

Extreme rainfall disrupts freshwater energy flux without altering food-web structure

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Extreme rainfall disrupts freshwater energy flux without altering food-web structure

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Abstract

Climate change is altering rainfall regimes, yet how these changes affect energy flux through food-webs remains poorly understood, limiting our ability to predict ecosystem responses across geographic scales. We conducted a coordinated experiment across Central and South America (18°N–29°S) using 210 freshwater microcosms to test how shifts in rainfall regimes and ecosystem size influence food-web structure and functioning. Increased rainfall amount reduced energy flux by disrupting decomposition and predation pathways, whereas rainfall frequency had no effects. These functional declines occurred without changes in food-web structure, revealing a decoupling between network structure and ecosystem functioning under hydrological disturbances. Larger ecosystems sustained higher energy flux and exhibited more trophically centralised food webs, with interactions concentrated at intermediate trophic levels. Our findings show that shifts in rainfall regimes can impair freshwater ecosystem functioning even when food-web structure remains unaltered, while larger ecosystems may buffer these effects by sustaining higher energy flux.

Keywords: climate change, species interactions, biodiversity, ecosystem functioning.

Introduction

Climate change is one of the most pervasive anthropogenic pressures on Earth¹ and is predicted to alter precipitation regimes in increasingly complex ways^{2,3}. These changes are expected to intensify the frequency of extreme hydrological events, such as floods and droughts, with profound yet still poorly understood consequences for biodiversity and ecosystem functioning, particularly in freshwaters^{4–10}. While research has traditionally focused on gradual shifts in average climate conditions, the ecological impacts of extreme events remain underexplored, despite their potential to trigger abrupt and cascading disruptions across ecological networks^{5,11}.

Most studies simulating precipitation extremes have been restricted to single trophic levels, particularly primary producers⁵. However, climatic disturbances often propagate across entire food webs, altering species interactions, trophic organisation, and energy transfer among consumers at multiple trophic levels^{12,13}. Since food webs integrate species interactions and energy flux (i.e., the transfer of energy through trophic links^{14,15}), food web structure is central to understanding ecosystem responses to climatic variability^{12,14,16}. Multitrophic interactions can buffer ecosystems against moderate disturbances, but extreme events can destabilise these networks, reducing their resilience and altering the distribution of energy^{4,12,16–18}. For instance, drought often reduces aquatic habitat size, connectivity, and resource availability, leading to simplified food webs and diminished functions such as decomposition and secondary production^{4,19}. Alternatively, by concentrating organisms within shrinking habitats, drought is expected to increase encounter and attack rates^{20,21}, thereby enhancing energy flux^{20,21}. In contrast, floods may increase connectivity and resource inputs but can also cause physical disturbance and biomass washout^{22,23}, disrupting trophic interactions, reducing encounter and attack rates and rewiring energy pathways^{24–26}. Energy flux is particularly sensitive to such environmental variability and provides an integrative measure of ecosystem functioning^{14,15}, but empirical evidence on how extreme rainfall shapes energy flux across food webs remains scarce. This gap is critical because the impacts of climatic stressors often vary across regions, meaning that broad generalizations require coordinated experiments across multiple sites^{5,27}. Thus, a macroecological, multitrophic approach is needed to identify general principles of ecosystem responses to extreme climatic events.

In addition to climate drivers, ecosystem size is a fundamental determinant of food web structure and function^{14,28,29}. Larger ecosystems typically sustain higher biodiversity, longer food chains, and more trophic interactions, which can stabilize dynamics and enhance energy transfer^{30–32}. These properties suggest that ecosystem size may buffer

ecosystems against climatic disturbances by maintaining interaction diversity and functional redundancy³³. However, empirical tests of this hypothesis are limited, particularly across broad geographic scales where size effects may interact with climate-driven stressors. Tank bromeliads provide an exceptional natural system for testing these ideas^{34,35}. They are distributed over broad environmental gradients across the Neotropics and host complex aquatic food webs comprising microorganisms, detritivores, and predators^{36,37}. This biodiversity underpins key ecosystem functions, such as decomposition, primary productivity, and nutrient cycling^{35,38,39} (Fig. 1a). Their structure allows for manipulative experiments while retaining natural ecological complexity, making them powerful model systems for studying how climatic variability and habitat attributes interact to shape food web dynamics^{8,34,35}.

Here, we leveraged tank bromeliads as natural microcosms and powerful model systems for testing climate-driven changes in freshwater ecosystems³⁵. We conducted a coordinated experiment spanning seven locations across Central and South America (18°N to 29°S, Fig. 1b) to investigate how extreme rainfall and ecosystem size influence food web structure and energy flux. We manipulated two rainfall parameters: (i) the mean daily amount of rainfall, μ ; and (ii) the distribution of rainfall events around this mean through time, k (i.e., a measure of evenness in the frequency distribution of rainfall; hereafter “frequency”). Reductions in both rainfall amount and frequency increase the proportion of days that bromeliads are empty of water. We implemented a response surface experimental design across all seven sites, applying ten levels of rainfall amount and three levels of rainfall frequency, for a total of 210 independent food webs. This design enabled us to compare ambient, baseline rainfall conditions informed by historical daily precipitation data at each site^{8,9} (see Methods) with extreme fluctuations in rainfall quantity (10–300%) and frequency (50–200%) relative to historical variability^{8–10,40}. Ecosystem size was measured as the maximum water-holding capacity of the bromeliad

by filling the plant to the point of overflowing^{29,39}, with volumes ranging from 73 to 1,726 mL (mean = 509 mL, SD = 370).

We hypothesised that (i) extreme rainfall events would directly reduce food web complexity and energy flux by disrupting community assembly and trophic interactions (Fig. 1c), (ii) larger ecosystem size would enhance both complexity and energy flux by providing more space for species and interactions, thereby partially mitigating rainfall impacts (Fig. 1d), and (iii) extreme rainfall events would exert indirect effects on energy flux through their influence on food web structure (Fig. 1e). More specifically, we expected rainfall-driven hydrological instability to simplify trophic organisation and reduce energy transfer through both decomposition pathways (from basal resources to detritivores) and predation pathways (from detritivores to predators) (Fig. 1a,e). In contrast, we predicted that larger ecosystems would buffer the effects of hydrological instability, maintaining more complex and energetically active food webs because rainfall-induced changes in water volume are proportionally smaller than in smaller ecosystems. By integrating large-scale manipulations with a mechanistic food web and energetic framework, our study provides novel empirical insights into how shifts in rainfall patterns and ecosystem size jointly regulate freshwater food web structure and functioning across the Neotropics.

