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Diane S. Srivastava

srivast@zoology.ubc.ca

University of British Columbia

A. Andrew M. MacDonald

Université de Sherbrooke

Olivier Dézerald

DECOD, L'Institut Agro, Ifremer, INRAE

Laura Melissa Guzman

University of Southern California

Mathias Mistretta Pires

Universidade Estadual de Campinas (UNICAMP)

Pierre Rogy

University of British Columbia

Jana S. Petermann

Paris-Lodron University of Salzburg

Angélica L. González

Rutgers, The State University of New Jersey

Eoin J. O'Gorman

University of Essex

Ulrich Brose

German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig

Régis Céréghino

Université de Toulouse, CNRS, IRD, Toulouse INP

Paula M. de Omena

Universidade Vila Velha

Pavel Kratina

Queen Mary University of London

Colette L. Ward

Fisheries and Oceans Canada

Benoit Gauzens

German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig

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Nicholas A.C. Marino
Universidade Federal do Rio de Janeiro
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University of British Columbia
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Universidade Federal do Rio de Janeiro
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Administración de Parques Nacionales
Céline Leroy
Université de Toulouse, CNRS, IRD, Toulouse INP
Bruno Corbara
Université Clermont Auvergne
Fabiola Ospina Bautista
University of Caldas
Gustavo Cauê de O. Piccoli
Universidade Estadual de Campinas (UNICAMP)
Barbara A. Richardson
University of Puerto Rico
Michael J. Richardson
University of Puerto Rico
Jacqueline T. Ngai
University of British Columbia
Guillermo Montero
IICAR-UNR-CONICET
Stanislas Talaga
Institut Pasteur de la Guyane
Gustavo Q. Romero
Universidade Estadual de Campinas (UNICAMP)

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Food web size and shape differ in their environmental control

Authors: Diane S. Srivastava[1*], A. Andrew M. MacDonald[2], Olivier Dézerald[3], Laura Melissa Guzman[4,5], Mathias Mistretta Pires[6], Pierre Rogy[1,†], Jana S. Petermann[7], Angélica L. González[8], Eoin J. O'Gorman[9], Ulrich Brose[10], Régis Céréghino[11], Paula M. de Omena[12], Pavel Kratina[13], Colette L. Ward[14], Benoit Gauzens[10], Ignacio M. Barberis[15], Pablo Augusto P. Antiqueira[9], Juliana S. Leal[16], Nicholas A. C. Marino[17], Michael C. Melnychuk[18], Vinicius F. Farjalla[17], Rodrigo Manuel Freire[19], Céline Leroy[20], Bruno Corbara[21], Fabiola Ospina-Bautista[22], Gustavo Cauê de O. Piccoli[23], Barbara A. Richardson[24], Michael J. Richardson[24], Jacqueline T Ngai[1], Guillermo Montero[25], Stanislas Talaga[26], Gustavo Q. Romero[23]

Affiliations:

[1]Dept. of Zoology & Biodiversity Research Centre, University of British Columbia; Vancouver, Canada.

[2]Département de Biologie, Université de Sherbrooke; Sherbrooke, QC, Canada.

[3]DECOD, L'Institut Agro, Ifremer, INRAE, Rennes, France.

[4]Biological Sciences Department, University of Southern California; Los Angeles, USA.

[5]Department of Entomology, Cornell University, Ithaca, USA.

[6]Departamento de Biologia Animal, Instituto de Biologia, Universidade Estadual de Campinas; Campinas, Brazil.

[7]Department of Environment and Biodiversity, Paris-Lodron University of Salzburg; Salzburg, Austria.

[8]Department of Biology & Center for Computational and Integrative Biology, Rutgers University; Camden, New Jersey, USA.

[9]School of Life Sciences, University of Essex; Wivenhoe Park, Colchester, UK.

[10]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany and Institute of Biodiversity, Friedrich Schiller University Jena; Jena, Germany.

[11]Centre de Recherche sur la Biodiversité et l'Environnement (CRBE), Université de Toulouse, CNRS, IRD, Toulouse INP; Toulouse, France .

[12]Laboratory of Aquatic Insect Ecology, Universidade Vila Velha; Vila Velha, ES, Brazil.

[13]School of Biological and Behavioural Sciences, Queen Mary University of London; Mile End Road, London UK.

[14]Great Lakes Laboratory for Fisheries and Aquatic Sciences, Fisheries and Oceans Canada; Burlington, Canada.

[15]Instituto de Investigaciones en Ciencias Agrarias de Rosario, Universidad Nacional de Rosario, Consejo Nacional de Investigaciones Científicas y Técnicas, Zavalla; Santa Fe, Argentina.

[16]Programa de Pós-Graduação em Ecologia, Universidade Federal do Rio de Janeiro; RJ, Brazil.

[17]Departamento de Ecologia, Instituto de Biologia, Universidade Federal do Rio de Janeiro; RJ, Brazil.

[18]Institute for the Oceans and Fisheries, University of British Columbia; Vancouver, Canada.

[19]Administración de Parques Nacionales; San Carlos de Bariloche, Río Negro, Argentina.

[20]Centre de Recherche sur la Biodiversité et l'Environnement (CRBE), Université de Toulouse, CNRS, IRD, Toulouse INP, Université Toulouse 3 – Paul Sabatier (UT3); Toulouse, France.

[21]LMGE, Université Clermont Auvergne; France.

[22]Departamento de Ciencias Biológicas, Universidad de Caldas; Colombia

[23]Laboratório de Interações Multitróficas e Biodiversidade, Departamento de Biologia Animal, Instituto de Biologia, Universidade Estadual de Campinas (UNICAMP); Campinas, SP, Brazil

[24]Luquillo LTER, Institute for Tropical Ecosystem Studies, University of Puerto Rico; San Juan, Puerto Rico

[25]IICAR-UNR-CONICET; Argentina

[26]Unité d'Entomologie Médicale, Institut Pasteur de la Guyane; Cayenne, French Guiana

[†]Present address: Department of Biology, McGill University, Montreal, Canada

*Corresponding author. Email: srivast@zoology.ubc.ca

Food-web structure governs community stability and ecosystem functioning, yet its environmental controls remain poorly understood. We analyzed 1,046 food webs from 26 Neotropical sites spanning broad environmental gradients in energy, temperature, hydrologic disturbance and ecosystem size to understand how these factors contribute to determining food web structure. All food webs were from the same widespread system and sampled using standardized methods. We found that food-web size increased with locally available energy and ecosystem size, but decreased with regional aridity and precipitation variability. In terms of shape, food webs became shorter and wider in regions with low primary productivity, high temperatures and drought-prone climates. Thus, food web size and shape were controlled by different environmental drivers acting at different spatial scales, likely reflecting divergence in the underlying mechanisms. Environmental effects on food web size were mediated by the abundance and traits of species, but food web shape was not. These findings reveal how local environmental conditions and regional climate structure ecological networks, providing a basis for forecasting food-web restructuring under environmental change.

Food webs describe how species interact in ecological communities, summarizing species diversity and the trophic pathways through which energy and matter flow. Among many structural descriptors, two are especially informative: food web size, which reflects the total number of species and interactions across trophic levels, and food web shape, which captures the distribution of species between versus within trophic levels (i.e. food web height versus width[1]). Food web size and shape are both linked to the ability of food webs to resist environmental perturbations and efficiently convert basal energy and nutrients into biomass[2,3]. Given the central role of food web structure in ecosystem resilience and functioning, it is surprising that we still struggle to understand how food web size and shape are determined by current environmental conditions, and therefore predict how these properties might respond to future environmental change[4].

Environmental conditions could affect food web structure through a wide range of mechanisms, including by determining energy input, modulating energy fluxes, filtering community composition, affecting metabolic efficiencies, determining interaction strengths, driving colonization-extinction dynamics, and influencing system stability[5–10]. Individually, environmental drivers – especially temperature, disturbance, available energy and ecosystem size - have been shown to affect food web structure[11–15]. However, because such drivers often mediate or interact with each other[e.g. 5,8,16–18], the effect of any single driver can only be properly tested through a causal framework that accounts for other plausible covariates. Furthermore, descriptors of food web structure are often conflated in analyses – for example, food web height could vary due to changes in either food web size or shape - complicating tests of causal mechanisms between environmental drivers and food web structure[19]. Finally, the scale of environmental drivers may determine how they influence food web structure, with small-scale heterogeneity shaping organism and population processes, and larger-scale bioclimatic gradients additionally affecting metacommunity processes[20]. Therefore, to fully understand the environmental control of food web structure, we need extensive surveys of food webs across multiple environmental gradients at both local and regional scales, coupled with detailed causal analysis and careful partitioning of effects on food-web size from those

on shape. Geographic replication of such surveys can establish robustness of patterns. To unravel the interplay between food web structure and environmental variation, we analyze here the structure of more than a thousand food webs spanning broad environmental and geographic gradients. We ask which are the dominant environmental drivers of food web structure, and whether food web size and shape are driven by the same types and scales of environmental drivers.

