig. 1). Previous analyses of this data set have established geographic trends in species richness, composition and abundance of individual taxa (Buckley *et al.*, 2003, 2010). Here, we turn our focus to network structure and metrics that summarize linkages and interactions among species within the *Sarracenia* food web. We calculated four categories of metrics: those related to complexity, food chain length, types of taxa and variation in trophic strategy (Table 1). We explore how the network structure of the *Sarracenia* food web varies systematically with broad-scale climate variables (e.g. mean temperature, annual precipitation), concentrations of nutrients from atmospheric nitrogen deposition that limit plant (= food web habitat) growth (Ellison, 2006), plant size and shape (Ellison & Gotelli, 2002; Ellison *et al.*, 2004) and three additional potential predictors of food web structure (resource availability, ecosystem size and the abundances of a potential keystone species).

We developed predictions of how food web structure would be related to known drivers (Post, 2002). Although Post’s (2002) framework specifically addresses measures of food chain length, we extended our analysis to several measures of food web complexity (Table 1). This is justified by the fact that many of the secondary consumers and top predators in the *Sarracenia* food web are omnivores (Fig. 2) and, as a result, measures of food chain length and complexity are highly correlated in this system (Table 2, Fig. 3). Furthermore, in an analysis of 14 well-studied webs (Vermaat *et al.*, 2009), food chain length, the proportion of omnivores and several measures of web complexity were positively correlated. Our first prediction is that food chain length and complexity of the *Sarracenia* food web will increase with potential resource availability (measured by microbial abundance, which is sensitive to prey inputs; Kneitel & Miller, 2002; Miller *et al.*, 2002; Hoekman, 2010a). Second, food chain length and complexity will increase with habitat volume (measured as the volume of fluid in an individual pitcher plant leaf; Spencer & Warren, 1996; Post *et al.*, 2000; Ellison, 2006). Third, atmospheric nitrogen deposition, which alters leaf morphology such

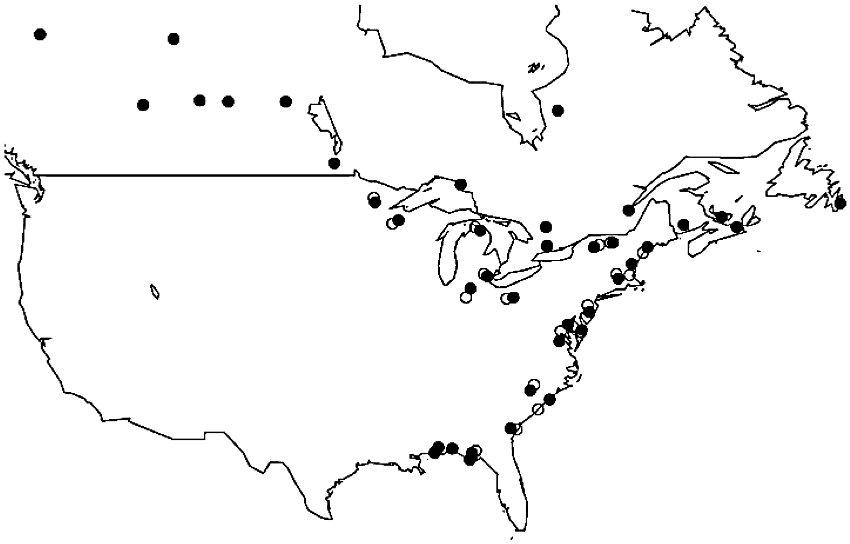

Figure 1 Map showing the 39 sites where *Sarracenia* food webs were sampled (solid circles) and National Atmospheric Deposition (NADP) sites (open circles) used for modelling nitrogen deposition.

