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# Food Web Complexity Underlies Biodiversity Effects on Ecosystem Functioning

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## **ABSTRACT**

**Biodiversity change has elicited widespread concern over the consequences for functions and services provided by ecosystems<sup>1-3</sup>. Despite extensive evidence for a positive effect of biodiversity on ecosystem functioning within a single trophic level<sup>4,5</sup>, how this biodiversity effect varies with multitrophic food web structure remains unresolved<sup>6</sup> even though most ecosystems contain two to six trophic levels<sup>7</sup>. We investigate how food web complexity modulates biodiversity-ecosystem functioning (BEF) relationships in nature by quantifying energy fluxes as proxies for two major ecosystem functions<sup>8</sup>—primary consumption and predation—in 318 highly-resolved, complex food webs from marine, lake, stream, and soil ecosystems. Ecosystem functioning increased consistently with taxon richness across all trophic levels and ecosystems, which arose from greater vertical diversity (i.e., maximum trophic level<sup>9</sup>) and trophic complementarity of predators in more taxonomically diverse food webs. Furthermore, predator trophic complementarity<sup>10,11</sup> increased predation fluxes in all freshwater ecosystem types. These findings highlight the threat of trophic downgrading to critical ecosystem functions (e.g., biological control and maintenance of biodiversity and ecosystem stability) provided by predators<sup>12,13</sup>, which are typically most vulnerable to anthropogenic disturbances<sup>14,15</sup>. Our study demonstrates that the consequences of biodiversity change are deeply entangled within the web of life, emphasizing the need to conserve the trophic complexity underlying positive biodiversity-ecosystem function relationships.**

## MAIN TEXT

Humans have vastly altered the diversity of life across the planet<sup>1,3</sup>. Virtually no ecosystem has escaped the influence of anthropogenic activities, which have not only caused global declines in biodiversity<sup>16</sup> but also widespread shifts in the composition of species assemblages<sup>17,18</sup>. These changes have motivated thousands of experimental studies, aimed at documenting the positive influence of biodiversity on ecosystem functioning<sup>6</sup>. Most evidence of the biodiversity-ecosystem functioning (BEF) relationship is derived from systems with minimal taxonomic and trophic complexity, particularly in terrestrial experiments, which often study only one trophic level<sup>6</sup>. However, biodiversity change is a highly complex process that drives concurrent changes in the structure of food webs. These webs describe the feeding interactions of species across various trophic levels, resulting in diverse ecosystem functions<sup>8</sup>. As most ecosystems comprise two to six trophic levels<sup>7</sup> that each perform unique functions and can respond differently to environmental change<sup>6,8</sup>, findings typically derived from primary producer communities in BEF experiments may be unable to explain consequences of biodiversity change for other trophic levels. Determining the mechanisms that underlie biodiversity effects on ecosystem functioning in natural food webs is therefore critical for establishing a generalised understanding of BEF relationships across trophic levels and ecosystem types<sup>6</sup>. Thus, to translate findings from experimental BEF research to real ecosystems<sup>4,19–21</sup>, it is imperative that we embrace the complexity of natural food webs by extending experimental and observational BEF research into the multitrophic realm.

Numerous conceptual reviews highlight the importance of multitrophic interactions for modulating BEF relationships<sup>6,8,22–26</sup>, which has been supported by theoretical investigations of model food webs describing the influence of food web structure on ecosystem functioning<sup>9,11,26,27</sup>. Such models demonstrate the impact of food web structure on the relationship between biodiversity and total biomass at different trophic levels<sup>26</sup> and

suggest that changes in food web structure alter multiple functions, such as biomass production and resource use<sup>27</sup>. Despite the large amount of theory, remarkably few empirical investigations exist and have only worked with simplified food webs<sup>28,29</sup> (< 20 taxa) and/or are restricted to specific ecosystems (e.g., <sup>28–31</sup>). Consequently, despite these important past contributions, our understanding of the BEF relationship in naturally complex food webs remains predominantly conceptual and lacks generality<sup>4</sup>.

A major challenge has been to determine which food web properties capture the underlying mechanisms that modulate BEF relationships in multitrophic systems<sup>25</sup>. Two main mechanisms have emerged from theoretical research: vertical diversity<sup>9</sup> and trophic complementarity<sup>10,11</sup> (Fig 1a). The *vertical diversity hypothesis*<sup>9</sup> proposes that primary productivity should be positively associated with the maximum trophic level of food webs due to increased predation pressure and top-down effects on primary consumption<sup>32</sup>. Ecosystem productivity has long been thought to directly constrain vertical diversity<sup>33–36</sup>, such that increased availability of basal resources supplies sufficient energy to sustain higher trophic levels. However, this constraint is likely weakened with decreasing ecosystem size<sup>33</sup> and increasing disturbance frequency, both of which inhibit biomass accumulation of more sensitive top-predator species<sup>14,15,37</sup>. By contrast, the *trophic complementarity hypothesis* suggests that dissimilarity of consumer-resource interactions enhances total rates of energy flux to consumers. This occurs when reduced overlap in trophic interactions allows for greater partitioning of resources among diverse consumers, thereby increasing the maximum rate of resource uptake (i.e., ecosystem functioning) at each trophic level<sup>11</sup>. Trophic complementarity in food webs is most likely constrained by taxonomic diversity<sup>10,11</sup> as variability in consumer-resource interactions depends on the diversity of consumer types<sup>38</sup> and resource heterogeneity<sup>39</sup>. Thus, unlike vertical diversity, the dependence of trophic complementarity on ecosystem productivity, size and disturbance should be mainly