A model system: aquatic food webs in bromeliads

To test these ideas, we conducted geographically-replicated surveys of the same system, using the same methods (see Materials and Methods): 1046 aquatic food webs housed within bromeliad plants in 26 Neotropical field sites. Sites differed substantially in food web composition[21] and spanned 47 degrees of latitude (Fig. 1, Supplementary Table 1). Water-filled bromeliads have been used extensively as model systems in ecology because of their contained dynamics and high natural replication[22–24]. Although bromeliads are small habitats, containing at most a few liters of water, the small size of most aquatic invertebrates mean that individual bromeliads can contain thousands of individuals and more than a dozen species. These aquatic food webs, dominated by invertebrates and micro-organisms[24,25], have been shown to have similar structure (e.g. number of trophic levels) to those of larger systems[26]. Although some terrestrial organisms interact with the system, consumptive interactions in these food webs are almost entirely aquatic[25]. Energy enters bromeliad food webs primarily from tree canopy detritus, but also autochthonous algal growth[27], both influenced by regional net primary productivity (NPP). Disturbance is predominantly hydrological and reflects extremes of aridity and precipitation, reducing organism survival through desiccation stress[28] or flushing of nutrients and organisms[21]. Bromeliad water temperatures are determined by the regional climate as modified by local canopy cover[29]. We tested key environmental drivers of food web structure at multiple scales: available energy (local: bromeliad detritus, regional: NPP), ecosystem size (local: bromeliad capacity), hydrologic disturbance (regional: aridity, monthly coefficient of variation in precipitation – hereafter "precipitation variability") and temperature (local: canopy openness, regional: mean annual temperature – hereafter "temperature").

We built unweighted food webs based on a hierarchy of information (in priority order: physiological and morphological constraints, gut content analyses, feeding trials, experiments, literature) expanded to close relatives (taxonomic scope for consumers based on similar diet, for resources based on similar morphology). With this method (details in Methods), we inferred the presence or absence of links for 86% of potential pairwise interactions, and estimated the remaining 14% from probabilistic models (Extended Data Fig. 1). As we assumed the same trophic structure of basal resources, microfauna and meiofauna for all food webs, inferences about food web structure apply primarily to the macroinvertebrate trophic levels whose species were directly observed. The method by which food webs are constructed and conceptualized determines their suitability for testing different theories[30]; here, we chose to use unweighted webs that integrate potential links over the aquatic lifespan of species, characterizing the trophic niche of species. This approach facilitates our subsequent tests of niche-based mechanisms while still enabling detection of

any other effects on food web structure that operate through shifts in species composition, for example network stability or energy flux effects[31]. We described food-web structure with 14 commonly used food-web metrics. As many of these metrics were correlated in our dataset, we discovered that most of the variance in food web structure could be captured by the first two components of a principal components analysis (PCA; Fig. 1, Extended Data Table 1). The food-web size component (PCA 1, 58% of total variance in food web structure) correlates with the number of species and links as well as their ratio, link density (Fig. 1). The food-web shape component (PCA 2, 23% of variance) increases with maximum number of trophic levels, proportion of species in the top trophic level and degree of omnivory (Fig. 1); thus, food webs with high shape scores are tall and narrow, whereas low-score food webs are short and wide.

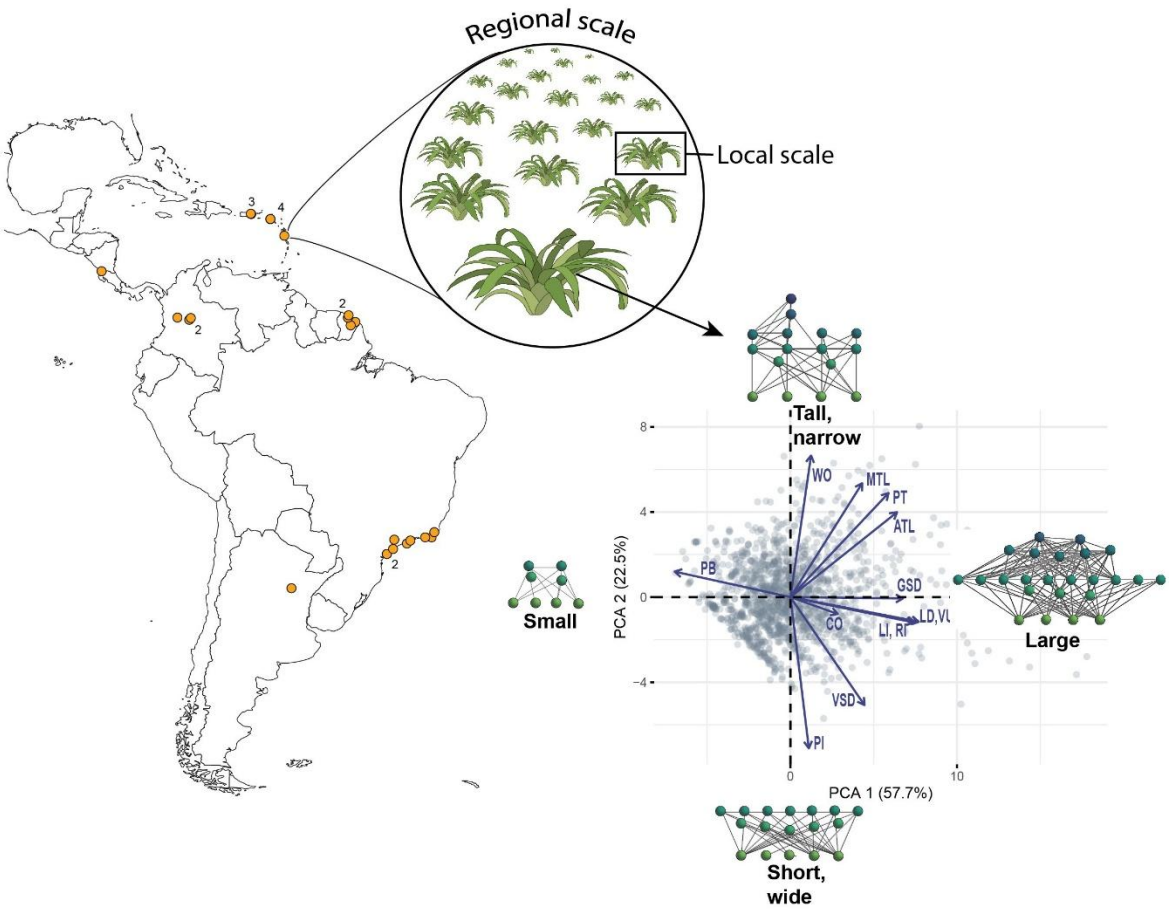


Figure 1. In 26 field sites in Central America, South America and the Caribbean (orange dots on map, numbers indicate the number of sites hidden by overlapping dots), we surveyed the aquatic fauna within each of many bromeliad plants (round inset). For each bromeliad, we constructed aquatic food webs based on invertebrate composition and trophic relationships. These food webs were described by 14 metrics, which were summarized by a principal components analysis (PCA, biplot of first two axes shown). The first PCA axis (PCA 1) primarily represents food-web size, from small to large, and the second

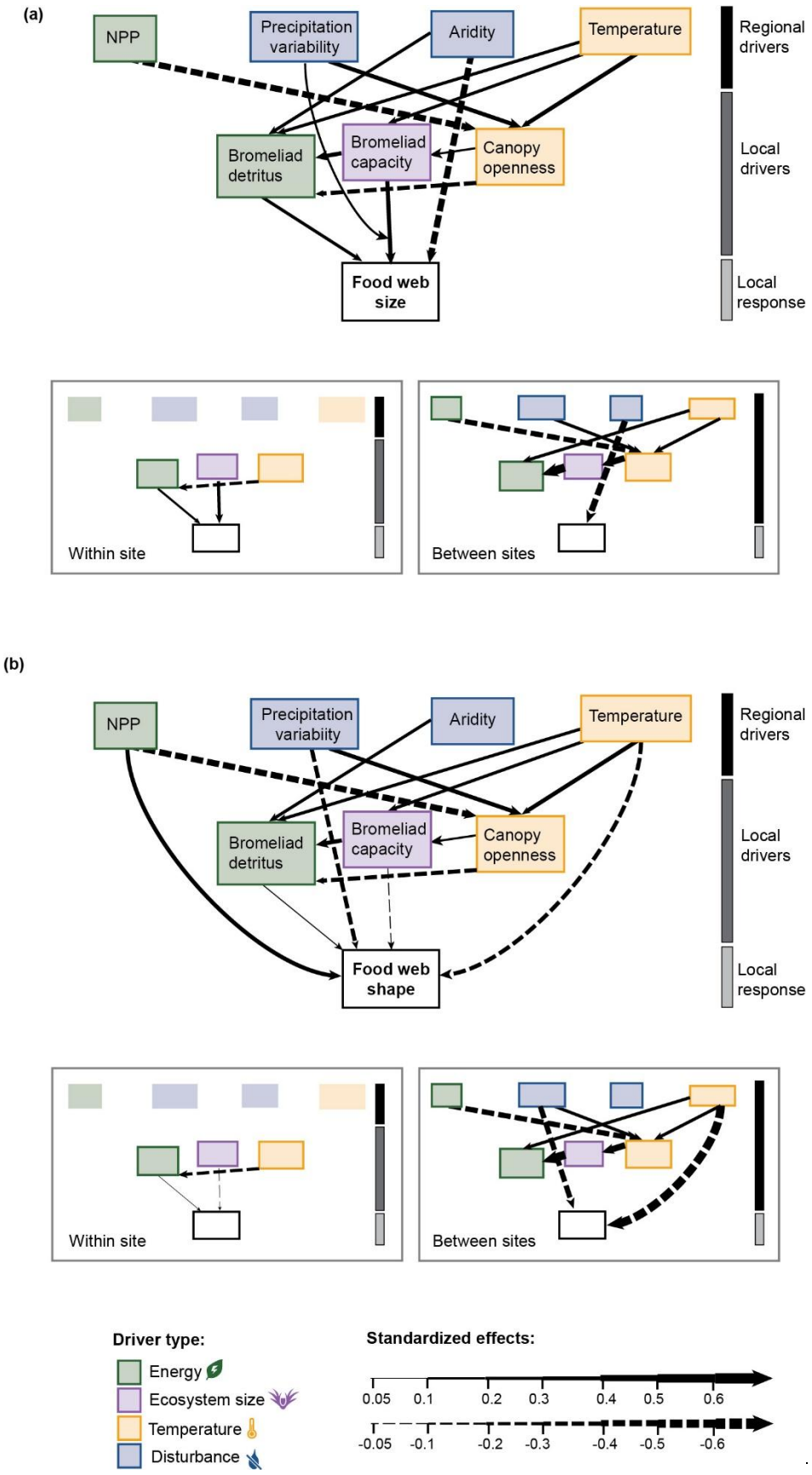
PCA axis (PCA 2) represents food web shape, from short and wide to tall and narrow. Illustrative food webs from the extremes of these axes are shown. The contribution of food-web metrics to the first two PCA axes is shown by labeled vectors: proportion basal species (PB), web omnivory (WO), maximum trophic level (MTL), proportion top species (PT), average trophic level (ATL), generality standard deviation (GSD), link density (LD), generality (GE), vulnerability (VU), number of links (LI), species richness (RI), connectance (CO), vulnerability standard deviation (VSD) and proportion intermediate species (PI).