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

Metric	Type	Definition*
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†	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 (no. of resources per taxon)
VulSD	Strategy	Normalized standard deviation of vulnerability (no. of consumers per taxon)
LinkSD	Strategy	Normalized standard deviation of links (no. of links per taxon)
MaxSim	Strategy	Mean across taxa of the maximum trophic similarity of each taxon to other taxa

*Definitions are taken from Dunne (2009) and Vermaat *et al.* (2009). For further information on food web metrics see Dunne (2009) and sources therein.
†Path is negatively correlated with complexity.

that pitchers have smaller openings and tubes (Ellison & Gotelli, 2002), will decrease food chain length and complexity. Fourth, food chain length and complexity will increase with the presence of the larvae of the pitcher-plant mosquito, *Wyeomyia smithii* (Coq.), an important filter-feeding predator in this system (Cochran-Stafira & von Ende, 1998; Kneitel & Miller, 2002; Ellison, 2006; Peterson *et al.*, 2008).

In addition to testing these predictions regarding food web structure, we also determined what percentage of the variance in food web structure could be accounted for by a suite of broad-scale climatic variables (a list of climate variables is available in Table 3 and Appendix S1 in Supporting Information). Climatic variables are highly correlated with biogeographic patterns of species richness across several taxa (Currie, 1991; Hawkins *et al.*, 2003). In the *Sarracenia* food web, total species richness is greater at higher latitudes that generally experience lower and more variable temperatures along with lower and more variable amounts of precipitation (Buckley *et al.*, 2003, 2010). We predict that food chain length and complexity will increase with latitude due to the greater probability of the presence of omnivores and top predators in high-latitude species-rich webs. Our final prediction is based on the previous finding that within-site com-

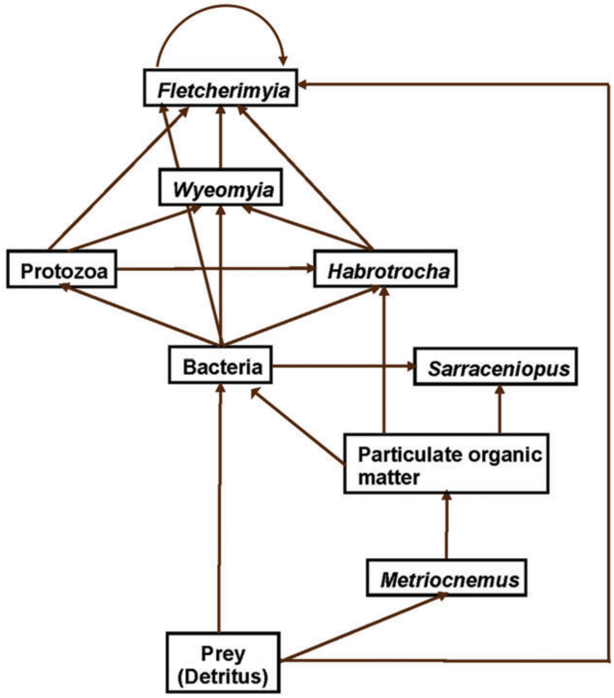

Figure 2 Main components of the *Sarracenia* food web. Captured prey is shredded by both midge (*Metriocnemus knabi*) and flesh fly (*Fletcherimyia fletcheri*) larvae into particulate organic matter (POM) and directly decomposed by bacteria. Bacteria also feed on POM along with mites (*Sarraceniopus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

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

Web metric	PC1	PC2
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

positional turnover shows an inverse relationship with latitude (Buckley *et al.*, 2010). We predict that within-site variability in food web structure will track compositional turnover and increase at lower latitudes due to the lack of trophic redundancy in the low-latitude species-poor pools (Baiser & Lockwood, 2011).

METHODS

The *Sarracenia* food web

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

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

Data collection

We sampled 20 pitchers at each of 39 sites for a total of 780 pitchers across the range of *S. purpurea* (Fig. 1). We determined the abundances of invertebrates, rotifers, protozoa and bacteria in each pitcher. We counted and identified all invertebrates in each pitcher and rotifers and protozoa in 0.1-ml subsamples using a phase-contrast microscope at 100×. Protozoa were identified to genus where possible and unidentified protozoa were not used in food web calculations (there were 16 unknown protozoa, 13 of which occurred in fewer than 2% of pitchers and three which occurred in 6–18% of pitchers). Bacterial abundances were estimated using serial dilutions (10^{-5} and 10^{-7}) for each leaf and plating out samples on half-strength Luria broth agar. Thus, only plate-culturable bacteria were included and identified by colony morphotypes. We calculated the density of the aforementioned taxonomic groups as abundance/ml in each pitcher. In total, 75 taxa were included in web calculations (see Food web metrics below). We determined the latitude for each site using the satellite global positioning system and recorded