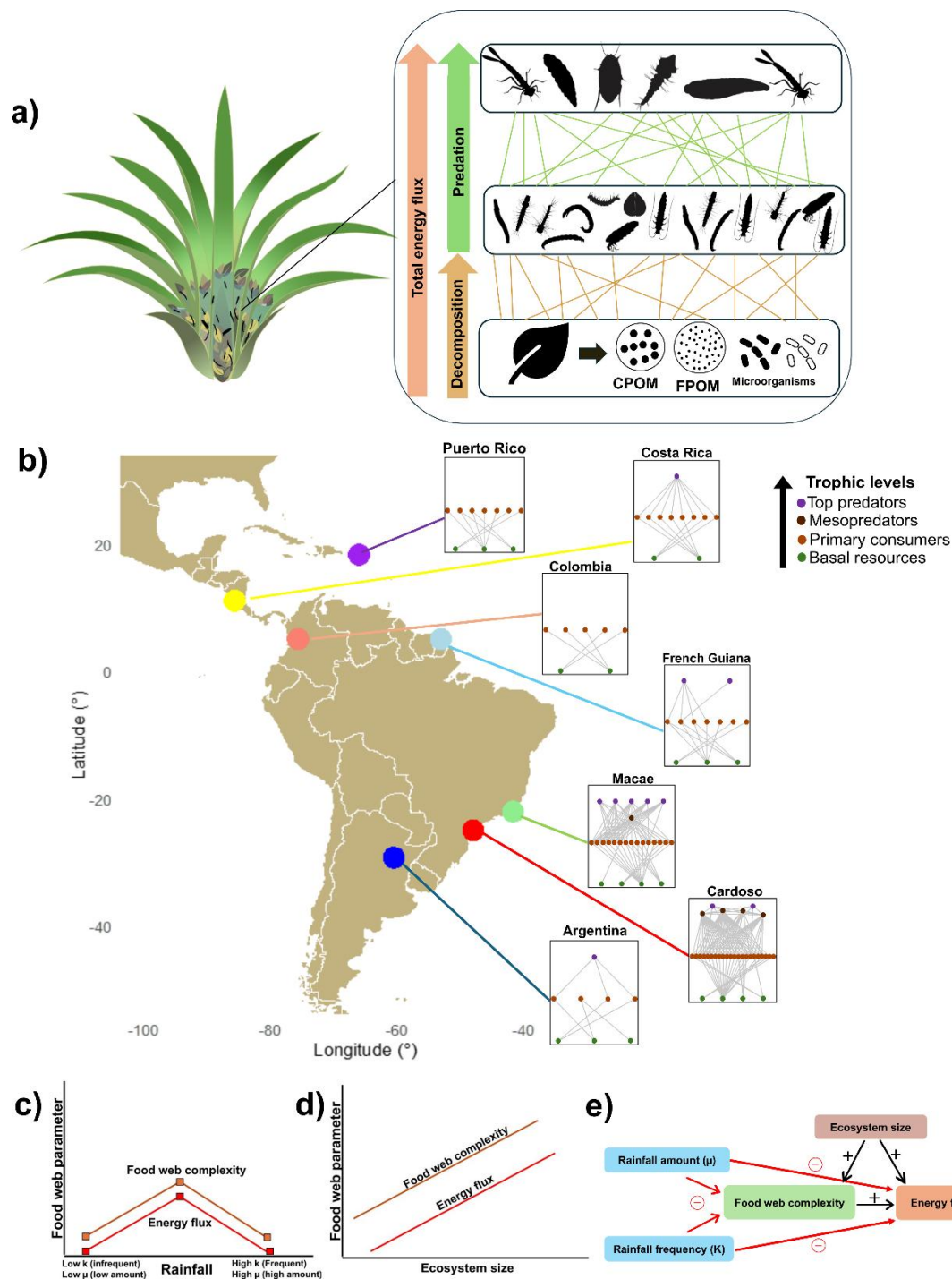


Figure 1. (a) Schematic representation of the detritus-based tank-bromeliad food web and associated energy flux pathways. Basal resources - including coarse particulate organic matter (CPOM), fine particulate organic matter (FPOM), and microorganisms - constitute the primary energy source for detritivores, supporting the decomposition pathway of energy flux. Detritivores are subsequently consumed by predators, forming the predation pathway. (b) Map of the seven study sites across the Neotropics, with representative food webs shown under ambient (baseline) conditions. (c-e) Conceptual framework illustrating the predicted effects of (b) rainfall amount and frequency and (c) ecosystem size on food web complexity and energy fluxes, highlighting (d) their direct and indirect influences. Note that negative effects of rainfall amount (μ) and frequency (k) on food web complexity and energy flux in (d) are hypothesised to be unimodal.

Results

Eleven metrics of food web structure (Extended data Table 1) were summarised using principal component analysis (PCA) to describe two key food web dimensions (Fig. 2a-b). The first axis represented a gradient of trophic centralisation, with positive values reflecting a redistribution of species and interactions toward intermediate trophic positions, associated with reduced proportions of basal and top species, increased food-chain length, and greater linkage density (Fig. 2b-c). The second axis described a gradient of trophic connectivity, with positive values indicating increased connectance, omnivory, and reduced vulnerability (Fig. 2b-c).