Results and Discussion

The environmental drivers of energy input, ecosystem size, temperature and disturbance collectively explained a substantial amount of variation in both food-web size (34% by fixed effects, 59% by both fixed and random effects) and food-web shape (36% and 67%, respectively) in piecewise structural equation models. Structural equation models test hypothesized causal relationships between variables, isolating the unique effect of each variable in relation to other variables. Our results suggest that food-web structure is determined by combinations of drivers operating at different scales. Of the seven proximate measures analyzed, all except canopy openness had direct effects on either food-web size or shape (Fig. 2, Extended Data Tables 2,3). Furthermore, strong causal paths among drivers meant that variables lacking a direct effect on a particular food-web metric often had indirect (mediated) effects *via* other drivers (Fig 3a).

Local energy affects food web size, regional energy affects food web shape

In general, we found that food-web size and shape differed in the types and scales of dominant environmental drivers. For example, while measures related to energy availability affected both food-web size and shape, size was largely affected by local proxies (detritus resources within bromeliads: Fig. 3a) whereas shape was more affected by regional measures (NPP between sites: Fig. 3a). Specifically, food webs were larger in bromeliads with more detritus, but were similarly-sized between sites differing in NPP. By contrast, food-web shape was more affected by regional NPP than local energy, with bromeliads in more productive sites having tall, narrow food webs (Fig. 3c). Such effects of NPP on food web shape are predicted to originate from combinations of bottom-up and top-down control. Classic models predict that increased bottom-up flow of energy through food webs overcomes inefficient energy transfer between trophic levels to enable the occupancy of higher trophic levels[15,32]. Increased occurrence of predators, especially large generalist species, can then exert strong top-down effects on prey species, reducing their standing stock abundance and diversity, resulting in tall but narrow food webs[10]. For example, the tallest and narrowest food webs are in Costa Rica, whereas the shortest and widest are in two French Guiana sites. Costa Rican rainforests have twice the productivity of those in French Guiana[33], and their bromeliads contain more large-bodied and long-lived top predators[34]. The strong consumptive effects of such predators result in food webs with more standing biomass in predator than prey trophic levels[35].



206

207 **Figure 2. Causal diagrams of the effects of four types of environmental drivers on (a) food-**
208 **web size, as represented by log PCA 1, and (b) food-web shape, as represented by log PCA**

2. Solid black lines represent significant positive effects, dashed black lines represent significant negative effects, and line thickness is proportional to effect size (see legend). Environmental drivers are coloured to indicate driver type. The spatial scale of drivers and responses is shown on the right margin. In the insets, causal models are repeated with the response and explanatory variables separated into within-site effects (i.e. after subtracting the site means, and so excluding regional drivers) and between-site effects (i.e. site means only for all drivers). We removed collinearity between regional bioclimatic variables with principal components analysis (PCA), representing drivers in models with appropriate PCA axes (Supplementary Table 6). All models were fit as piecewise structural equation models, and met global tests of directed separation (Fisher's C: $p > 0.05$).

Ecosystem size affects food-web size more than shape

Bromeliad capacity had strong, positive effects on food-web size but only minor effects on food-web shape. The relationship between food-web size and bromeliad capacity was partially mediated by detritus (Fig. 2a): larger plants capture more falling detritus, which support larger food webs as shown above. However, most of the effect of capacity on food-web size was independent of detritus (Fig. 3a) and may reflect not energetic limitation but effects of disturbance: smaller capacity bromeliads dry out more frequently[36], and desiccation is a major source of invertebrate mortality[28]. Studies in other systems have shown that effects of habitat size on food web structure can be mediated by multiple mechanisms apart from simple energetic limitation, such as disturbance[16], patch dynamics[6], network stability[37], body-size distributions[8], cross-ecosystem coupling[14] and altered interaction types and strengths[5].

Regional temperature flattens food-web shape, indirectly increases food-web size

Temperature was a key driver of food web shape. In warmer sites, food webs were shorter and wider (Fig. 3e). A similar flattening of food web shape at higher temperatures has been observed in a range of other freshwater systems[13,38,39]. Metabolic theory predicts such a response, for two reasons. First, temperature often increases metabolic rates more than can be sustained by feeding rates, decreasing energetic efficiencies and starving higher trophic levels[7,40]. Second, the effects of higher temperatures on such metabolic asymmetries are exacerbated for larger organisms, so when predators are larger than their prey they will be particularly impacted [41]. While the first reason is consistent with our results, the second is unlikely: bromeliad food webs have few gape-limited predators and so are generally not size-structured. Thus, mean body mass was uncorrelated with food web shape, and so could not mediate effects of temperature on this metric (Extended Data Table 4, Supplementary Table 2).

Food web size is also predicted to be directly affected by temperature through effects on interaction stability[9,39,42]. However, in our study, effects of temperature on food-web size were indirect rather than direct, driven by bromeliad plants being larger and containing more detritus in warmer sites. Bromeliad morphology, like that of many plants, shows both inter- and intraspecific responses to climate[43]. This result illustrates the important ways that non-

trophic interactions, here the ability of bromeliads to create habitat, can mediate the effects of temperature on trophic networks[44,45]. Although there are iconic marine examples of how changes in the extent or complexity of habitat-forming species (e.g. sea grass, corals) can mediate the effects of warming on food webs, such non-trophic mediation has rarely been considered in freshwater systems[45].

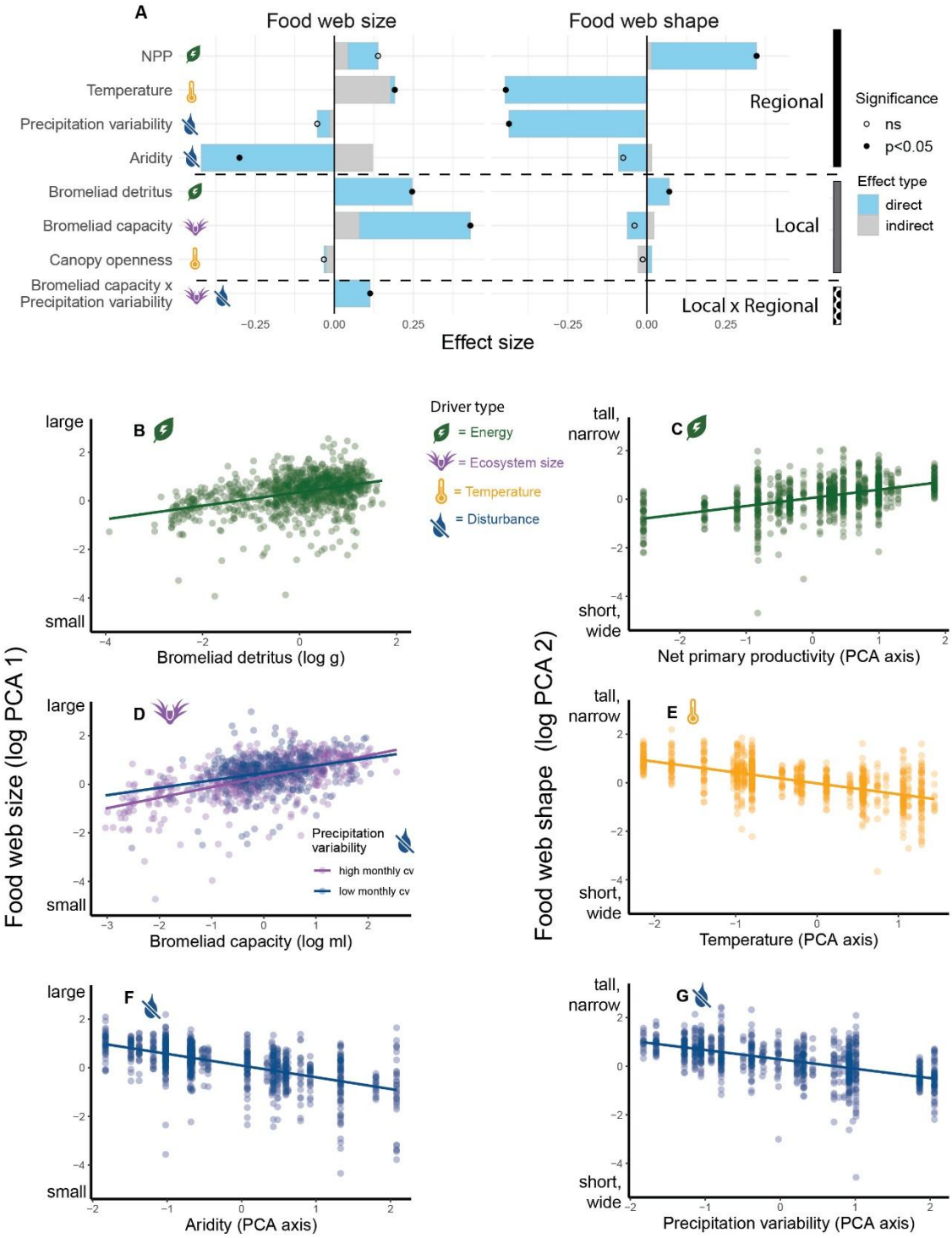


Figure 3. Effects of environmental drivers on food-web size (i.e. number of species and links) or shape (i.e. height relative to width). (A) Total, direct and indirect effect sizes of