indirect<sup>40,41</sup>. As anthropogenic activities alter ecosystem productivity and size through the introduction of novel ecological disturbances<sup>3</sup>, humans are not only driving changes in taxonomic diversity but also in food web complexity that likely underpins the functioning and stability of ecosystems. However, the relative importance of multitrophic mechanisms for maintaining ecosystem functioning in real, complex food webs remains untested, posing a major limitation for understanding and predicting ecosystem-scale consequences of biodiversity change<sup>12</sup>.

Here we analyse contributions of vertical diversity and trophic complementarity to the relationship between taxon richness and multitrophic ecosystem functioning (i.e., functions carried out simultaneously by different trophic levels) (Fig. 1) in 318 highly resolved, complex food webs that describe 144,020 interactions among 15,521 populations from marine (n = 131), lake (n = 48), stream (n = 74), and soil (n = 65) ecosystems located worldwide (Fig. 2). We first estimate energy fluxes from resources to consumers using an adaptation of the food-web energetics approach<sup>8,42</sup>, whereby energy fluxes to consumer populations (food web nodes) are balanced by energetic losses estimated by whole population metabolism, assimilation efficiencies, and loss of energy to predators<sup>43</sup>. This allows us to quantify two major ecosystem functions in complex food webs: primary consumption (total outflux from primary producers and detritus) and predation (total outflux from consumers; i.e., secondary consumption) that exhibit wide-ranging variation across productivity and temperature gradients present in each of the ecosystems (Supplementary Fig. 1-2). We then estimate the effect of taxon richness on ecosystem functioning in complex food webs across ecosystem types and investigate how two different dimensions of food-web complexity (vertical diversity and trophic complementarity) modulate the BEF relationship. Accordingly, along gradients of primary productivity, we test how multitrophic taxon diversity (i.e., the number of food web nodes resolved to the species, genus or family level) affects ecosystem

functioning by increasing vertical diversity and trophic complementarity (Fig. 1b). Increased taxonomic diversity enables a higher maximum trophic level (vertical diversity), which could lead to concurrent increases in trophic complementarity as higher vertical diversity increases trophic niche availability across trophic levels (Fig. 1b); i.e., consumers feed on resources from different trophic levels to avoid competition. Alternatively, trophic complementarity could increase orthogonally to vertical diversity. This could occur when increased consumer richness leads to greater trophic complementarity within trophic levels (i.e., horizontal niche partitioning), while holding vertical diversity constant (Fig. 1a, bottom right panel). As such, variation in trophic complementarity can arise from changes in both vertical and horizontal diversity. We expect that greater vertical diversity (i.e., maximum trophic level) will increase total predation but reduce primary consumption due to increased top-down control of primary consumers<sup>9,35</sup> (Fig. 1b). We further hypothesise that greater trophic complementarity (i.e., dissimilarity of trophic interactions) will enhance both primary consumption and predation due to increased partitioning of resources by consumers<sup>10</sup> (Fig. 1b). By exploring variation in multiple dimensions of food web complexity that capture a suite of trophic processes (e.g., trophic cascades and niche partitioning), we unveil how the multitrophic structure of ecosystems determines the role of biodiversity in maintaining functions in natural, complex ecosystems.

## RESULTS & DISCUSSION

The cross-ecosystem analysis revealed consistently positive effects of taxon richness on rates of primary consumption (linear mixed effects model coefficient  $\beta = 0.85 \pm \text{SE } 0.11$ ,  $\text{df} = 305$ ,  $p < 0.001$ ) and predation ( $\beta = 1.89 \pm \text{SE } 0.20$ ,  $\text{df} = 305$ ,  $p < 0.001$ ) (Fig. 3a). This positive bivariate relationship, between taxon richness and multitrophic ecosystem functioning in

complex food webs, was also observed for total energy flux (Extended Data Fig. 1a). Furthermore, these positive diversity effects remained significant after controlling for consumer density as a covariate, indicating that consumer density did not bias estimated effects of taxon richness on primary consumption ( $\beta = 0.95 \pm \text{SE } 0.10$ ,  $\text{df} = 304$ ,  $p < 0.001$ ) and secondary consumption ( $\beta = 1.77 \pm \text{SE } 0.02$ ,  $\text{df} = 304$ ,  $p < 0.001$ ). Across the full range of taxon richness observed in the 318 food webs—from ten taxa in an eastern Canadian intertidal rock pool to 159 taxa in central German forest soils—we found a predicted increase of  $1875 \text{ J day}^{-1} \text{ m}^{-2}$  in primary consumption (1297% increase) and of  $375 \text{ J day}^{-1} \text{ m}^{-2}$  in predation (7050 % increase). These consistent positive effects of taxon richness were reflected in a cross-ecosystem structural equation model (SEM) (Fig. 3b-c). Notably, part of the large variability observed in bivariate BEF relationships was explained by variation in vertical diversity and predator trophic complementarity of food webs, such that effects of taxon richness on predation rates observed across all food webs were conditional on variation in maximum trophic level and predator trophic complementarity (Fig. 3b; Supplementary Table 1). These results support our main hypothesis that taxon richness directly and indirectly affects ecosystem functioning (predation rates) in food webs via multiple dimensions of food web complexity (Fig. 3b-c). Specifically, we found significant variation in taxon richness and maximum trophic level across the gradient of estimated primary productivity that produced positive relationships with predator complementarity and total predation across all food webs (Fig. 3b-c). These findings were highly robust to simulated variations in input parameters used to estimate primary consumption and predation fluxes (see Supplementary Methods and Supplementary Fig. 3).