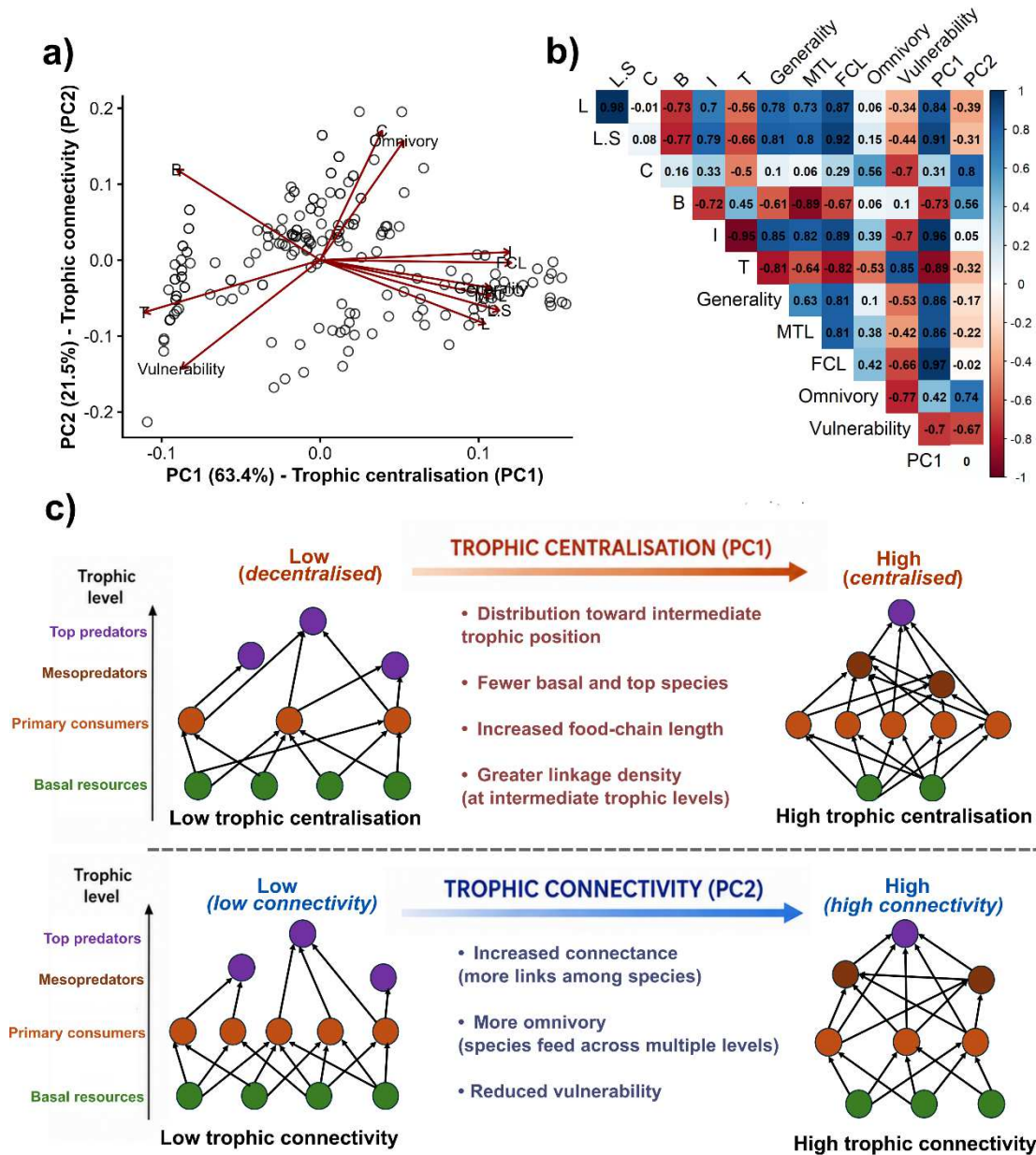


Figure 2. Empirical and conceptual dimensions of food-web structure. (a,b) Multivariate characterization of food-web structure across study sites. (a) Principal component analysis (PCA) biplot showing the ordination of sites (grey circles) based on food-web structural metrics, with vectors (red arrows) indicating the loadings of each metric. (b) Correlation matrix between food-web metrics and the first two principal components. Cell colours represent Pearson correlation coefficients (r), with red indicating negative and blue indicating positive relationships. For full definitions, see Extended data Table S1. (c) Conceptual representation of food-web organisation along the two principal axes identified in the PCA. Based on their correlations with the original food-web metrics we interpret PC1 as a gradient of trophic centralisation and PC2 as a gradient of trophic connectivity. Top panels show increasing trophic centralisation, with interactions concentrated at intermediate trophic levels, reduced basal (B) and top species (T), greater linkage density and generality. Bottom panels show increasing trophic connectivity, with higher connectance and omnivory and less vulnerability. Nodes denote trophic groups (green - basal, orange – primary consumers, brown – mesopredators and purple - top predators), and arrows indicate feeding interactions.

Multigroup piecewise structural equation models (pSEM) revealed that increases in rainfall amount did not affect food web structure but reduced total energy flux (Fig. 3a), indicating that structure and function were decoupled under high rainfall. Specifically, increased rainfall amount directly decreased decomposition and predation pathways underlying energy flux, although the effect on the predation pathway was only consistent across all study sites when we accounted for direct effects of trophic centralisation (Fig. 3c, Extended data Fig. 1). When we accounted instead for the direct effects of trophic connectivity, rainfall amount significantly impacted decomposition or predation pathways only at Cardoso Island in Brazil and/or Costa Rica (Fig. 3d-e, Extended data Fig. 1). Overall, models that included trophic centralization rather than trophic connectivity explained more variance in energy fluxes, whether via the decomposition or predation pathway (r-squared values in Fig. 3). Rainfall frequency had no detectable influence on any component of food-web structure or energy flux (Fig. 3).