drivers on food web structure from SEMs in Fig. 2. Total effects, represented by circles, are the sum of direct and indirect effects (stacked bars). Significance of total effects was determined through bootstrapping. Drivers are distinguished in terms of their spatial scale (local vs. regional) and type (following colours and icons in Fig. 2), only significant interactions shown. The strongest direct effects are illustrated for food-web size (B, D, F) and food-web shape (C, E, G). In all cases, partial residuals of the specific driver are used in combination with median values of other variables to visualize the direct effect. We used a principal component analysis (PCA) to remove correlations between the four climate variables, and so net primary productivity, temperature, aridity and precipitation variability are all plotted as their respective PCA axes (Supplementary Table 6). In order to show the interaction in panel D, the PCA values for precipitation variability were divided into two categories, low monthly coefficient of variation (cv), based on PCA score <0, and high monthly cv (PCA score >0).

Disturbance shrinks food-web size, and flattens food-web shape

Food webs were also strongly affected by conditions linked to hydrologic disturbance. Food-web size decreased in sites with high aridity or a strong coefficient of variation in precipitation, where bromeliads are likely to dry (Fig. 3d,f). The decline in food-web size with variable precipitation was particularly acute in small bromeliads (Fig. 3d), whose shallow tanks can dry out quickly. Although bromeliad capacity, monthly variation in precipitation, and annual estimates of aridity affect hydrological disturbance at different time scales, there is remarkable consistency in their effects.

Food-web shape was also affected by hydrologic disturbance, becoming shorter and wider in sites with variable precipitation (Fig. 3g). Dynamic models of food-web assembly predict frequent disturbance to result in attenuated trophic structure, in part because predators can only colonize habitats where sufficient prey are already established[46,47]. Although drought is particularly prevalent in small aquatic systems such as bromeliads, hydrologic variability has been shown to be the dominant determinant of food web structure even in much larger aquatic systems, such as rivers or ponds[1,16,48]. Our insights on the mechanisms underlying food-web structure in bromeliads may thus inform a wide range of freshwater systems.

Food-web size and shape: different drivers, different mechanisms

So far, we have demonstrated that food-web size and shape differed in the scale of dominant environmental drivers, and this disparity was particularly evident for drivers related to energy and temperature. Food-web size was affected by both local- and regional-scale drivers, whereas food-web shape was primarily affected by regional bioclimatic drivers. We now examine some potential mechanisms underlying this pattern.

We first exclude two potential artefacts. The first possibility is that environmental conditions measured at the local (bromeliad) scale may still act as regional-scale drivers if the mean attributes of bromeliads differed between sites. However, even when we subtract site means from local environmental variables, our SEMs of food-web size and shape still show the

same patterns (Supplementary Tables 3,4). The second possibility is that regional climate shapes the size and trophic structure of the regional species pool (often called the "meta-web"), and these effects are then passively transmitted to local food webs[49]. However, there is no effect of climate, or any other environmental variables, on the structure of meta-webs (Supplementary Table 5).

We suggest, instead, that food-web size and shape may often differ in the scale of their environmental determinants because of fundamental differences in the underlying mechanisms. We posit that food web size is often influenced by community assembly mechanisms, which include both numerical and trait-based mechanisms, with the former particularly important in neutral theory and the latter in niche theory. By numerical effects we refer to environmental conditions that restrict the total number of individuals in a community, but are neutral with regard to their traits. For example, reductions in total community abundance can affect food web structure through stochastic loss of rare species, which are often at high trophic levels[50]. By trait-based mechanisms we refer to the differential effects of environmental conditions on the performance and persistence of species based on their attributes. For example, environmental filtering of the dominant traits can affect food web structure when these traits are rare, influence trophic efficiency, or are associated with specific trophic roles[51]. In general, we found that numerical and trait-based mechanisms explained a substantial part of the effect of environmental conditions (local and regional) on food web size. However, these mechanisms accounted for very little of the effect of regional bioclimatic drivers on food web shape (Fig. 4).

Specifically, we used structural equation models to ask if the effect of each environmental driver on food web structure could be mediated by the total abundance of macroinvertebrates in the community (numerical effects) or by community-weighted trait axes (Extended Data Table 5) representing four major facets of macroinvertebrate life history[52]. A significant mediating path between two variables in a structural equation model suggests a causal role for the mediator. We found strong numerical limitation and weaker trait-mediated effects on food web size under conditions where invertebrate survival or colonization is limited by frequent desiccation: small-capacity plants, especially under variable precipitation, and more arid climates (Fig. 4b). For example, the invertebrates in small-capacity plants were few in number and dominated by either pelagic or defended benthic taxa, attributes associated with small food webs (Extended Data Table 4,5). Low detrital quantity also limited food web size through strong numerical effects, offset slightly by trait-mediated effects (Figure 4b). Numerical effects are expected from energetic limitation, but may also reflect the physical role of detritus in providing refuges from predators. Indeed, low detritus conditions favoured species with morphological defenses and dormant stages (Extended Data Table 4,5). It is plausible that such trait combinations reduced consumptive effects, thereby bolstering food-web size.

By contrast, numerical and trait-based mechanisms explained very little of the effect of regional bioclimatic drivers on food web shape. Even though bioclimatic drivers favoured certain trait axes[51], these were not trait axes that strongly affected food web shape. For example, traits correlated with drought resistance occur at all trophic levels in the food web[28].

Instead, the patterns we found in food web shape were often consistent with predictions from metabolic theory, energetic constraints, or disturbance-induced dynamics, as detailed earlier. While definitive attribution of these mechanisms will require careful experimentation and field parameterization of models, our results point to a disjunct between the mechanisms underlying food-web size and those underlying food-web shape. This disjunct in mechanisms means that food-web size and food-web shape can be controlled by different types of scales and environmental drivers. Such decoupling is unlikely to be unique to bromeliads and may occur in many other systems.

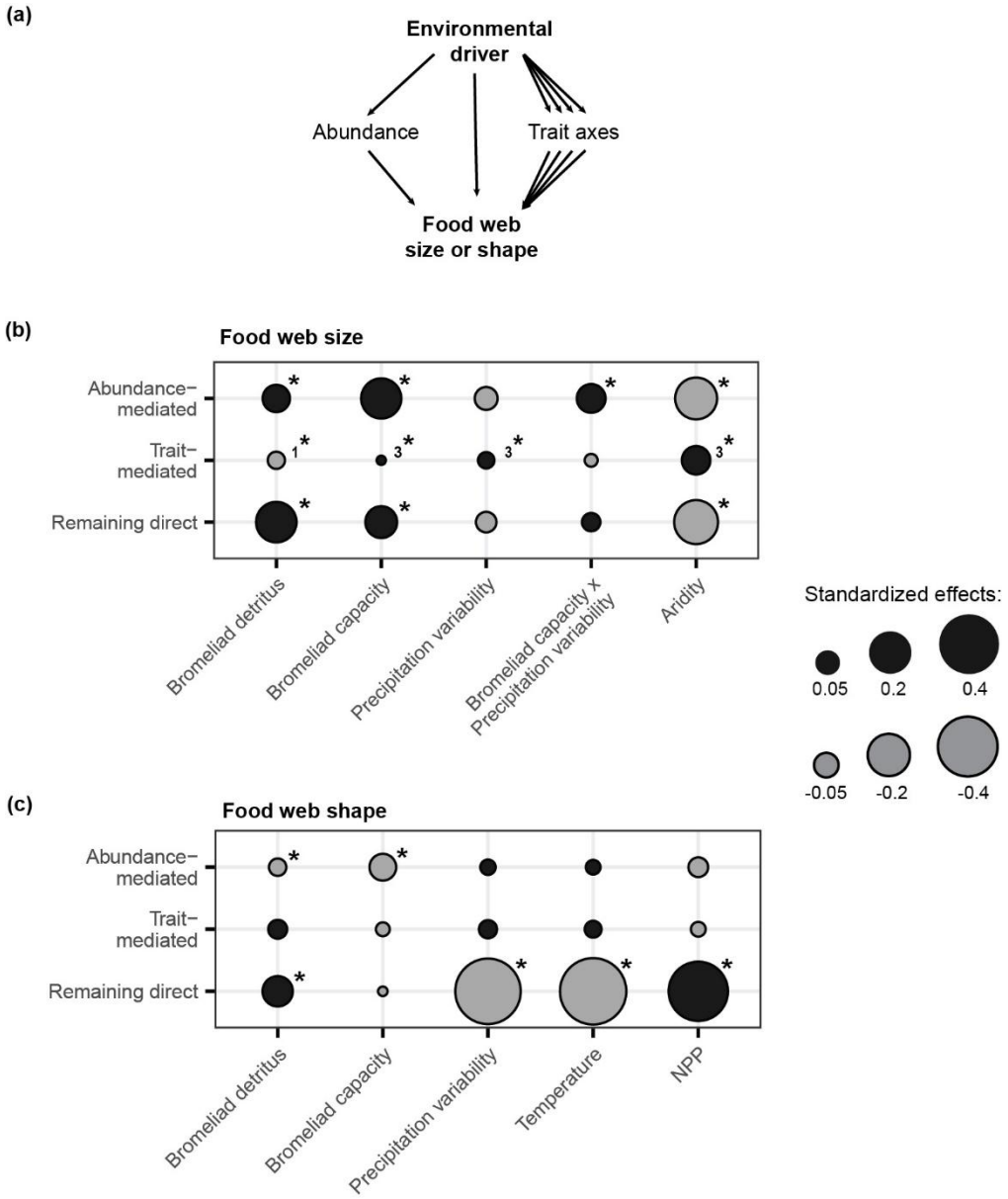


Figure 4. Potential mediation of environmental effects on food web structure by either total invertebrate abundance or invertebrate trait axes. (a) We partitioned the direct, partial effect of each environmental driver on either food web size or shape into effects mediated by total abundance of the macroinvertebrate community ("abundance-mediated") or by the net sum of four community-weighted trait axes ("trait-mediated"), or