Our cross-ecosystem food web analyses confirm the prevalent role of vertical diversity and trophic complementarity in maintaining predation rates in food webs<sup>2</sup>. Therefore, changing biodiversity is likely to have the strongest impacts on predation rates

when coupled with a loss or gain of species at the highest trophic levels and with unique prey choice. Since large-bodied predators are predicted to be the most sensitive organisms to environmental change<sup>14,15,37</sup>, biodiversity loss is likely to be characterised by ‘trophic downgrading’<sup>12</sup> and trophic niche compression<sup>44</sup> that have far-reaching consequences for ecosystem processes. Notably, we find that predation fluxes scale superlinearly with taxon richness in food webs, suggesting ecosystems could face a four-fold loss in predation rates under pessimistic scenarios of 50% biodiversity loss by the end of this century<sup>45</sup>. These findings exemplify the potential risk of species loss to the critical ecosystem functions provided by predators, such as natural biological control<sup>46,47</sup>, maintenance of biodiversity at lower trophic levels<sup>48,49</sup>, and regulation of ecosystem stability<sup>12,50</sup>. This positive superlinear scaling of predation with biodiversity further suggests predators have greater *per capita* feeding rates on their prey, indicating stronger top-down control in more diverse food webs, which could also lead to reduced stability<sup>33</sup>. Indeed, we find evidence of reduced food web stability with higher *per capita* feeding rates of predators on their prey, which was greatest in more complex food webs (Extended Data Fig. 3; Supplementary Table 2). However, the net decline in food web stability with food web complexity was notably weak despite strong concurrent increases in maximum trophic level and *per capita* predation rate. In line with previous studies, this points to the prominent influence of other stabilizing mechanisms (e.g., energy channel asymmetry<sup>50</sup>, weak trophic loop weights<sup>51</sup>, and trophic omnivory<sup>33,52</sup>) that modulate potentially destabilising effects of strong top-down control in more diverse, naturally assembled food webs.

We hypothesised that food web structure would equally determine effects of taxon richness on ecosystem functioning driven by primary consumers and predators. However, our findings suggest that functions performed by predators could be more strongly constrained by structural properties of food webs compared to primary consumption such as herbivory and

decomposition (but see ecosystem-specific analysis of lake food webs; Fig. 4e). Accordingly, taxon richness appeared to directly explain variation in primary consumption rates, irrespective of variability in food web complexity (Fig. 3; Supplementary Table 1). This finding was further supported by our analysis of total food web energy flux (with predation and primary consumption combined), whereby taxon richness was the main driver of total energy flux, with only a very weak relationship between maximum trophic level and total energy flux. This was despite relatively strong direct and indirect effects of taxon richness on maximum trophic level and trophic complementarity, respectively (Extended Data Fig. 1; Supplementary Table 3). We further assessed whether other food web properties, namely average trophic omnivory and food web connectance, could play a hidden role in modulating the observed relationships between taxon richness and ecosystem functioning by reconstructing the cross-ecosystem SEM with these two additional food web properties. However, we found the inclusion of trophic omnivory and connectance had no significant influence on the proportion of variance explained in either primary consumption or predation (Extended Data Fig 2; Supplementary Table 4), suggesting that other aspects of environmental variation are more likely to contribute to the remaining unexplained variation in ecosystem functioning than these additional dimensions of food web complexity.

Effects of taxon richness on multitrophic ecosystem functioning proved to be similarly consistent among each ecosystem type, such that seven of eight bivariate BEF models detected positive effects of diversity on primary consumption and predation (Fig. 4a; Supplementary Table 5). This positive diversity effect held for five of the eight models when consumer densities were included as a covariate (Supplementary Table 6); significant positive relationships were no longer detected for stream food webs, suggesting that collinearity of taxon richness and consumer abundance could mask positive effects of diversity on ecosystem functioning. Strong consistency was also found using a SEM framework with

food web properties that describe multitrophic BEF mechanisms, such that taxon richness had a net positive effect on all functions across all ecosystem types (Fig. 4b-e; Supplementary Tables 7-10). This was even the case for predation when consumer density was included as an additional endogenous variable in an alternative SEM for stream food webs (Supplementary Fig. 4; Supplementary Table 11). Thus, the only statistically non-significant bivariate relationship observed between taxon richness and primary consumption in lakes likely resulted from an indirect negative taxon richness effect via maximum trophic level, which was obscured in the bivariate BEF model (Supplementary Table 5). This finding suggests that biodiversity effects on ecosystem functioning may be often misinterpreted due to variability in food web structure, particularly in ecosystems where trophic cascades may be the strongest, such as some aquatic ecosystems<sup>53</sup>. Similar to the cross-ecosystem analysis, these findings remained qualitatively consistent when subjected to simulated variation in input parameters used to estimate consumer energy fluxes (see Supplementary Methods and Supplementary Fig. 5).