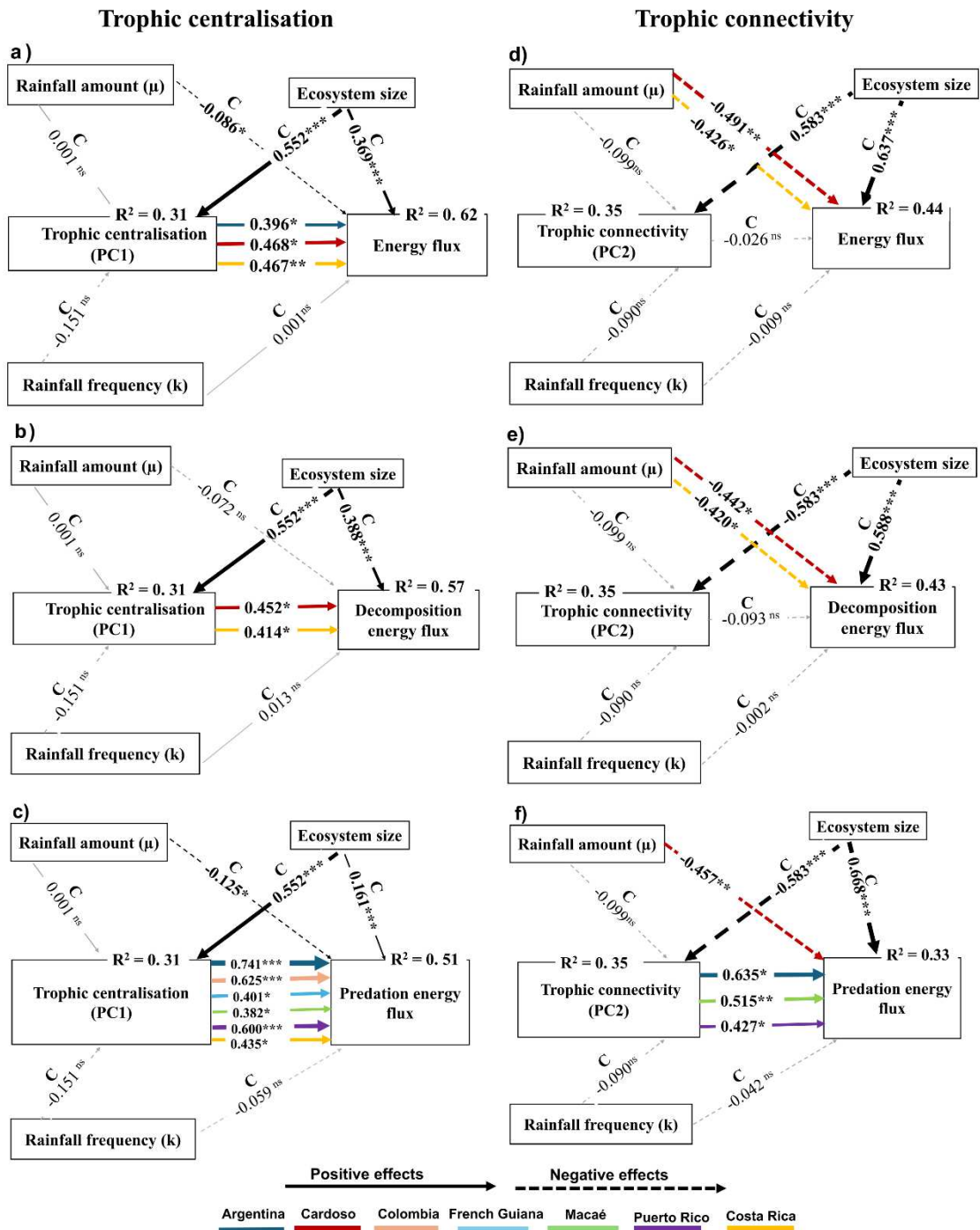


Figure 3. Direct and indirect effects of rainfall variability and ecosystem size on energy fluxes mediated by food-web structure. Multigroup piecewise structural equation models showing the effects of rainfall amount (μ), rainfall frequency (k), and ecosystem size on (a, d) total energy flux, (b, e) decomposition energy flux, and (c, f) predation energy flux. Panels a-c show models mediated by trophic centralisation (PC1), whereas panels d-f show models mediated by trophic connectivity (PC2). Solid arrows indicate positive effects, and dashed arrows indicate negative effects. Arrow widths are proportional to standardized path coefficients (values shown). Grey arrows denote non-significant paths ($P > 0.05$). Black arrows represent significant constrained (C) effects, estimated jointly across all sites when effects did not differ among locations, whereas coloured arrows indicate significant site-specific (S) effects that varied among sites and are shown separately for each location. Model fit is indicated by R^2 values at each response node.

Increasing ecosystem size altered food-web structure by promoting trophic centralisation (Fig. 3a-c) and reducing connectivity (Fig. 3d-f), patterns that were consistent across all sites. Ecosystem size also had direct positive effects on all energy fluxes across all sites, and indirect positive effects in some sites (Figs. 3, S1). Although ecosystem size also had indirect negative effects on predation energy flux, such effects were restricted to three sites and insufficient to offset the positive direct effect of ecosystem size (Fig. 3f). We also explored the role of species richness as a mediator of energy flux. Larger ecosystems supported greater species richness (Extended data Fig. 2a), which in turn enhanced total energy flux (Extended data Fig. 2b, $R^2 = 0.72$, $P < 0.001$). Species richness also emerged as a strong predictor of the food web structural properties (Extended data Fig. 2c,d). Together, these findings indicate that ecosystem size influences energy flux both directly and indirectly through its effects on biodiversity and trophic organisation.

Linear mixed-effects models with site as a random factor consistently outperformed quadratic counterparts for all response variables (Table S1), indicating that linear relationships best captured the influence of rainfall variability and ecosystem size on food web structure and energy flux. This lack of support for nonlinear responses contrasts with expectations that extreme climatic events would generate threshold or unimodal effects on ecosystem functioning. These findings also support the linear responses presented by pSEM results (Table S2-S3; Figs. S2-S3).

Discussion

Climate change does not affect ecosystems uniformly; instead, its impacts depend on how perturbations propagate through ecological networks. Here, we show that rainfall alteration and ecosystem size influence energy flow through fundamentally distinct pathways. Increased rainfall amount reduced energy flux pathways, indicating that