not mediated by these variables ("remaining direct"). These four trait axes for bromeliad macroinvertebrates were previously established[52], and are described in Extended Table 5. (b, c) We calculated the standardized effect size for each of the abundance-mediated, trait-mediated and remaining direct paths (Extended Data Table 4). Mediated paths were considered significant (*) when both the path from the environmental variable to the mediator and from the mediator to the food web metric were significant ($p<0.05$). We examined significance separately for each trait axis, and next to each trait-mediated symbol we indicate, with a numeral (1-4), any trait axis that was significant. To ensure that the effects of environmental drivers on food web structure were independent of other environmental drivers, we conducted this analysis within an SEM. Specifically we restricted the SEMs in Figure 2 to those drivers with significant direct effects on food web structure (to prevent model overfitting), and then added total abundance and weighted trait axes as mediators (Supplementary Table 2).

Implications

In this study, we demonstrate strong effects of local and regional environments on food webs. As climate variables such as temperature, aridity and precipitation variability affected food web shape and size, these results point to potential flattening and shrinking of food webs in a future with warmer, drier conditions. In the case of temperature, no local conditions – not even shade from trees – was able to mitigate the effects on food-web shape. There was also no interaction between local energy availability and temperature, contrary to previous results[17,18]. Instead, regional energy (NPP) was more effective in countering the flattening of food-web shape in warm climates. Our results do suggest that an increase in ecosystem size might mitigate the effects of aridity and variable precipitation on food-web size – in part because these determinants of drought disturbance all reduced food-web size via the same mechanism: fewer total individuals. In general, many invertebrate populations show evidence of widespread declines in abundance[53], and our study points to the consequences of such declines for food web structure. Finally, this study shows the power of coupling causal modelling with comprehensive assessment of environmental drivers and food-web responses across continental-scale gradients. In a rapidly changing world, such integrative approaches are critical for predicting and mitigating effects of environmental change on food webs.

Methods

Compiling the database

The Bromeliad Working Group (BWG) database[54] consists of data on field sites, habitats, sample dates, bromeliad characteristics, macroinvertebrates in each bromeliad, and taxonomic information and traits for each macroinvertebrate morphospecies. From this database, we selected sites and bromeliads with adequate plant-level environmental data and detailed taxonomic information for aquatic macroinvertebrates within bromeliads. In total, we included for analysis 1046 bromeliads sampled for aquatic macroinvertebrates between 26 different field sites (Supplementary Table 1). Field sites varied in latitude from 29.4° S (Argentina) to 18.3° N (Puerto Rico), in longitude from 73.9° W (Colombia) to 41.5° W (Brazil) and in elevation from sea level (Brazil, French Guiana) to 3050 m (Colombia). This area covers much of the distributional extent of tank-forming Bromeliaceae. In a few cases, bromeliads were sampled across a large spatial gradient within a single study. To delimit ecologically-distinct sites within such gradients, we used a threshold of > 50% Jaccard dissimilarity in macroinvertebrate composition[54]. Field sites varied in the number and attributes of bromeliads sampled, and the habitats and years sampled (Supplementary Table 1).

All aquatic macroinvertebrates were censused in each bromeliad. These invertebrates were extracted from each bromeliad by dissection, by washing, or by pipetting the water from each leaf as suitable to each site. Apart from this variation, sampling of invertebrates in all sites followed the same protocol. For each bromeliad plant, all invertebrates seen by a naked eye were carefully removed, counted, and identified. Across all sampled bromeliads reported in this study, 435 invertebrate morphospecies (88% insects, 12% annelids and other invertebrates) were recorded. Although abundance data was recorded at the level of morphospecies (i.e. morphologically uniform biological units), the realized level of taxonomic identification ranged from species (13%) to genus (37%), subfamily (11%), family (32%), order (0.4%), and higher levels from subclass to phylum (6%).

Basal resources and zooplankton groups

Although we had information on the composition of bacteria, fungi or zooplankton for a limited number of bromeliads in some sites, this was not comprehensive enough to construct species-level food webs across the majority of the database. Instead, we follow the approach

of many studies in collapsing the lower levels of the food web into broad categories of organisms. Based on previous studies[e.g. 55], we assumed all bromeliads contained two sizes of zooplankton: "microzooplankton" include microscopic pelagic fauna (< 0.2 mm) such as amoebae, rotifers, and ciliates, whereas "mesozooplankton" are larger meiofauna (0.2 - 1 mm) such as copepods and mites. We further assumed that all bromeliads have five broad types of basal resources: algae (phytoplankton and periphyton), bromeliad tissue (leaves and stem), coarse particulate organic matter ("CPOM"), fine particulate organic matter ("FPOM"), microorganisms (i.e. bacteria and fungi in water column and on organic matter). Here, CPOM refers to all submerged dead plant matter, largely tree leaves, that is ≥ 0.1 mm in diameter, whereas FPOM is < 0.1 mm in diameter and is a combination of detrital fragments and invertebrate feces.

Defining the food web

We combine multiple sources of information to reconstruct the trophic fundamental niche of all nodes (i.e. macroinvertebrate morphospecies and basal resources) in the meta-web of each site. We focus on the fundamental rather than realized trophic niche, reasoning that in the bromeliad system it is impossible to know what each individual actually consumed during their lifetime in any particular bromeliad. For example, remnants of resources may not be visible in guts if the resource was ingested in liquid form (e.g. piercing predators) or has been excreted after consumption. We ask of each invertebrate species: what feeding relationships are possible over its aquatic lifespan given the other species in the species pool of the site? As the majority of consumption in the aquatic food web is by aquatic organisms, we do not consider terrestrial species in our analysis (details: Supplementary Note 1).

Step 1: Combining multiple sources of information into food web matrices

Creating site-level food webs is a multi-step process (Extended Data Fig. 1). In Step 1, we use five empirical sources of information and inference between related species to fill in an interaction matrix with the value 1 (trophic link within the fundamental niche) and 0 (trophic link not within the fundamental niche), leaving some missing values (coded "NA"). In brief (details: Supplementary Note 2), we compiled information on: forbidden links (0 = known morphological and physiological constraints of species, otherwise NA; 15 rules); gut contents (1 = potential prey recorded from gut of consumer, otherwise NA; based on 3443 gut dissections); feeding trials (1 = potential prey consumed by consumer with 95% power, 0 =

potential prey not consumed, NA = insufficient evidence; based on 848 feeding trials); field experiments with bromeliad invertebrates (1 = significant decrease in potential prey abundance when consumer added, 0 = no significant decrease, NA = insufficient evidence; based on 167 experimental treatments); and published pairwise interactions for invertebrates from other freshwater systems (1 = consumption reported, 0 = lack of consumption reported, NA = insufficient evidence; based on 767 studies compiled by us, a published database of 20,823 freshwater invertebrate interactions[56] and a database of food types and feeding groups for 850 taxa[52]).

Step 2: Expanding information through taxonomic inference

When direct information about a pairwise interaction was not available in Step 1, we were often able to infer this information from closely-related species (Extended Data Fig. 1). Such inference assumes conservation through evolutionary time of the traits that enable consumers to feed on certain resources, or that allow prey to escape predation by certain consumers. We determined the taxonomic scope of such inference independently for the roles of consumer and resource as follows.

We defined consumer taxonomic scope as the highest taxonomic level of the consumer that maintains the same consumer degree (either primary, meaning that they only consume basal resources, or secondary, meaning that they can consume other macroinvertebrates). For example, a species of *Culex* has a consumer taxonomic scope of tribe, as all species within the Culicini tribe are primary consumers, but the same is not true at the next highest taxonomic level, the Culicinae subfamily, which includes the predatory genus *Toxorhynchites*. A similar definition of consumer scope has informed other food web algorithms[56]. We used a previously compiled database of feeding groups for bromeliad invertebrates[52] to determine, for each consumer taxa in our database, which higher taxonomic levels were homogeneous with respect to consumer degree (details: Supplementary Note 3). If taxa at a specific taxonomic level were neither entirely primary consumers nor secondary consumers, then the consumer's taxonomic scope has been exceeded and inference is not possible.

We defined resource taxonomic scope as the highest taxonomic level that maintains similar vulnerability to a predator[56]. Vulnerability is strongly influenced by morphology, although behavioural traits can also be important. As morphological traits are generally conserved

among arthropods generally up to the family level[57], we chose this as the taxonomic scope for arthropods. For the few non-arthropod prey in our database, we allowed the resource taxonomic scope to be as high as phylum as, specifically within bromeliad non-arthropods, prey morphology is well conserved.

For each information source, original information about pairwise trophic interactions was expanded to other pairwise interactions within the overlap of resource and consumer scopes.