Both maximum trophic level and trophic complementarity modulated the effect of taxon richness on ecosystem functioning (Fig. 4b-e; Supplementary Tables 7-10), with some notable variation in the relative importance of multitrophic BEF mechanisms among ecosystems. Ecosystem-specific analyses revealed a relatively strong role of maximum trophic level in modulating the biodiversity-predation flux relationship in marine, soil and lake food webs, whereby food webs with more trophic levels had higher rates of predation (Fig. 4b-d; Supplementary Tables 7-8 & 10). In lake ecosystems, SEM results even reveal evidence of a trophic-cascade effect of taxon richness on primary consumption, whereby higher maximum trophic level reduced primary consumption rates (Fig. 4e; Supplementary Table 10). Although it is difficult to infer a trophic cascade from these analyses (also noting relatively high uncertainty around the estimation of this effect; Supplementary Fig. 5), given

that increased vertical diversity may also increase suppression of intermediate trophic levels<sup>54,55</sup>, the detection of this effect only in lakes aligns with evidence that trophic cascades can be stronger in lake ecosystems<sup>53</sup>. In contrast to findings from our cross-ecosystem analysis of BEF relationships in food webs, there was a strong influence of predator trophic complementarity on predation only in the two freshwater ecosystems: streams and lakes (Fig. 4; Supplementary Tables 9-10). These apparent differences between cross-ecosystem versus within-ecosystem analyses demonstrate how fundamental biological differences among ecosystem types must be considered in predictions of the functional consequences of biodiversity change. For example, soils had the highest maximum trophic level (Supplementary Fig. 2d), which may arise from the additional trophic level of decomposers that consume microbial resources as well as basal detrital resources<sup>56</sup>. The more constrained variation in predator trophic complementarity across the 65 soil food webs (Supplementary Fig. 2f) also could have reduced the likelihood of detecting trophic complementarity effects on ecosystem functioning. In contrast, all three aquatic ecosystem types had more variable food web properties (except primary consumer trophic complementarity; Supplementary Fig. 2e), thus increasing the likelihood of detecting effects of both maximum trophic level and trophic complementarity on ecosystem functioning. Despite a greater range of food-web complexity in aquatic systems, we still found no evidence of a trophic complementarity effect in marine food webs. This could be due to a stronger influence of wider-ranging primary productivity on ecosystem functioning (Fig. 4; Supplementary Figure 2 and 3) that overrides any modulating effect of food web complexity in this system. The greater variation in food web properties observed in aquatic food webs may be attributed to the wider variety in dimensionality of foraging search space, ontogenetic diet shifts, and food chain lengths, as these habitats incorporate both benthic and water column foragers<sup>57</sup>. Ultimately, this variation

could give rise to the natural variation in trophic complementarity required to significantly influence the relationships between biodiversity and ecosystem functioning.

This study presents consistent evidence for the integral role of food web structure in modulating the relationship between biodiversity and ecosystem functioning in real ecosystems. However, there is still notable unexplained variance in multitrophic ecosystem functioning across ecosystems in our analyses, as well as many direct effects of taxon richness on ecosystem functioning that appear not to be modulated by maximum trophic level or trophic complementarity. Other structural properties that describe food web complexity, such as food web connectance and trophic omnivory<sup>58</sup>, could further explain biodiversity effects on ecosystem functioning and stability in naturally complex multitrophic ecosystems, though we found no evidence to support this in our data (Extended Data Fig. 2). Additionally, environmental gradients that underlie the observed variation in taxonomic richness and food web properties likely create context-dependencies that could weaken or intensify multitrophic BEF relationships<sup>59</sup>. Although we analytically and statistically incorporate geographic variation in environmental temperature and primary productivity in our analyses, other gradients such as anthropogenic stressors may further explain critical variation in the relative influence of different food web properties on ecosystem functioning. Furthermore, inconsistency in the construction of empirical food web datasets, such as differences in taxonomic resolution of basal resources, sampling intensity, and approach to assigning trophic links, poses a significant challenge to describing generalised BEF effects in food webs. Most notably, it is possible that our inability to detect effects of food web complexity (i.e., particularly trophic complementarity) on primary consumption resulted from poorer taxonomic resolution of basal resources (e.g., phytoplankton, bacteria, etc.) and associated definitions of feeding links. While this has long been recognised as a widespread constraint in

food web ecology, this highlights the critical need for better global standards in food web data generation<sup>60</sup>.

Until now, BEF research has been heavily constrained to within trophic levels, lacking explicit consideration of the vast complexity of trophic interactions that shape species assemblages and their influence on the environment<sup>6,8</sup>. By understanding how the architecture of food webs influences energy flows and ecosystem functioning, as well as the inherent variability of these biological mechanisms across different ecosystem types, we can advance our ability to predict the consequences of ecosystem-scale shifts as Earth's biodiversity changes.