hydrological forcing can constrain ecosystem functioning across multiple compartments of the food web, weakening energy flux from basal to apex levels, which partially supports our first prediction (H_1 - Fig. 1b). Notably, these responses in energy flux, a measure of ecosystem functioning, occurred without detectable changes in food-web structure, revealing that ecosystem processes can respond directly to environmental conditions without requiring trophic network reorganisation^{7,39,41}. This decoupling between structure and function suggests that climatic disturbances may impair ecosystem functioning well before detectable changes emerge in biodiversity or network topology. Rainfall-driven disturbance, therefore, appears to operate primarily through direct physiological and behavioural constraints on consumers and decomposers rather than through structural network reconfiguration. Excess water likely impairs the biomass⁸, functional composition^{8,40}, and activity of both microbial decomposers and macroinvertebrate predators⁴², compromising key ecosystem processes. Such hydrological disturbances, comparable to flood-induced flushing in river systems⁴³, can displace organisms from bromeliads²², disrupt community assembly, and temporarily simplify food web structure, thereby reducing total energy flux. Although the food web may recover structurally over time, energy flux does not necessarily return to pre-disturbance levels, indicating a lag in functional recovery^{8,40}. These findings align with evidence that altered hydrology reduces detrital processing and limits energy availability to higher trophic levels^{44–46}. Notably, rainfall frequency had no significant effect on food web structure or energy transfer, whereas rainfall amount emerged as the primary driver, likely because intense rainfall generates stronger ecosystem-level disturbances (e.g., flushing) than shifts in rainfall frequency alone. Together, these results underscore that the magnitude of hydrological forcing plays a dominant role in shaping energy flow under climate change.

By contrast, ecosystem size influences energy flux through a structural pathway, mediated by biodiversity and the organisation of interactions, consistently evident across all study sites. Larger systems support higher species richness and redistribute interactions toward intermediate trophic levels, increasing trophic centralisation. This reorganisation enhances the energy transfer across the network, through both predation and decomposition pathways, consistent with our predictions (H_2 and H_3 – Fig. 1c-d) and theoretical expectations that larger ecosystems sustain longer food chains, greater biomass, and more complex interaction pathways^{28–30,47}. Importantly, the stronger effect of trophic centralisation relative to connectivity indicates that how interactions are arranged across trophic levels is more consequential than their overall connectivity. Networks with greater trophic centralisation may facilitate energy flow by concentrating interactions within intermediate trophic compartments, reducing losses and increasing transfer efficiency⁴⁸. Our results also suggest that larger ecosystems may buffer the effects of rainfall by sustaining higher rates of energy flux through greater biodiversity and more complex trophic organisation. This stabilising effect is likely driven by a combination of greater resource availability^{47,49}, increased redundancy⁵⁰, and the presence of alternative energy pathways (e.g., via predation and decomposition), which collectively reduce the sensitivity of ecosystem processes to disturbance. These findings underscore the central role of ecosystem size in modulating both the structural and functional dimensions of food webs^{31,32} and suggest that conserving or restoring larger freshwater habitats may help sustain ecosystem functioning under increasingly variable rainfall regimes.

Trophic centralisation consistently impacted energy flux across all pathways, whereas trophic connectivity exerted more context-dependent influences, most evident in predation-related fluxes. These contrasting patterns highlight the need to move beyond single-metric descriptions of food-web complexity, as emphasised in ecological network

theory⁵¹⁻⁵³. While increasing species richness promoted trophic centralisation, it reduced overall connectivity, indicating that biodiversity can reorganise networks in opposing ways, consistent with evidence that diversity and connectance are not monotonically coupled^{54,55}. This contrast also helps explain the weaker and more variable functional role of connectivity, whose effects likely depend on local species composition, interaction strengths, and the degree of functional redundancy within the food web^{55,56}. Because systems with higher generality tend to include more redundant interactions^{56,57}, trophic centralisation (positively associated with linkage density and generality) may encompass a greater proportion of functionally substitutable links (i.e., redundant) than trophic connectivity (Fig. 2). In highly redundant networks, additional links can create alternative pathways for energy flow and stabilise ecosystem functioning, whereas in more specialised communities, changes in connectivity may have limited consequences. These results indicate that the organisation of interactions across trophic levels, rather than overall complexity alone, determines the magnitude of energy flux through food webs.

In conclusion, our study shows that ecosystem responses to climate change depend not only on the magnitude and type of climatic forcing, but also on how energy pathways are organised within ecological networks. Hydrological disturbance impaired ecosystem functioning by reducing energy flux, with no detectable changes in network structure, revealing that functional declines can precede structural reorganisation. In contrast, larger ecosystems sustained higher energy flux through increased biodiversity and the reorganisation of trophic interactions, potentially buffering the consequences of hydrological variability for ecosystem functioning. This distinction demonstrates that structure and function are not intrinsically coupled but instead depend on the mechanisms through which environmental change propagates across ecological networks. By disentangling these contrasting responses across a broad biogeographic gradient, our study provides a framework for understanding how climate-driven hydrological changes

affect ecosystem functioning. More broadly, our findings suggest that structural properties of ecological networks alone may not fully capture responses to environmental disturbances, highlighting the need to integrate functional measures into assessments of ecosystem functioning under climate change.

Methods

Study site and experimental design. We performed a coordinated experiment across the Neotropics, manipulating the amount and frequency of rainfall entering natural micro-ecosystems. Our goal was to investigate the effects of variation in rainfall on food web dimensions and energy flux using aquatic macroinvertebrate communities inhabiting tank bromeliads. We replicated the experiment at seven sites and six countries across Central and South America (from 29°S to 18°N), including Las Gamas (Argentina), Cardoso and Macae (Brazil), Colombia, Pitilla (Costa Rica), French Guiana, and Puerto Rico. Detailed site descriptions and the experimental manipulations are provided in Srivastava et al.⁸ and Romero et al.⁹.

Rainfall manipulation. We experimentally simulated the rainfall variation for each site using procedures described in previous studies^{8,9}. We used daily rainfall data from the past five years at each site to determine the number of days with recorded rainfall amounts. We fitted these data to a negative binomial distribution characterized by the parameters μ and k . The parameter μ indicates the average daily rainfall, while k represents the frequency of rainfall events relative to this average over time. Since climate change impacts each site differently, our precipitation manipulations are proportional to current conditions at each site and preserve the temporal autocorrelation structure unique to each location. The treatment combinations varied μ by 30-fold and k by 4-fold around the ambient conditions, using a response surface design with 30 unique μ and k

combinations. The “ $\mu 1k1$ ” denotes the ambient (control) treatment combination. The various treatment combinations were created by multiplying the control value of μ by 0.1, 0.2, 0.4, 0.6, 0.8, 1, 1.5, 2, 2.5, and 3, and the control value of k by 0.5, 1, and 2. The range of μ and k values used in the experiment was generally broader than those recently observed at the sites during the experimental period⁸, meaning that the highest and lowest values represent extreme rainfall conditions. The experiment lasted 60 days, after which time the bromeliads were dissected and washed, and their contents were removed entirely and separated to collect the organisms and organic matter. All organisms were preserved in 70% ethanol and later counted, measured, and identified at the lowest possible taxonomic level.