Ranking information types in Step 1 and 2

We compiled all information in Steps 1 and 2 into a single value for each pairwise interaction (possible values: 1, 0, NA), prioritizing information where present in the order: forbidden links > gut contents > feeding trials > experiments in bromeliads > literature from other systems. We considered forbidden links first, in order to impose these fundamental constraints of morphology and physiology[58]. We considered gut contents, based on the actual diet of consumers in bromeliads, to be more reliable source of information on realized trophic interactions than feeding trials, where conditions (artificial containers, no choice experiments) were abstracted from that of natural bromeliads. Information from our experiments in bromeliads was considered even less reliable as consumption is generally inferred (addition of one species leads to decreased survival in another) rather than observed. The least reliable source of information was judged to be that from literature sources, as these sources inevitably were based on freshwater systems other than bromeliads.

By ranking these sources of information, we could use the first one or zero recorded for a pairwise interaction as the final interaction value. As a check, we examined the concordance in pairwise interactions between information sources. In many cases, all information sources with definitive interaction values (i.e. 1 or 0) agreed unanimously on a particular pairwise interaction value. Species pairs without unanimous agreement typically involved gut contents and forbidden links (2% of all inferred links showed such a conflict), potentially reflecting the passive ingestion of detrital particles or microorganisms during invertebrate prey capture.

Step 3: Estimating missing interactions with a probabilistic model

After Step 1 and 2, we were able to infer presence of absences of links for 86% of potential pairwise interactions in all sites, leaving 14% of pairwise combinations with no data. In Step 3 (Extended Data Fig. 1), we use the filled cells in the matrix to estimate, for each missing

value, the probability that the unknown link exists (i.e. takes the value 1). These probabilistic models (see Supplementary Note 4) use no secondary source of information to inform this process, but instead borrow information from across the matrix to parametrize a niche of resources for each consumer[59]. As the probabilistic niche model uses existing information rather than adding new information, it is judged the weakest of the methods for inferring links, and so is placed last in the rank order of information sources. Therefore, the resulting networks have 1s and 0s for interactions inferred from Step 1 and 2 and the remaining interactions are assigned probabilities using the niche model in Step 3.

Step 4: Validation with stable isotopes

We validated the models in three field sites with small, intermediate and large species pools (Extended Data Fig. 1). We found a general correspondence between the mean trophic level of species estimated by our algorithm with that estimated from field data on relative $\delta^{15}N$ values of the same invertebrate species in bromeliads (see Supplementary Note 5, Supplementary Fig. 1). As the first estimate of trophic level is unweighted by energy flux and the second metric weighted, the correspondence is not expected to be perfect.

Bromeliad-level food web metrics

To create food web matrices at the bromeliad scale, we filtered the site-level food web matrices to include only those species found within the specific bromeliad.

In order to describe food web structure at either scale, links need to either exist (take the value 1) or not (take the value 0). However, following Step 3 at least some links are represented by probabilities. We therefore generated 100 possible versions of the food web in each bromeliad using independent Bernoulli random draws from the estimated pairwise interaction probabilities.

For each of the 100 Bernoulli-based food webs, we estimated structural metrics at both the species-level and the food web level (see Supplementary Note 6) and then averaged these food web metrics over all 100 versions of the food web. We used principal components analysis (PCA) to efficiently summarize the 14 food web structural metrics into a limited number of structural dimensions (Extended Data Table 1). We included both bromeliad-level and site-level food webs in this PCA so that we could directly compare PCA scores between levels. We scaled all metrics before conducting the PCA.

539 **Bromeliad environmental variables**

540 Within each field site, bromeliads were characterized with three environmental variables:
541 total detritus, water-holding capacity, and canopy openness[see also 54]. The total detritus in a
542 bromeliad was defined as the dry mass of all detritus, ranging in size from intact leaves down
543 to fine particles greater than 100 μm (the 0 - 100 μm particle range, excluded simply to
544 expedite filtering, is highly correlated with the > 100 μm mass). Water-holding capacity was
545 estimated by filling the emptied bromeliad with water until it overflowed. Canopy openness
546 was determined immediately over the center of the bromeliad, and ranged from 1 (open) to 0
547 (closed), with values homogeneous amongst bromeliads within a field site for 22 of the 26
548 sites. In a few cases, measurements of detritus were for a narrower size range of particles than
549 required or actual rather than maximum water was measured. Here, predictive models were
550 used to estimate the missing data based on other measured variables[54].

551 **Regional environmental variables**

552 We downloaded, from online databases and for each of our site locations, data on net primary
553 productivity (NPP), annual mean temperature, annual precipitation, and precipitation
554 seasonality (renamed "precipitation variability" throughout this study to prevent readers from
555 misinterpreting this variable, calculated as the monthly coefficient of variation in
556 precipitation, as a measure of seasonality). We calculated aridity and potential
557 evapotranspiration by combining solar radiation measures with downloaded monthly
558 precipitation, minimum temperature and maximum temperatures values. All data was
559 compiled and averaged for the period 2000-2013, covering the temporal extent of our
560 bromeliad data, and at a spatial resolution of 1km (10km for NPP). We downscaled regional
561 environmental variables for a few sites that were closer than one raster and averaged data for
562 sites that spanned multiple rasters. Full details of data sources and procedures are given in
563 Supplementary Note 7.

564 There were varying degrees of collinearity between the site-level bioclimatic variables (NPP,
565 aridity, annual mean temperature, annual precipitation, precipitation variability). As it is
566 difficult to include such collinearity at the group-level in piecewise structural equation
567 models, we removed this collinearity using a PCA. The first four axes of this PCA axis
568 (Supplementary Table 6) accounted for 96% of the total variation. Axis 1 (43.7%) correlated
569 best with aridity, Axis 2 (27.9%) was dominated by precipitation variability, Axis 3 (14.3%)

correlated with annual mean temperature, and Axis 4 (9.7%) correlated with NPP. The fifth bioclimatic variable, annual precipitation, was not clearly aligned with any one axis, and so could not be isolated by the PCA. We therefore did not consider this variable further.

Modelling environmental control of food web metrics

We developed piecewise structural equation models (pSEMs) to individually explain food web size and shape as represented by the first two axes of the PCA of food web structural metrics. These pSEMs included both bromeliad-level and regional environmental variables, as well as causal pathways within and between these two levels of environmental variables. All environmental variables were centered and scaled prior to analysis to ensure that they were comparable. We accounted for non-independence of bromeliads within sites through a random effect for site in the underlying linear mixed effect models. We did not include temporal random effects within sites after initial analyses revealed temporal effects to be minor.

We first used an AIC-based model selection process to determine the following aspects of pSEM structure: (1) whether bromeliad capacity and detrital content are better modeled on linear or logarithmic scales; (2) whether linear or quadratic functions better represented the effects of each of three variables related to hydrological disturbance – precipitation variability, aridity and bromeliad water – as disturbance can have unimodal effects; (3) whether the best models had no interactions between environmental variables in their effects on food web structure, or only interactions within a class of driver (where class is one of energy, disturbance, temperature, ecosystem size), or both within-class and cross-class interactions. The within-class interactions for energy were bromeliad detritus × NPP, for temperature were canopy openness × annual mean temperature, and for disturbance were bromeliad capacity × aridity or precipitation variability. We considered only cross-class interactions that were predicted from theory, specifically the interaction between energy and temperature (i.e. bromeliad detritus × annual mean temperature) and between ecosystem size and energy (i.e. bromeliad capacity × NPP).

In sum, we evaluated pSEMs (Extended Data Table 6) that represented all six possible combinations of (1) and (2) and all eight possible combinations of (1) and (3). We did not consider models that combined (2) and (3) as such models would have fit so many paths that they would be difficult to interpret. We used AIC from the piecewiseSEM R package[60] to

compare pSEMs, choosing the best model as that with the lowest AIC. If two models were < 2 AIC units apart, we chose the model with fewer terms (Extended Data Table 7).

Once the best pSEM model structure was determined, we examined residual plots of each generalized linear models within the pSEM with the DHARMa R package[61] and log-transformed response variables when needed. After variable transformation, we reran the pSEM model selection procedure. We also tested for spatial autocorrelation with the DHARMa R package, confirming that Moran's I was neither strong nor significant (absolute Moran's $I < 0.4$, $p > 0.05$).

We evaluated the robustness of each final pSEM with Fisher's C, which measures the deviation of the model from the observed variance-covariance matrix, and ensured that there were no missing paths through tests of directed separation (must have $p > 0.05$). The direct path coefficients and their error was extracted and used to evaluate which paths were significant.

For each of the environmental drivers in our pSEM, we estimated their direct, indirect and total effects on the food web structure response. A direct effect occurs when there a potential driver and a response variable are connected by a causal path, and this causal path is not interrupted by a mediating variable. An indirect path occurs when another variable acts as a mediator between the driver variable and the response variable. There may be multiple indirect paths between any particular driver and response variable, and we sum all such paths to generate the overall estimate of the indirect effect. Finally, total effects refer to the sum of direct and indirect effects. To calculate these effect sizes, we used the semEff function from the semEff R package[62], with 1000 permutations and the 'optimx' optimizer.

For each pSEM, we also isolated effects of within-site variation from between-site variation in bromeliad capacity, detritus and openness on food web structure. Specifically, to isolate within-site variation in these environmental variables, we subtracted site means from values and reran the pSEMs. As regional climate variables have by definition no within-site variation, such variables are not included in within-site pSEMs. To isolate between-site variation in these environmental variables, we replaced bromeliad-level values with their site means and reran the pSEMs.