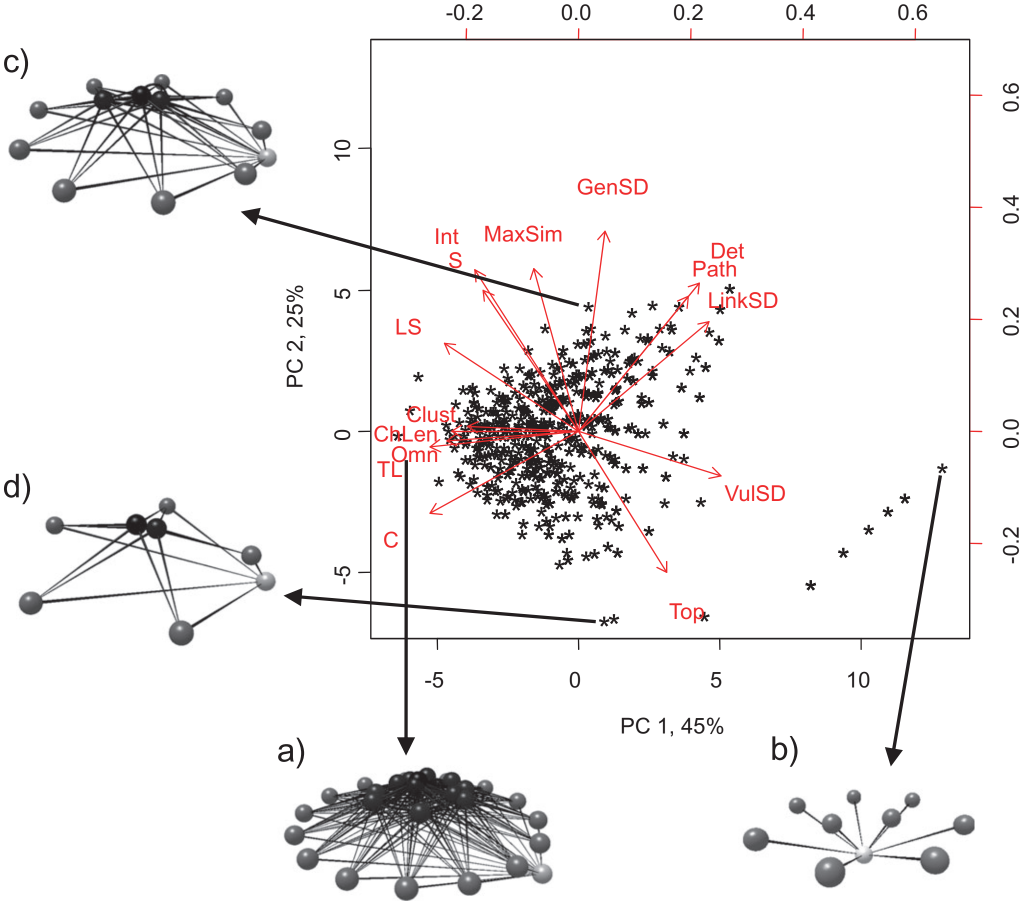

Figure 3 Principal components analysis (PCA) of food web metrics (see Table 1 for web metric definitions) calculated for 780 *Sarracenia* food webs. Component 1 is related to complexity and chain length and component 2 is related to trophic redundancy and variation in prey and predator strategies. These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

the total volume of pitcher fluid for each pitcher (see Buckley *et al*., 2003, 2010, for details on site selection, leaf selection, sampling protocol and a complete list of species found in all food webs).