Food web and energy flux variables.

Food web metrics. Trophic interactions were estimated through stomach content analysis based on morphological identifications of prey remains, together with field observations, feeding trials, and the literature (Supplementary data). Food webs were then constructed for each bromeliad in the experiment.

We assessed the likelihood of feeding interactions using a combination of predator-prey identity, body size ratios, and relevant traits of both predators and prey⁵⁸. Predators were categorized into two functional groups based on their feeding strategies - piercers and engulfers - which were determined by their mouthpart morphology. Interactions were classified as likely when engulfer predators were between 2 and 1000 times larger than their prey^{59,60}. For piercers, which are capable of attacking larger prey, interactions were classified as likely when predators were between 1000 times larger and 10 times smaller in body mass than their prey^{61,62}. Additionally, drawing on prior work and observations conducted by our group, we identified a set of unlikely interactions; those constrained by prey unpalatability, morphological or behavioural defences, or

spatial mismatches in microhabitat use among bromeliad macroinvertebrates (Table S4). These were treated as “forbidden links”, meaning that they were excluded from potential feeding relationships even when body size ratios suggested a possible match. By integrating all these criteria, we built a global interaction matrix for each bromeliad system. This matrix captured all likely feeding interactions, along with associated data on average biomass, total biomass, and total abundance for each consumer and resource involved (Supplementary data).

Eleven metrics were quantified to characterise food web structure (Extended data Table 1) using the Cheddar⁶³ package in R⁶⁴. Definitions of food web metrics and their type were based on Baiser et al.⁶⁵ (Extended data Table 1). Complexity metrics relate to the number of nodes (i.e., taxa) and links. Trophic height metrics relate to the number of trophic levels and food chains in the web. Trophic distributions of taxa describe the proportions of taxa found at the bottom, middle, and top of the food web. Dietary strategy relates to variation in the number and similarity of predators and prey among species in a web (Extended data Table 1).

To identify the major dimensions of food web structure, we carried out a principal component analysis (PCA) with the food web variables previously standardised and centred (Fig. 1a). The first two PC axes represented the majority of variation present in the original eleven variables (axis 1 = 63.4% and axis 2 = 21.5%; Fig. 1a) and were used as two independent dimensions of food web structure. These two axes were interpreted by assessing their correlation strength with each original food web metric (Fig. 1b). The first PC axis was negatively associated with the proportion of basal and top species, and positively associated with the proportion of intermediate species, capturing a gradient of trophic centralisation. Higher values along this axis therefore reflect food webs dominated by intermediate, generalist consumers with numerous trophic links, indicative of a more centralised and internally connected structure (Fig. 2b,c). In contrast, the second PC axis

represented variation in trophic connectivity, characterised by positive associations with connectance and omnivory, and negative associations with species vulnerability. This axis thus describes a shift towards more densely interconnected food webs with increased prevalence of omnivorous interactions (Fig. 2b,c).

Energy flux. Energy flux within food webs was estimated using the fluxweb⁶⁶ package in R. This method assumes an energetic steady state, meaning that for each consumer species, the rate of energy gained through consumption (energy input) is balanced by the rate of energy lost through metabolic processes and predation (energy output). To implement this approach, we utilized the "*fluxing*" function parameterized with: (1) binary predation matrices for each food web; (2) biomass data for each species, derived from individual body mass measurements⁹; (3) assimilation efficiencies adjusted for temperature dependencies and resource types (e.g., plant, detritus, or invertebrate)⁶⁷; (4) species preferences (w_{ij} 's) depending on resource biomasses; and (5) metabolic rates estimated using the average of species body masses and temperatures specific to each experimental bromeliad, following the methodology of Brown et al.⁶⁸.

The bromeliad ecosystem comprises multiple trophic compartments, ranging from basal resources - such as coarse and fine particulate organic matter (CPOM and FPOM) and microorganisms - to a variety of multitrophic consumers. Basal resources are consumed by detritivores, initiating the first energy flux pathway, while detritivores themselves serve as prey for higher trophic levels, contributing to consumer-driven energy flux (Fig. 1a). Accordingly, we estimated distinct energy pathways within the bromeliad food web, which correspond to key ecosystem functions. First, we quantified decomposition as the energy transferred from basal resources to detritivores through the consumption of microorganisms, CPOM, and FPOM (Fig. 1a). Next, we calculated predation as the energy transferred from detritivores to their predators. Finally, total

energy flux within each food web was estimated as the sum of these two pathways - decomposition and predation - equating to the total amount of carbon flowing through the food web. Here we did not quantify herbivory, because this pathway is less important in tank bromeliads ecosystem compared to decomposition⁶⁹. Energy flux units are given in Joules per second.

Statistical analyses. We used piecewise structural equation modelling (pSEM)⁷⁰ to assess the causal effects of rainfall changes on multiple dimensions of trophic interactions (PC scores) and energy flux through food webs across the Neotropics. We evaluated one model for each food web dimension (PCs) and energy flux component (decomposition, predation, total energy). We calculated the magnitude of an indirect effect from a path A to C through B in a pSEM is obtained by multiplying the direct path coefficients of A on B and B on C⁷⁰. We used multigroup analysis using local estimations to assess (a) model-wide estimates where parameters were allowed to vary among groups (“free model”) and (b) constrained models where parameters were fixed within seven groupings (sites). We considered the seven sites as the grouping variable. We constructed a pSEM in which all parameters were free to differ between sites and a model in which all parameters were fixed (constrained to a single value determined by all sites). We compared the free model with the constrained model in which pathway coefficients were held constant across sites. Non-significant differences between models indicated consistent pathway coefficients across sites, while significant differences suggested site-specific variation. Since the models differed significantly, we proceeded to identify which specific pathways differed among sites. Nonsignificant pathways associated with site-specific parameters were removed to create the most parsimonious models (Fig. 3). These models were fitted using generalized linear models (GLM) with Gaussian distributions.