We ran similar pSEMs for species pool-level food webs (Supplementary Note 8, Supplementary Fig. 2).

Mediation of environment-food web relationships by abundance and traits

Finally, we examined potential mediation of paths from environmental drivers to food web structure by either total invertebrate abundance or community-weighted trait axes. For the latter, we used four trait axes (Extended Data Table 5) previously identified as capturing the major independent gradients in invertebrate traits[52,54]. In total, each path between an environmental driver and a food web metric in the original pSEM was replaced by five potential mediators (total abundance, four trait axes) so to make the new pSEM efficient we only considered significant paths from the original pSEM. We calculated the indirect effect via each potential mediator, summing this over the four trait axes to calculate the net trait effect (Supplementary Table 2). In addition, for the response of food web shape (PCA2), we replaced the four trait axes with abundance-weighted mean body mass in the above analysis to evaluate the theoretical prediction that high temperature and low energy favoured lower body masses, which in turn led to changes in food-web shape. In this pSEM, there was a significant positive correlation between total abundance and mean body mass. Such correlations can complicate the partitioning of mediating paths. This correlation could be represented in the pSEM as either abundance determines body mass or body mass causes abundance, but in neither case did body mass significantly mediate the effect of any environmental driver on PCA2. Thus, we can conclude that body mass is not a meaningful mediator of environmental effects on food-web shape.

Software

Unless otherwise stated, all analysis were completed using R 4.4.2.

Data availability

All data are available on the Open Science Framework[63]:
https://doi.org/10.17605/OSF.IO/S5BQU

Code availability

All R scripts are available on the Open Science Framework[63]:
https://doi.org/10.17605/OSF.IO/S5BQU

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Author contributions: Following the CRediT roles, with contributions in rank order.

Conceptualization: DSS, AAMM, OD, PR, JSP, ALG, EJO'G, UB, GQR, PK, BG, CLW, LMG, MMP, RC, PMO, IMB, PAPA, JSL, NACM, VFF, MCM

Methodology: AAMM, DSS, MMP, LMG, PR, NACM, UB, PK, CLW, BG, OD, ALG, EJO'G

Investigation: DSS, RC, OD, PMO, GQR, JSL, RMF, CL, BC, LMG, JSP, IMB, NACM, MCM, VFF, GCOP, AAMM, ALG, PK, PAPA, FO-B, BAR, MJR, JTN, GM, ST

Visualization: DSS, PR, LMG, AAMM

Funding acquisition: DSS, GQR

Project administration: DSS, GQR, UB

Writing – original draft: DSS, MCM, CL, EJO'G

Writing – review & editing: EJO'G, JSP, ALG, CLW, GQR, MCM, OD, LMG, MMP, UB, AAMM, PR, RC, PMO, PK, BG, IMB, PAPA, JSL, VFF, RMF, CL, BC, FO-B, BAR, MJR, JTN

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Additional information

Extended Data and Supplementary Materials are available for this article.

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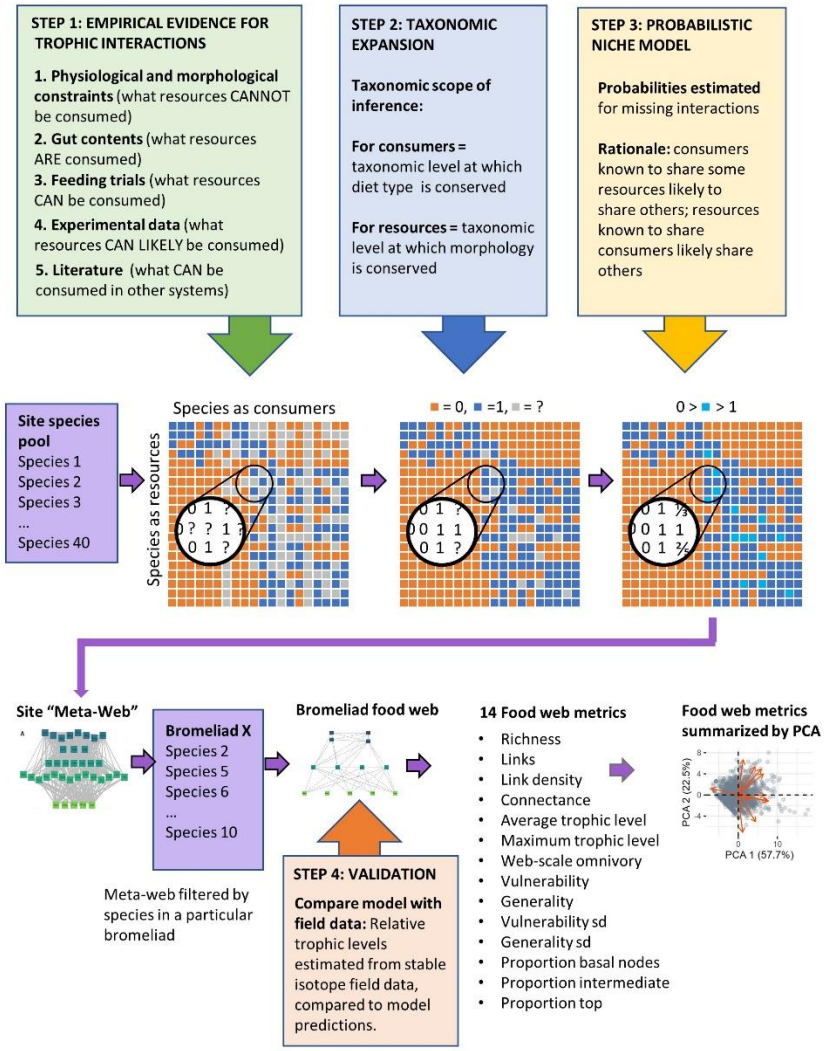
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Extended Data Figure 1. The reproducible workflow used in this study for inferring food webs from species composition data based on empirical evidence, taxonomic expansion, and probabilistic modeling. We show here an idealized site-level food web matrix that is intentionally smaller than the ones generated in this study so that the matrix cells can be easily visualized. The matrix cells are filled with numbers between 0 and 1 indicating the likelihood that a trophic interaction is with the fundamental niches of the interacting organisms. We use a question mark in this figure to indicate when the matrix cell value is unknown, although in the code this is technically a "NA" value. Once the food webs were created, we summarized their structure using a principal components analysis of 14 food web metrics.

Extended Data Table 1. Contributions (%) of each of 14 food web structural metrics to the first three principal component axes (% variance explained by each in parentheses) of a principal component analysis. The first two axes were selected to be analyzed in this study.

	PCA axis 1 (57.7%)	PCA axis 2 (22.5%)	PCA axis 3 (10.6%)
Richness	10.8	0.7	4.6
Links	11	0.7	0.5
Links density	11.7	0.7	2.1
Connectance	1.6	0.3	44.9
Average trophic level	8.1	8.1	3.3
Maximum trophic level	3.7	14.5	5.1
Web omnivory	0.3	22.4	0.7
Vulnerability	11.7	0.7	2.1
Generality	11.7	0.7	2.1
Vulnerability SD	3.9	13	7.8
Generality SD	9	0	9.9
Proportion basal	9.5	0.7	9.2
Proportion intermediate	0.2	25.5	7.3
Proportion top	6.8	12.1	0.5

Extended Data Table 2. Standardized estimates for effects of predictors on responses within a piecewise structural equation model (SEM_1_1_0, defined in Extended Data Table 6), ultimately explaining variation in log PCA 1 (a proxy of food web size). “Aridity”, “NPP”, “Temperature” and “Precipitation variability” refer to PCA axes that load predominantly on each of these variables respectively. Significant p-values are indicated in boldface. Overall the pSEM did not deviate from the observed variance-covariance matrix ($\chi^2_4 = 3.79$, $p = 0.44$ and Fisher’s $C_{(df = 8)} = 7.07$, $p = 0.53$).

Response	Predictor	Estimate	SE	DF	P
PCA 1 (log)	NPP	0.087	0.121	30.2	0.476
PCA 1 (log)	Bromeliad detritus (log)	0.275	0.043	771.1	**0.000**
PCA 1 (log)	Canopy openness	-0.010	0.076	52.2	0.899
PCA 1 (log)	Temperature	0.004	0.113	27.0	0.970
PCA 1 (log)	Bromeliad capacity (log)	0.378	0.039	1045.6	**0.000**
PCA 1 (log)	Aridity	-0.442	0.113	28.2	**0.001**
PCA 1 (log)	Precipitation variability	-0.037	0.115	26.2	0.748
PCA 1 (log)	NPP × Bromeliad detritus (log)	-0.020	0.040	698.6	0.624
PCA 1 (log)	Temperature × Canopy openness	0.004	0.076	47.1	0.955
PCA 1 (log)	Aridity × Bromeliad capacity (log)	0.025	0.039	1010.2	0.518
PCA 1 (log)	Variability × Bromeliad capacity (log)	0.128	0.029	1045.2	**0.000**
Bromeliad capacity (log)	Aridity	0.125	0.093	24.0	0.190
Bromeliad capacity (log)	Canopy openness	0.127	0.038	649.9	**0.001**
Bromeliad capacity (log)	Temperature	0.294	0.094	25.2	**0.005**
Bromeliad detritus (log)	Bromeliad capacity (log)	0.324	0.027	1041.4	**0.000**
Bromeliad detritus (log)	Canopy openness	-0.333	0.035	958.3	**0.000**
Bromeliad detritus (log)	NPP	0.109	0.105	27.6	0.308
Bromeliad detritus (log)	Temperature	0.251	0.104	27.1	**0.023**
Bromeliad detritus (log)	Aridity	0.274	0.103	26.0	**0.013**
Canopy openness	Temperature	0.357	0.143	25.9	**0.019**
Canopy openness	Precipitation variability	0.380	0.142	25.6	**0.013**
Canopy openness	NPP	-0.467	0.143	25.9	**0.003**

Extended Data Table 3. Standardized estimates for effects of predictors on responses within a piecewise structural equation model (SEM_1_0_0, defined in Extended Data Table 6), ultimately explaining variation in log PCA 2 (a proxy of food web shape). “Aridity”, “NPP”, “Temperature” and “Precipitation variability” refer to PCA axes that load predominantly on each of these variables respectively. Significant p-values are indicated in boldface. Overall the pSEM did not deviate from the observed variance-covariance matrix ($\chi^2_4 = 3.79$, $p = 0.44$ and Fisher’s $C_{(df = 8)} = 7.07$, $p = 0.53$).