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**Figure 1. The hypothetical role of food web complexity in mediating biodiversity effects**

**on ecosystem functioning.** (a) Ecosystem functioning (primary consumption [blue] and predation [red]) should increase with taxon richness in food webs, which is expected to positively correlate with multiple dimensions of food web complexity: maximum trophic level and trophic complementarity. However, residual variation in the BEF relationship may be explained by differences in trophic complexity among food webs. Hypothetical increases (denoted by positive arrows) in vertical diversity (blue y-axis in food webs depicting increased maximum trophic level) and trophic complementarity (blue x-axis in food webs depicting increased trophic dissimilarity) compared to a reference low-diversity food web (upper left panel) illustrate how these two mechanisms could independently contribute to enhanced primary consumption and predation fluxes with increasing taxon richness (from six to nine taxa, or nodes). Coloured food web nodes represent different taxa across trophic levels. (b) We predict that effects of taxon richness on ecosystem functioning are modulated by vertical diversity and trophic complementarity (‘trophic compl.’), which directly and indirectly enhance primary consumption and predation fluxes in food webs. Variation in taxon richness and food web complexity is expected to arise as a result of environmental gradients such as primary productivity. Arrows denote hypothesised positive (green), negative (brown) and non-linear (grey) effects.

**Figure 2. Geographic distribution of the 318 food webs across four major ecosystem types.** Example food webs are shown in zoomed insets, with vertical axes to denote maximum trophic level and horizontal axes to denote mean trophic complementarity (as in hypothetical food webs shown in Fig. 1a). Trophic complementarity ranges between 0 and 1, whereby a value of 1 indicates 100% dissimilar interactions among consumers (i.e., zero overlap in resource-use by consumers). Food web nodes are divided into basal resources (grey), primary consumers (blue), and secondary consumers (red), with trophic interactions (links) denoting energy fluxes from resources to their consumers. Links in blue and red illustrate primary consumption and predation, respectively.

**Figure 3. Positive effects of taxon richness on multitrophic functioning rely on vertical diversity and trophic complementarity.** (a) Marginal effects of taxon richness on ecosystem functioning derived from bivariate analyses of all 318 food webs for predation (red) and primary consumption (blue). Predation and primary consumption fluxes are expressed in  $\text{J day}^{-1} \text{m}^{-2}$ . Solid trend lines and associated 95% CI denote statistically significant relationships ( $p < 0.05$ ) derived from the log-transformed LMM models. (b) Outcomes of the cross-ecosystem SEM (Fisher's  $C_{16} = 19.03$ ,  $P = 0.27$ ; Supplementary Table 1) testing the effects of taxon richness on primary consumption and predation via maximum trophic level ('Max TL'), trophic complementarity of primary consumers ('1° consumer complementarity'), and trophic complementarity of predators ('predator complementarity'), with (c) associated effect plot summarising direct effects (solid bars) derived from the SEM and indirect effects (hatched bars) mediated by other food web properties. Arrow widths are scaled to standardised path coefficients (numbers adjacent to arrows) from the SEM to indicate relative effect sizes. Green arrows in (b) indicate positive effects, and the double-headed arrow denotes correlated errors. Grey arrows indicate the absolute, non-directional effect size of

quadratic relationships derived from Cohen's  $f^2$  (see Methods). Red and blue bars in (c) denote standardised effects of food web properties on predation and primary consumption, respectively. 'Trophic compl.' = trophic complementarity; 'Max TL' = maximum trophic level.

**Figure 4. Positive effects of taxon richness on ecosystem functioning are mediated by food web complexity across ecosystems.** (a) Marginal effects of taxon richness on ecosystem functioning derived from bivariate analyses across ecosystems (Supplementary Table 5), with associated SEMs (Supplementary Tables 7-10) testing the effects of taxon richness on primary consumption and predation via maximum trophic level ('Max TL'), trophic complementarity of primary consumers ('1° consumer compl.'), and trophic complementarity of secondary consumers ('predator compl.') for (b) marine (n = 131), (d) soil (n = 65), (d) stream (n = 74), and (e) lake (n = 48) food webs. Solid trend lines and associated 95% CI (a) denote statistically significant relationships ( $p < 0.05$ ) derived from log-transformed GLS and LMM models. Green, brown, and grey arrows (b-e) indicate positive, negative and absolute non-linear effects, respectively; double-headed arrows denote correlated errors; dashed arrows indicate non-significant effects that were retained in the minimum adequate models (i.e., with the lowest AIC score following model simplification). Arrow widths are scaled to the standardised path coefficients from each SEM to indicate relative effect strengths. Effect plots next to each SEM show direct effects on ecosystem functioning (solid bars) and indirect effects that are mediated by other food web properties (hatched bars) derived from the SEMs. Standardised effects of food web properties on predation and primary consumption are denoted by red and blue bars, respectively. 'Trophic compl.' = trophic complementarity; 'Max TL' = food web maximum trophic level. Y-axis scales vary among panels in (a) to aid visual interpretation of within-ecosystem relationships.