To validate the robustness of the SEM results, we applied linear mixed effects

models⁷¹ (LMMs) with rainfall amount, rainfall frequency, and ecosystem size as fixed effects, and sampling site as a random intercept to account for spatial heterogeneity. We tested both linear and quadratic terms for rainfall amount and frequency to evaluate potential non-linear responses to climatic variability. We analysed five response variables: trophic centralisation, trophic connectivity, total energy flux, decomposition flux, and predation flux. Model selection based on Akaike Information Criterion (AIC) consistently favoured the simpler linear models over their quadratic counterparts (Table S1), indicating that linear relationships most accurately described the influence of rainfall variability and ecosystem size on food web dynamics - thus corroborating the results obtained from the SEM framework. Accordingly, we report only the results from the linear models.

To quantify the effects of ecosystem size on species richness, we fitted linear mixed-effects models (LMMs) with ecosystem size as a fixed effect and sampling site included as a random intercept to account for spatial heterogeneity. We then used a similar modelling framework to test how species richness influences food-web structure and energy flux, fitting LMMs with species richness as a fixed effect and sampling site as a random intercept.

Additionally, to explore how these predictor variables affect food web structure and energy dynamics across different geographic contexts, we conducted site-specific linear models for each of the seven study locations. Analysing each site independently allowed us to account for local ecological conditions and capture context-dependent responses to environmental variability. Model assumptions were assessed by visual inspection of residual distributions and homoscedasticity.

Data availability

The data supporting the findings of this study are available via Figshare Digital Repository at <https://doi.org/10.6084/m9.figshare.33307629>

Code availability

The main codes to reproduce the analyses and figures of this study are publicly available on Figshare Digital Repository at <https://doi.org/10.6084/m9.figshare.33307629>

Competing interests

The authors declare no competing interests.

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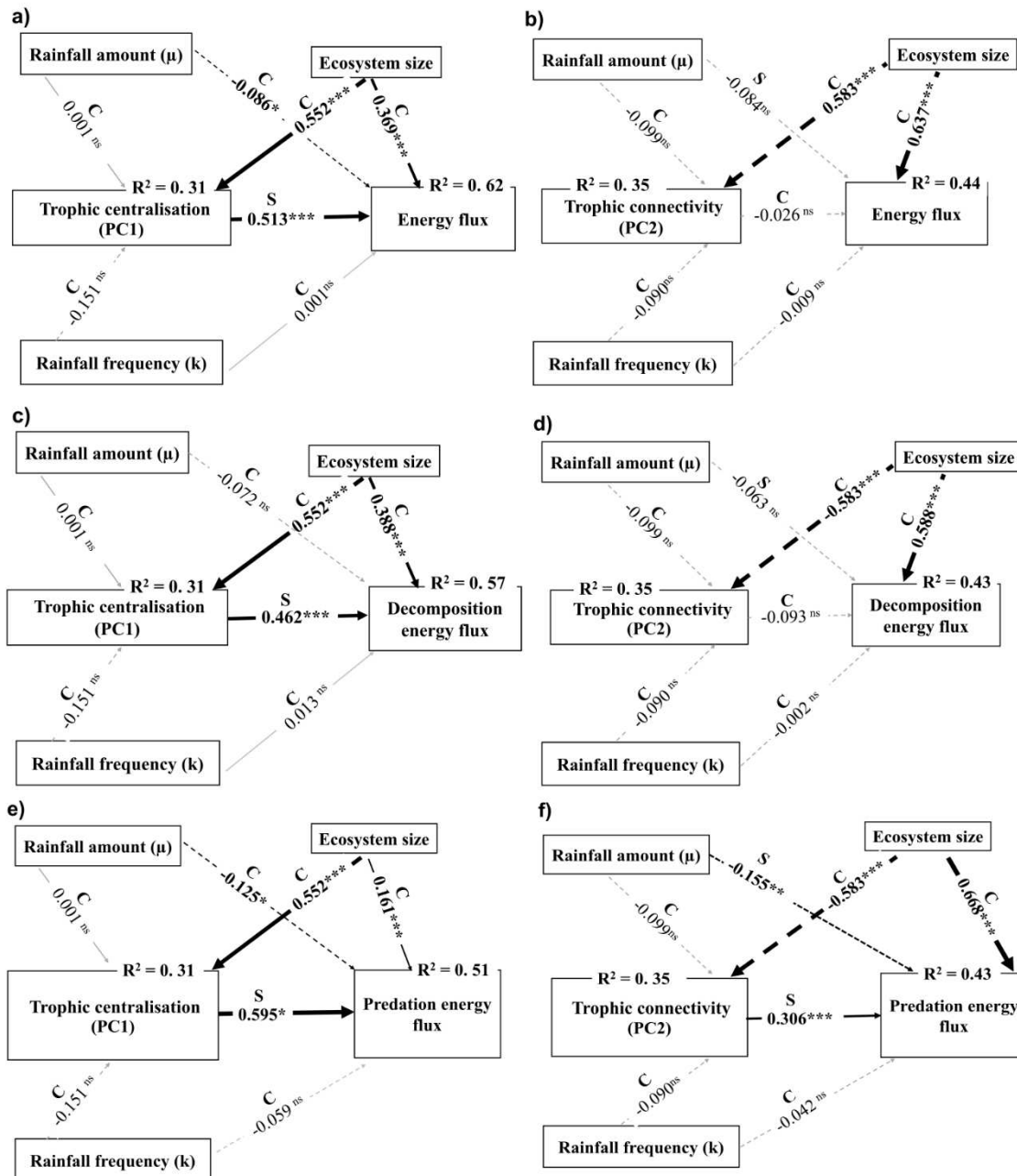
Author contributions

G.Q.R., D.S.S., R.C., V.F.F., F.O.B., I.M.B., J-F.C., B.C., D.A.M., C.L., and G.C.O.P. conceived the idea, designed the global experiment, and developed it with P.A.P.A, O.D., E.H., T.B.A., J.S.L., G.M., R.F., S.L.A. and A.B.A.C. P.A.P.A drafted the paper with inputs from G.Q.R, E.J.O’G and R.C.P. P.A.P.A, G.Q.R. and B.G performed the statistical analyses and P.A.P.A drafted the figures. D.S.S. created rainfall schedules, G.Q.R., D.S.S., I.M.B., F.O.B., R.C., V.F.F., E.H., D.A.M. and G.M. coordinated site-level experiments. All authors provided critical revisions and contributions to subsequent versions of the manuscript.