Food web metrics

Feeding interactions (hereafter links) between the species of the *Sarracenia* food web were assigned based on previous studies (Addicott, 1974; Forsyth & Robertson, 1975; Heard, 1994; Cochran-Stafira & von Ende, 1998; Miller *et al*., 2002; Butler *et al*., 2008) and direct observation. We constructed an $n \times 2$ matrix for each of the 780 food webs, where the n rows are the number links; the first column of the matrix contains the predator species identity and the second column contains the prey species identity for each link. We used NETWORK3D (Williams, 2010) to calculate a suite of 15 metrics that characterize complexity, chain length, type of taxa and variation in trophic strategy for the *Sarracenia* food web (Table 1). Because metrics for most well-studied food webs co-vary to some degree (Vermaat *et al*., 2009), we used principal components analysis (prcomp in R version 2.11.1; R Development Core Team, 2009) to account for the covariance structure of the food web metrics.

Nitrogen data

Pitcher plants receive atmospheric nitrogen (in the form of NH_4 and NO_3) from the rain and snowmelt that fill the pitchers. This atmospheric deposition can affect pitcher morphology and habitat structure for the food web (Ellison & Gotelli, 2002) and pitcher plant population dynamics (Gotelli & Ellison, 2002). We estimated deposition levels at each sampling site during the year of the survey to investigate these potential effects on food web structure. We used nitrogen deposition from National Atmospheric Deposition Data (NADP) monitoring stations that were closest to our sample sites in the United States (US; Fig. 1); deposition data for Canada are comparatively sparse and geographically distant from our sample sites. Therefore, for consistency, we estimated nitrogen deposition (total $N = NH_4 + NO_3$ as precipitation-weighted mean concentration in mg l^{-1}) at all our

Table 3 Factor loadings for the first two principal components axes describing climatic variation across our 39 sites (C-PC1 and C-PC2). C-PC1 explained 78% of the variation and C-PC2 explained 14%. C-PC1 describes latitudinal variation in temperature and precipitation. Sites with high scores on this axis were at high latitudes, had short growing seasons with low mean temperatures and precipitation, and had high annual variation in both of these variables. Sites representative of these conditions were located in the northern US and Canada (Fig. 1). Sites with low scores are located at low latitudes and experience higher mean temperatures and precipitation, but lower variability in both variables. Climatic variables are defined in Appendix S1. See http://cres.anu.edu.au/outputs/anuclim.php for further information about climatic variables.

Variable	C-PC1	C-PC2
Mean diurnal temp. range	–0.04	0.72
Temperature seasonality	0.33	0.06
Temperature annual range	0.33	0.14
Annual precipitation	–0.31	–0.24
Precipitation seasonality	0.22	0.43
Growing season days	–0.32	0.21
Annual mean temperature	–0.33	0.18
Mean min. temperature	–0.33	0.12
Mean max. temperature	–0.33	0.23
Mean monthly precipitation	–0.31	–0.24
Latitude	0.33	–0.12

sites (i.e. US + Canadian sites) in the summer quarter (July–September) using the AURAMS model (Moran *et al.*, 2008) and used this estimate as a predictor variable for all sites in our analyses of *Sarracenia* food webs The estimates for US sites were well-correlated with empirical NADP data ($r = 0.66$, $P < 0.0001$), and we assumed similar accuracy for Canadian sites. Further details on modelling nitrogen deposition are given in Appendix S2.

Climatic data

Spatially referenced climatic data for all sites were obtained using the program ANUSPLIN from the Landscape Analysis and Application Section of the Canadian Forest Service (McKenney *et al.*, 2006). Climate data for points nearest to the study site locations were queried in ArcGIS 9.0. We included 10 climate variables that quantify precipitation and temperature across our 39 sites (Appendix S1). The 10 climate variables and latitude were highly correlated (see Appendix S3 for correlation matrix). To account for the interdependency of these measures, we conducted a principal components analysis (prcomp in R version 2.11.1; R Development Core Team, 2009) and used the first two principal components axes (which we refer to as C-PC1 and C-PC2) as predictor variables. Climate variables and latitude were transformed to standard deviation units for the principal components analysis. To ensure that any one climate variable did not account for the majority of the variation in a given food web metric, we ran a set of preliminary univariate regressions with each climate variable, latitude, C-PC1 and C-PC2 as predictor variables and food web metrics as response variables. We ranked models using the Akaike information criterion (AIC), and used the AIC score to select the best fitting model(s) among the candidate set (Burnham & Anderson, 2002). If any single climate variable, latitude or C-PC2 had a ΔAIC < 2 when compared with C-PC1 we selected that variable for further consideration in the regression models described below. If no single variable distinguished itself as a better fit (ΔAIC < 2) than C-PC1, then C-PC1 was selected for further consideration in the regression models described below. C-PC1 was the climate variable used in regression models for all but one case.