Response	Predictor	Estimate	SE	DF	P
PCA 2 (log)	Bromeliad detritus (log)	0.079	0.032	1045.0	**0.015**
PCA 2 (log)	Canopy openness	0.016	0.038	1019.0	0.683
PCA 2 (log)	Bromeliad capacity (log)	-0.066	0.030	1034.2	**0.028**
PCA 2 (log)	Aridity	-0.090	0.118	25.7	0.452
PCA 2 (log)	Precipitation variability	-0.386	0.118	25.9	**0.003**
PCA 2 (log)	Temperature	-0.448	0.119	26.7	**0.001**
PCA 2 (log)	NPP	0.337	0.119	26.9	**0.009**
Bromeliad capacity (log)	Aridity	0.125	0.093	24.0	0.190
Bromeliad capacity (log)	Canopy openness	0.127	0.038	649.9	**0.001**
Bromeliad capacity (log)	Temperature	0.294	0.094	25.2	**0.005**
Bromeliad detritus (log)	Bromeliad capacity (log)	0.324	0.027	1041.4	**0.000**
Bromeliad detritus (log)	Canopy openness	-0.333	0.035	958.3	**0.000**
Bromeliad detritus (log)	NPP	0.109	0.105	27.6	0.308
Bromeliad detritus (log)	Temperature	0.251	0.104	27.1	**0.023**
Bromeliad detritus (log)	Aridity	0.274	0.103	26.0	**0.013**
Canopy openness	Temperature	0.357	0.143	25.9	**0.019**
Canopy openness	Precipitation variability	0.380	0.142	25.6	**0.013**
Canopy openness	NPP	-0.467	0.143	25.9	**0.003**

Extended Data Table 4. Partitioning the direct effects of environmental variables (columns in tables) on (a) food web size (log PCA1) and (b, c) food web shape (log PCA2). “Aridity”, “NPP”, “Temperature” and “Precipitation variability” refer to PCA axes that load predominantly on each of these variables respectively. For each environmental variable in (a,b), the direct effect is partitioned between pathways mediated by total abundance, community-weighted means (“CWM”) of four trait axes and the residual (i.e. unexplained) direct effect. The net trait effect is calculated as the sum of the four trait-mediated paths, and is shown in Fig. 4. In (c), the community-weighted means of trait axes are replaced by the community-weighted mean body mass. In all tables (a-c), boldfaced values indicate significant direct effects or mediating paths (for a mediating path to be significant, both component paths must also be significant). For example, the mediating path of bromeliad capacity - total abundance - log PCA1 (estimate = 0.182, this table) is the product of a significant direct effect of bromeliad capacity on total abundance (estimate = 0.444 in Supplementary Table 2), and a significant direct effect of total abundance on log PCA1 (estimate = 0.409 in Supplementary Table 2). Bold italicized values for net traits indicate that at least one trait axis was a significant mediator.

(a)

Mediator	Bromeliad capacity (log)	Aridity	Bromeliad detritus (log)	Precipitation variability	Precipitation variability x bromeliad capacity (log)
Remaining direct	**0.099**	**-0.227**	**0.185**	-0.028	0.02
Total abundance	**0.182**	**-0.202**	**0.065**	-0.039	**0.075**
CWM trait axis 1	0.0012	-0.0039	**-0.0080**	-0.0023	-0.0069
CWM trait axis 2	-0.0066	-0.0241	0.0122	-0.0031	0.0014
CWM trait axis 3	**0.0084**	**0.105**	-0.0230	**0.0322**	-0.0040
CWM trait axis 4	0.0018	-0.0040	0.0024	0.0086	0.0024
Net traits	***0.0047***	***0.0731***	***-0.0164***	***0.0141***	-0.0071

(b)

Mediator	Bromeliad capacity (log)	Precipitation variability	Temperature	NPP	Bromeliad detritus (log)
Remaining direct	-0.002	**-0.447**	**-0.461**	**0.355**	**0.064**
Total abundance	**-0.044**	0.0068	0.0057	-0.0168	**-0.0109**
CWM trait axis 1	-0.0002	0.0017	-0.0002	-0.0060	0.0034
CWM trait axis 2	-0.0079	-0.0034	0.0021	0.0017	0.0132
CWM trait axis 3	0.0015	0.0058	0.0015	0.00056	-0.0038
CWM trait axis 4	0.0020	0.0086	0.0062	-0.0022	0.0018
Net traits	-0.0047	0.0127	0.0097	-0.0059	0.0146

(c)

Mediator	Bromeliad capacity	Precipitation variability	Temperature	NPP	Bromeliad detritus
Remaining direct	-0.006	**-0.434**	**-0.451**	**0.344**	0.081
Total abundance	**0.044**	0.007	0.005	-0.018	-0.011
CWM body mass	0.000	0.000	0.000	0.000	0.000
Net traits	0.000	0.000	0.000	0.000	0.000

Extended Data Table 5. Four invertebrate trait axes were based on a PCA analysis of 64 traits by previous studies as described in Methods. Each trait axis can be interpreted based on its correlation with these traits, and we provide here the top trait correlations (r = Pearson correlation coefficient), positive and negative, for each axis.

	Trait Axis 1	**Trait Axis 2**	**Trait Axis 3**	**Trait Axis 4**
Top traits negatively correlated with axis (r ≤ -0.5)	No resting stage (r = -0.67); Flat ovoid body (r = -0.57); Sclerotized exoskeleton (r = -0.54)	Siphon/spiracle respiration (r = -0.69); Active dispersal (r = -0.65)	Sclerotized spines (r = -0.75); Surface swimmer (r = -0.63); Dorsal plates (r = -0.59);	Full water swimmer (r = -0.60); Adults aquatic (r = -0.59); Flat elongate (r = -0.58)
Top traits positively correlated with axis (r ≥ 0.5)	Consumes living microphytes (r = 0.75); Nymphs aquatic (r = 0.73); Diapause or dormancy (r = 0.70)	Tube builder (r = 0.81); case or tube defence (r = 0.81); Asexual reproduction (r = 0.72)	No correlations greater than 0.42	Consumes dead plant litter (r = 0.67); Shredder (r = 0.51)

Extended Data Table 6. Formulation of 14 piecewise structural equation models. Within driver interactions = Detritus x NPP, Canopy openness x Temperature, Bromeliad capacity x Aridity, Bromeliad capacity x Precipitation variability. Cross-driver interactions = Bromeliad capacity x NPP, Detritus x Temperature.

Model name	Bromeliad detritus and capacity: scale	Interactions between local and regional drivers	Hydrology variables: linear or non-linear
SEM_0_0_0	linear	none	all linear
SEM_1_0_0	logarithmic	none	all linear
SEM_0_1_0	linear	within-driver interactions	all linear
SEM_1_1_0	logarithmic	within-driver interactions	all linear
SEM_0_2_0	linear	cross-driver interactions	all linear
SEM_1_2_0	logarithmic	cross-driver interactions	all linear
SEM_0_3_0	linear	within- and cross-driver interactions	all linear
SEM_1_3_0	logarithmic	within- and cross-driver interactions	all linear
SEM_0_0_1	linear	none	quadratic: Bromeliad capacity
SEM_1_0_1	logarithmic	none	quadratic: log(Bromeliad capacity)
SEM_0_0_2	linear	none	quadratic: Aridity
SEM_1_0_2	logarithmic	none	quadratic: Aridity
SEM_0_0_3	linear	none	quadratic: Precipitation variability
SEM_1_0_3	logarithmic	none	quadratic: Precipitation variability

985 **Extended Data Table 7**. Comparison of AIC values for 14 potential forms of SEM models,
986 for each of two response variables. Model formulations, named here by a code, are
987 described in detail in Extended Data Table 6. Responses are the first two axes of a PCA
988 summarizing food web structural metrics, with PCA 1 representing food web size and PCA 2
989 food web shape; these two axes were log transformed to normalize residual plots. For each
990 response variable the model with the lowest AIC value (boldface) was selected (asterisk).
991 Models within two AIC values of each other were considered equally informative, and in this
992 case the simplest model was selected.

993

Model name	**Log PCA 1**	**Log PCA 2**
SEM_0_0_0	8745.1	8330.1
SEM_1_0_0	8055.6	**7824.3 ***
SEM_0_1_0	8741.4	8334.6
SEM_1_1_0	**8042.6***	**7825.3**
SEM_0_2_0	8744.0	8332.8
SEM_1_2_0	8045.4	7827.3
SEM_0_3_0	8744.7	8337.7
SEM_1_3_0	**8042.6**	7827.2
SEM_0_0_1	13780.4	13401.0
SEM_1_0_1	11744.0	11530.2
SEM_0_0_2	11820.2	11408.9
SEM_1_0_2	11129.2	10900.7
SEM_0_0_3	12056.0	11643.3
SEM_1_0_3	11362.8	11135.1

994

Supplementary Files

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