## **METHODS**

### **Food web data collation**

We compiled 318 food web datasets from 12 studies<sup>56,61–70</sup> across 15 different countries that contained information on trophic interactions and food web topology, body size, and population biomass densities (partially hosted in the GATEWAY v.1 database<sup>57,71</sup>). Body mass of consumers in food webs measured as dry weight (83% of all food webs) was converted to fresh mass (g) by multiplying by a factor of four<sup>72</sup>. Food web datasets were distributed across four different ecosystem types: marine ( $n = 131$ ), terrestrial soils ( $n = 65$ ), streams ( $n = 74$ ), and lakes ( $n = 49$ ) (Fig. 2), ranging widely in primary productivity, environmental temperature, and taxon richness (Supplementary Fig. 2). We initially screened food web datasets to include only those where consumer nodes were resolved to at least the genus level and that included both primary and secondary consumers. Because many food web datasets lacked body size and biomass information for primary producers, we focused our analyses on two general ecosystem functions associated with heterotrophic consumer interactions: rates of 1) primary consumption (i.e., the sum of herbivory and decomposition) and 2) predation.

### **Estimating population energy expenditure, feeding preference, and trophic efficiency**

To estimate primary consumption and predation rates in complex food webs using the food-web energetics approach<sup>8,43</sup>, we first needed to quantify the energetic losses of each population across the 318 food webs. To do so, we estimated metabolic expenditure (i.e., population energetic demands due to metabolism of consumed resources) and assimilation efficiency (the proportion of energy that is assimilated from consumed resources and allocated to metabolism and biomass production). Individual metabolic rates,  $I$ , were

calculated based on generalised allometric and thermal scaling of organism metabolism<sup>73</sup> using the formula:

$$\ln(I) = \ln(i_0) + 0.71 \ln(M) - E/kT \quad (1)$$

where  $i_0$  is a normalisation constant,  $M$  is organism body mass, and  $E/kT$  is the Vand't Hoff-Arrhenius relationship described by the activation energy, ( $E = 0.69$ ), Boltzmann's constant ( $k = 8.62 \times 10^{-5}$ ), and the absolute temperature in Kelvin,  $T$ . We parameterized normalization constants separately for invertebrates ( $i_0 = 17.17$ ) and ectothermic vertebrates ( $i_0 = 18.47$ ) based on estimated model intercepts for mass-metabolism scaling relationships from Brown *et al.*<sup>73</sup>. For each food web node (i.e., a consumer population in a local food web), we calculated consumer population energy use,  $X_j$ , as  $X_j = I \cdot N_j$  where  $N_j$  is the population density of consumer  $j$ .

To partition energy fluxes from multiple resources to consumer nodes, we estimated the preference of a consumer  $j$  on resource  $i$  out of all exploited resources  $k$ , as:

$$W_{ij} = \frac{w_{ij}B_i}{\sum_k w_{kj}B_k} \quad (2)$$

where  $w_{ij}$  is the biomass-independent preference of  $j$  on  $i$  and  $B$  is resource biomass. We estimated the efficiency of energy assimilation from resources ingested by consumer populations in food webs,  $\varepsilon_i$ , by scaling according to resource-consumer interactions and environmental temperature. Specifically, we estimated the proportion of assimilated energy from a given resource pool,  $i$ , at a given absolute temperature,  $T$ , calculated as

$$\varepsilon_i = \frac{e^{\hat{\varepsilon}_{0,i}} e^{\frac{E_{\varepsilon,i}(T-T_0)}{kTT_0}}}{1 + e^{\hat{\varepsilon}_{0,i}} e^{\frac{E_{\varepsilon,i}(T-T_0)}{kTT_0}}} \quad (3)$$

where  $\epsilon_0$  is a normalisation constant,  $E_\epsilon$  is the activation energy,  $k$  is Boltzmann's constant, and  $T - T_0$  is absolute temperature (K) normalised to 20°C ( $T_0$ : 293.15 K)<sup>74</sup>. We specified different  $\epsilon_0$  values for the three main resource types, animal (predation), plant (herbivory), and detritus (detritivory), for each trophic interaction within food webs, according to Lang *et al.*<sup>74</sup>. This allowed for multiple possible assimilation efficiencies per consumer population where they fed on multiple resource types in a food web (i.e., omnivores).

### Quantifying multitrophic ecosystem functioning using energy fluxes

To estimate flows of primary consumption (herbivory and detritivory) and predation, we employed the food web energetics approach<sup>8,43</sup> in the 'fluxweb' R package<sup>75</sup> to quantify fluxes of energy from resources to consumers along trophic links across the 318 food webs. Fluxes were calculated solving:

$$\sum_i W_{ij} \epsilon_i F_j = X_j + \sum_k F_k W_{jk} \quad (4)$$

where  $F_j$  represents the sum of ingoing fluxes to node  $j$ . This bioenergetic framework<sup>8,51,76</sup> was developed to use readily accessible biological information, allowing the system of equations to be fully defined (i.e., without missing parameters), thus producing a unique solution for each calculated flux of energy. From those fluxes, primary consumption was calculated as the sum of fluxes flowing from basal nodes to their consumers (i.e., the sum of outgoing fluxes from basal resources). Predation was similarly calculated as the sum of fluxes flowing from non-basal nodes to other consumer nodes (i.e., the sum of outgoing fluxes from animal populations)<sup>46</sup>. Furthermore, we estimated top-down effects of predators on prey by calculating *per capita* predation rates ( $Pr_i$ ) as  $Pr_i = \frac{\sum_j F_{ij}}{N_i}$ , where  $F_{ij}$  is the energy flux from prey node  $i$  to its predators  $j$ , and  $N_i$  is the population density of prey  $i$ <sup>46</sup>. Finally, we determined local stability

of each food web from the community Jacobian matrix, whereby the off-diagonal elements are derived from calculated energy fluxes (see Supplementary Methods).