Data analyses

Pitcher scale

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

We built a set of candidate models for each response variable that included a null model (i.e. random intercept only), global model (with random intercept and all predictor variables entered), univariate models for each predictor variable and all subsets of variables that had a P-value < 0.1 for the slope coefficient in both the global and univariate models (model structure is given in Appendix S4). We ranked models using the AIC, and used the AIC score to select the best fitting model(s) among the candidate set (Burnham & Anderson, 2002). We calculated the variance explained (R^2) by the fixed effects in mixed-effects models using Xu's (2003) method (see Appendix S5 for calculation).

Site scale

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

We used linear models (lm in R v.2.11.1) to assess the influence of predictor variables on structural turnover at each of our 39 sites. We regressed structural turnover (the CV of each food web metric for the 20 pitchers at each of the 39 sites) on C-PC1, and the CVs of pitcher volume, mosquito abundance and bacterial abundance. The model for the food web metric 'Top' (see Table 1 for definition) included the climate variable CV of precipitation instead of C-PC1 based on the climate variable model selection (see Climatic data). We used the CV of pitcher volume, mosquito abundance and bacterial abundance for this analysis because we were interested in how pitcher-to-pitcher variation of predictor variables within each site was correlated with pitcher-to-pitcher variation in food web metrics across all pitchers within each site.

We built a set of candidate models for each response variable that included a global model, univariate models for each predictor variable and all subsets of variables that had a P-value < 0.1 for the slope coefficient in both the global and univariate models. We ranked models using the AIC, and used this score to select the best fitting model(s) among the candidate set (Burnham & Anderson, 2002). We calculated the adjusted R^2 to determine the proportion of variance explained by each model.

Predictor variables

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

RESULTS

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

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

Principal components analysis of climatic variables and latitude

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

Resource availability, food chain length, and food web complexity

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

Habitat size, food chain length and food web complexity

Pitcher volume, which is a measure of ecosystem size, was positively correlated with the number of links per species, species richness, mean trophic level, chain length and the percentage of omnivores, and was negatively correlated with variation in links per species at the pitcher scale (Table 4). At the site scale, variation in pitcher volume was positively correlated with structural turnover in the clustering coefficient (Table 5; Fig. 4c). As predicted, we observed increases in several measures of web complexity with ecosystem size at the pitcher scale and increases in structural turnover with the CV of ecosystem size at the site scale. However, chain length increased with ecosystem size only at the pitcher scale and showed no relationship with variation in pitcher volume at the site scale.

Nitrogen deposition, food chain length and food web complexity

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

Table 4 Top ranked mixed models with site as a random effect describing network structure for the *Sarracenia* food web at the pitcher scale. Metrics for which the top model was the null model (intercept only) or where the ΔAIC < 2 between the null model and the top model are not included. See Table 1 for definitions of web metrics.

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

*R^2 calculated using the methods of Xu (2003) for assessing the fit of mixed models.
Vol = pitcher volume; AIC, Akaike information criterion.

Table 5 Top ranked linear models describing structural turnover (coefficient of variation of food web metrics) for the *Sarracenia* food web at the site scale. Only models significant at a *P*-value of 0.05 with an adjusted $R^2 \geq 0.05$ are shown. See Table 1 for definition of web metrics.