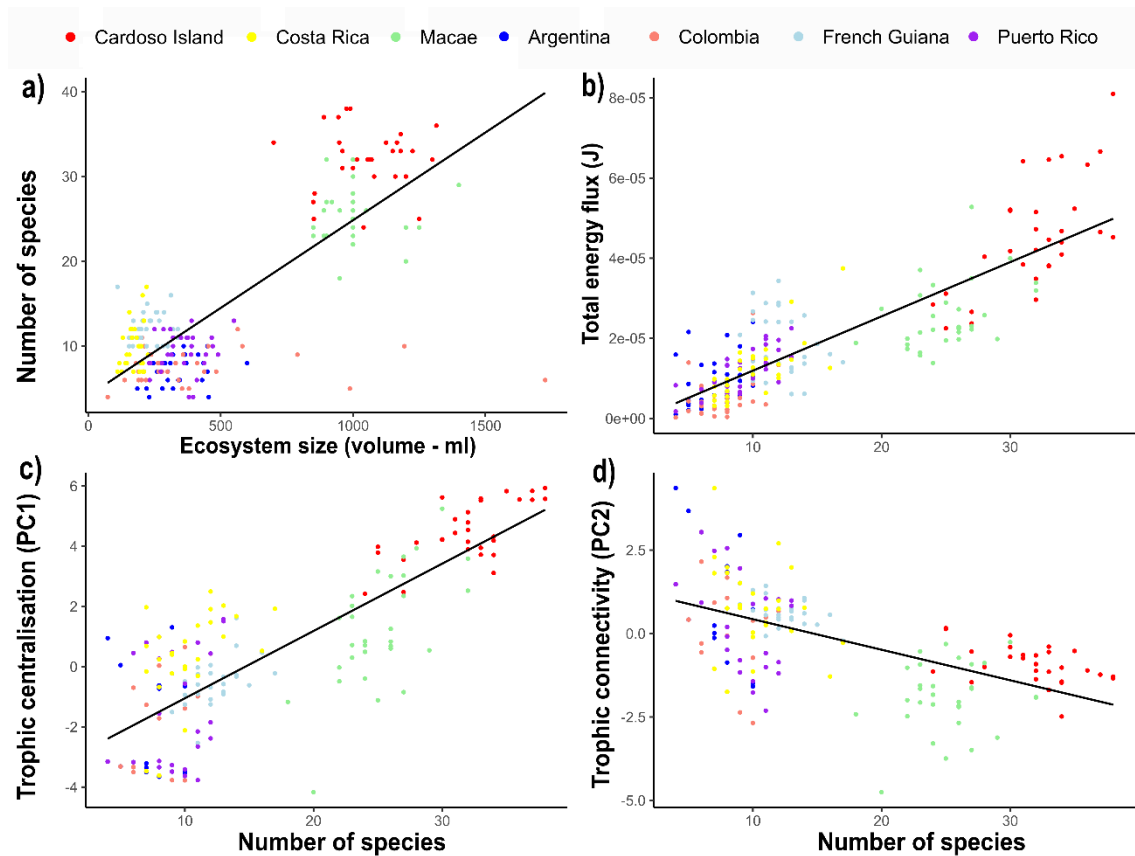
Extended data

Extended data Table S1. Definitions and abbreviations of the principal food web metrics used in this study, following established formulations in previous studies^{63,65}.

Food web metrics	Type
L – number of links	Complexity
L/S - linkage density (number of links per species)	Complexity
C – Connectance (L/S^2)	Complexity
B - fraction of basal species (species with no prey)	Trophic distribution of taxa
I - fraction of intermediate species (species with both predators and prey)	Trophic distribution of taxa
T - fraction of top species (species with no predators)	Trophic distribution of taxa
G - standard deviation of generality (normalized number of resources per taxon)	Dietary strategy
V - standard deviation of vulnerability (normalized number of consumers per taxon)	Dietary strategy
Omnivory - standard deviation of prey averaged trophic level	Dietary strategy
MTL - mean trophic level ($1 + \text{MTL of prey}$)	Trophic height
FCL - average food chain length	Trophic height



Extended Data Figure 1. Multigroup piecewise structural equation models showing indirect effects of rainfall and ecosystem size on energy fluxes via food web structure. Structural equation models (SEMs) evaluate the effects of rainfall mean (μ), rainfall variability (k), and ecosystem size on three components of ecosystem functioning: total energy flux (**a, b**), energy flux from decomposition (**c, d**), and energy flux from predation (**e, f**). These effects are mediated by two key food web structural axes: trophic centralisation (**a, c, e**) and trophic connectivity (**b, d, f**). Arrows represent causal paths; numbers indicate standardized path coefficients (averaged across sites where applicable). Paths labelled "C" represent constrained (i.e., globally estimated) coefficients that did not differ significantly among sites ($P > 0.05$), while paths labelled "S" represent site-specific effects that varied significantly across the gradient. Arrow widths are proportional to effect sizes. Coefficients of determination (R^2) for each endogenous variable are reported within boxes.



Extended Data Figure 2. Influence of ecosystem size on species richness and how species richness mediates structural (trophic centralisation and trophic connectivity) and functional (energy flux) properties of food webs. Panels show relationships between **(a)** ecosystem size (volume in mL) and number of species (species richness) (*Linear model-LM*, $R^2 = 0.66$, $P < 0.001$), and between the number of species and **(b)** total energy flux in J (*LM*, $R^2 = 0.72$, $P < 0.001$), **(c)** trophic centralisation (PC1) (*LM*, $R^2 = 0.64$, $P < 0.001$) and **(d)** trophic connectivity (*LM*, $R^2 = 0.31$, $P < 0.001$). Each point represents a replicate bromeliad food web sampled across seven Neotropical sites, indicated by colour (see legend). Black lines denote linear model fits.

Supplementary Files

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