### **Describing food web vertical diversity and trophic complementarity**

The trophic level of a node,  $TL$ , is defined as 1 plus the average trophic level of its prey (i.e., prey-averaged trophic level), scaled by relative energy fluxes:

$$TL_i = 1 + \frac{1}{|P_i|} \sum_j TL_j \quad (5)$$

where  $|P_i|$  represents the number of prey of node  $i$  and with trophic levels of basal nodes set to 1. The trophic similarity  $TS_{ij}$  between consumer  $i$  and  $j$  represents the similarity in their diets, estimated with a Jaccard index:

$$TS_{ij} = \frac{|P_i \cap P_j|}{|P_i \cup P_j|} \quad (6)$$

$P_i$  represents the set of prey of consumer  $i$  and  $|P_i \cap P_j|$  is the cardinality of the intersection of  $P_i$  and  $P_j$  (i.e., the number of prey common to consumer  $i$  and  $j$ ). To estimate a metric of trophic complementarity, we calculated trophic dissimilarity between two consumers as  $1 - TS_{ij}$ . Primary consumer trophic complementarity was defined as the food web average dissimilarity between consumers feeding on basal nodes only and predator trophic complementarity was defined as the food web average dissimilarity between consumers feeding on at least one non-basal node.

### **Statistical analysis**

To quantify the relationship between taxon richness and multitrophic ecosystem functioning using the full global dataset of 318 food webs across ecosystems, we constructed random-intercept linear mixed effects models (LMMs) using the ‘nlme’ package in R<sup>77</sup>, with either primary consumption or predation as the response variable and total taxon richness of food webs as a fixed effect. To account for hierarchical data structure, we included food web study ID (i.e., study source of each dataset;  $n = 12$ ) nested within ecosystem type (marine, soils, streams, and lakes) as random effects. Model variance structure was inspected for homogeneity of variance and normality of residuals, after which all variables were log-transformed to meet parametric model assumptions. In cases where notable heteroscedasticity of variance was still observed after log-transformations were applied, we refit models with a ‘varIdent’ variance function to account for different variances among food web studies, and/or a ‘varPower’ variance function to account for systematic heterogeneity of variance across the range of taxon richness<sup>78</sup>. We then identified the best fit model using the Akaike Information Criterion (AIC), followed by a likelihood ratio test to determine which variance functions to retain in our minimum adequate models. For our within-ecosystem analyses, we applied the same procedure to quantify BEF relationships within the stream ecosystem type (i.e., random intercept LMMs with study ID as a random effect and including variance functions). However, for the marine, soil, and lake food web analyses, we constructed generalised least squares (GLS) models so that we could account for different variance structures in model residuals, but with only fixed effects as there were not enough separate food web studies included for these ecosystem types to warrant the inclusion of study ID as a random effect (i.e.,  $< 3$  studies, and therefore levels, per ecosystem type).

We applied structural equation modelling with piecewise SEM<sup>79</sup>, which uses directed tests of separation<sup>80</sup> to determine the conditional independence of multiple response and predictor variables in a multivariate framework. This approach allowed us to determine the

direct and indirect effects of taxon richness on primary consumption and predation rates in food webs, via maximum trophic level and trophic complementarity of food webs as intermediary (endogenous) variables within the structural equation models. To do so, we first constructed a maximal model that included the effects of NPP on taxon richness and maximum trophic level, all possible effects of taxon richness on food web properties, the effects of maximum trophic level on trophic complementarity of primary consumers and predators, and their effects on both ecosystem functions quantified in food webs (according to Fig. 1b). We additionally specified correlated errors between pairs of variables where we assumed no causal relationship: predator trophic complementarity with primary consumer trophic complementarity, predator trophic complementarity with primary consumption, primary consumer trophic complementarity with secondary consumption, and primary consumption with predation. For the global dataset (i.e., with all ecosystem types combined) and for within-ecosystem SEMs, we employed the same model structures described above, using LMMs with study ID included as a random effect (global and stream food web analysis) and GLS models (marine, soil, and lake analyses), the inclusion of variance functions where necessary to ensure all assumptions of parametric tests were met. Due to likely non-linear relationships between NPP and food web properties (particularly taxon richness), we also fit component models with a quadratic polynomial term and compared against the equivalent linear model (without the quadratic term) using AIC to determine whether quadratic terms should be included in SEMs. Once individual component models were assessed and corrected for any violation of assumptions, we constructed the SEMs based on these component models following the piecewiseSEM approach<sup>79</sup>, whereby the structure of hypothetical path diagrams was examined for missing paths by calculating Fisher's *C* and comparing against a chi-squared distribution. If the resulting *P*-value of the causal model is  $> 0.05$ , this infers that the hypothesised paths are consistent with the data and

the SEM cannot be rejected<sup>80</sup>. We performed model simplification on the maximal SEMs by sequentially removing non-significant predictors from each model until there was no further reduction in AIC score of the SEM of  $\geq 2$  units.