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

Predator–prey interactions, food chain length and food web complexity

Mosquito abundance was not correlated with food web structure at the pitcher scale. However, variation in mosquito abundance at the site scale was positively correlated with structural turnover in two measures of chain length – mean trophic level and mean chain length (Table 5, Fig. 4a,b). Although the hypothesized relationship between mosquito abundance and chain length was observed at the site scale, food web complexity did not increase with mosquito abundance at the pitcher scale and variation in mosquito abundance within sites did not increase structural turnover in complexity metrics.

Biogeographic correlates of food chain length, and food web complexity

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

Overall, network structure of the *Sarracenia* food web was only weakly influenced by all predictor variables at the pitcher scale across 780 webs. The best-fit models left a large portion (> 95%) of the variance in food web structure unexplained at the pitcher scale (Table 4). At the site scale, predictor variables explained more (8–35%) of the variance in structural turnover in food webs (Table 5).

DISCUSSION

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

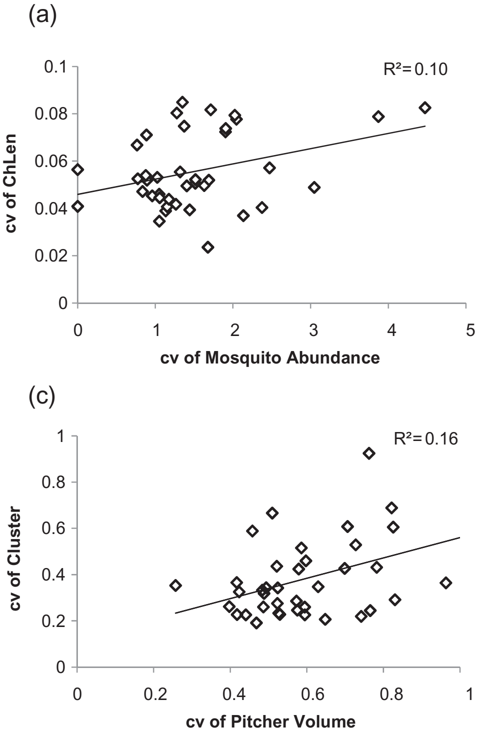

Figure 4 Univariate models showing the relationship between variables (other than C-PC1) and structural turnover – CV (coefficient of variation) of food web metrics – for the *Sarracenia* food web at the site scale ($P < 0.05$ for all models). See Table 1 for web metric definitions.

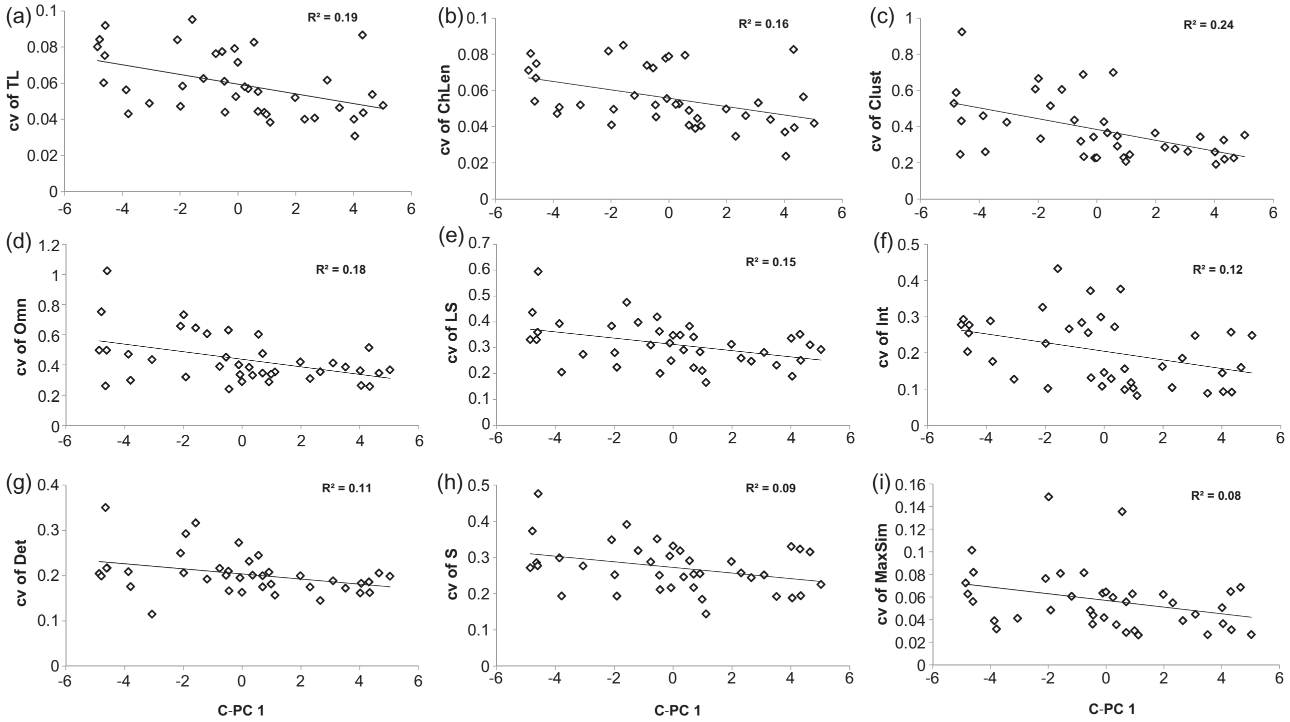

Figure 5 Univariate models showing the relationship between C-PC1 and structural turnover, i.e. variation in network structure between webs within each site as measured by the CV (coefficient of variation) of each food web metric, for the *Sarracenia* food web at the site scale. Structural turnover significantly decreased ($P < 0.05$) with C-PC1 and thus latitude for (a) chain length, (b) mean trophic level, (c) clustering coefficient, (d) % omnivores, (e) linkage density, (f) % intermediate species, (g) % detritivores, (h) species richness, and (i) maximum trophic similarity.

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

Although mosquito abundance had no effect on food web structure at the pitcher scale, increased variation in mosquito abundance between pitchers was positively correlated with structural turnover in chain length and mean trophic level within sites. Mosquito larval density varied from 0 to over 11 larvae ml^{-1}. The simple presence of *W. smithii* can increase metrics related to chain length (Kitching, 2001; Post & Takimoto, 2007) or at high densities, extirpate intermediate consumers through predation (Addicott, 1974; Kneitel, 2007), concomitantly decreasing chain length. Mosquito abundance was not related to any measures of food web complexity, suggesting that the observed keystone effects of increased bacterial and protozoan diversity (Cochran-Stafira & von Ende, 1998; Peterson *et al.*, 2008) were not manifested in food web metrics related to complexity (consistent with Kneitel & Miller, 2002).

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

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

Overall, our results show that the commonly observed relationship between ecosystem size and food chain length (Spencer & Warren, 1996; Post *et al.*, 2000; Takimoto *et al.*, 2008; McHugh *et al.*, 2010) is extended to several measures of network structure in the *Sarracenia* food web, and that biogeographic patterns of species richness and compositional turnover influence food web structure. However, our predictor variables leave a large portion of variability in food web structure unexplained. We suggest that stochastic assembly processes related to dispersal and arrival order and timing of propagules (Kneitel & Miller, 2003; Miller & Kneitel, 2005; Chase, 2010) that are not captured in our snapshot data set may be the driving influence behind food web structure in the *Sarracenia* system. A study assessing assembly trajectory is necessary to explicitly test the hypothesis that stochastic assembly processes are the main determinant of network structure in the *Sarracenia* food web.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Climatic variables (and latitude) used in climate variable principal components analysis and regressions.
Appendix S2 Methods for modelling nitrogen deposition.
Appendix S4 Correlations among climatic variables and latitude.
Appendix S4 Mixed effect models for the pitcher-scale analysis using function lme in package nlme in R v.2.11.1.
Appendix S5 Xu's (2003) method for calculating the variance explained (R^2) by the fixed effects in a mixed-effects model.

BIOSKETCH

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