From the final minimum adequate SEMs, we then summarised the direct and indirect effects of taxon richness, maximum trophic level, and trophic complementarity using the standardised (z-transformed) path coefficients from each SEM<sup>79</sup>. However, for models with quadratic terms for NPP included, we needed to estimate compound standardized path coefficients, which we achieved using Cohen's  $f^2$  to estimate relative effect strength<sup>81</sup>. Cohen's  $f^2$  is defined as

$$f^2 = \frac{R_{included}^2 - R_{excluded}^2}{1 - R_{included}^2} \quad (7)$$

Where  $R_{included}^2$  is the conditional  $R^2$  from the full model including the linear and non-linear effects of NPP, while  $R_{excluded}^2$  is the conditional  $R^2$  from the reduced model without NPP included (both its linear and non-linear components). Indirect effects of taxon richness, maximum trophic level, and trophic complementarity on primary consumption and predation were calculated by multiplying standardised path coefficients along identified pathways within each SEM. All analyses were carried out in R version 4.5.0<sup>82</sup>. All data and code used to produce the results in this study can be found on the Zenodo open research repository (<https://zenodo.org/records/15883665>).

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## DATA AVAILABILITY

All data used in this study is available from Zenodo:

<https://doi.org/10.5281/zenodo.20130985>

## CODE AVAILABILITY

Code for computing food web properties, energy fluxes, stability, net primary productivity, and statistical analyses is available from Zenodo: <https://doi.org/10.5281/zenodo.20130985>

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## **AUTHOR CONTRIBUTIONS**

ADB, UB, NE, DGC, DPG, JH, MJ, EJO, DO, DMP, BR, CV, and BG designed the study.

ADB assembled the datasets and ADB, EB, BR, and BG conducted the analysis. UB, MB, SLE, DPG, ROH, DIK, SK, PK, MM, JRM, MCN, EJO, DO, DMP, RAS, VSS, AJT, and CV contributed data. All authors contributed to discussions on study design, analysis and interpretation. ADB wrote the manuscript with contributions from all authors.

## **COMPETING INTERESTS**

The authors declare no competing interests.

## **ADDITIONAL INFORMATION**

Supplementary Information is available for this paper.

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**Extended Data Figure 1. Dependence of total energy flux through food webs on taxon**

**richness and food web complexity.** (a) The relationship between taxon richness and total energy flux in food webs across ecosystem types ( $\beta = 1.24 \pm \text{SE } 0.14$ ,  $\text{df} = 305$ ,  $p < 0.001$ ).

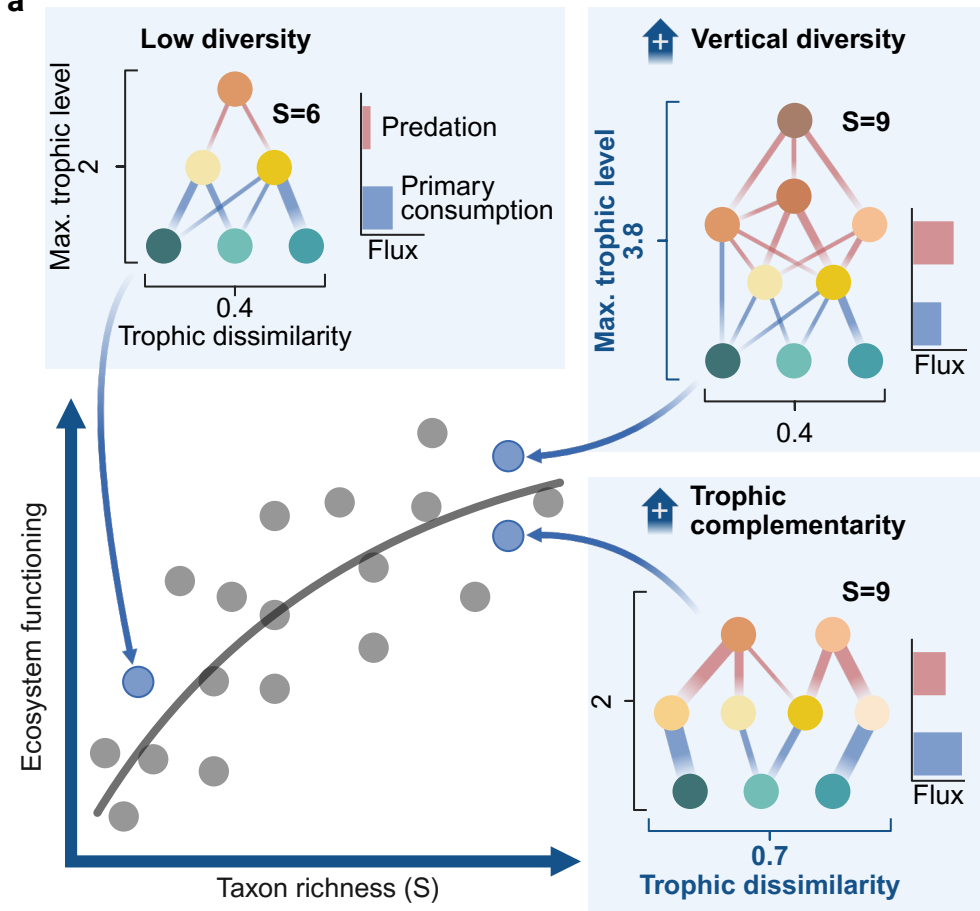
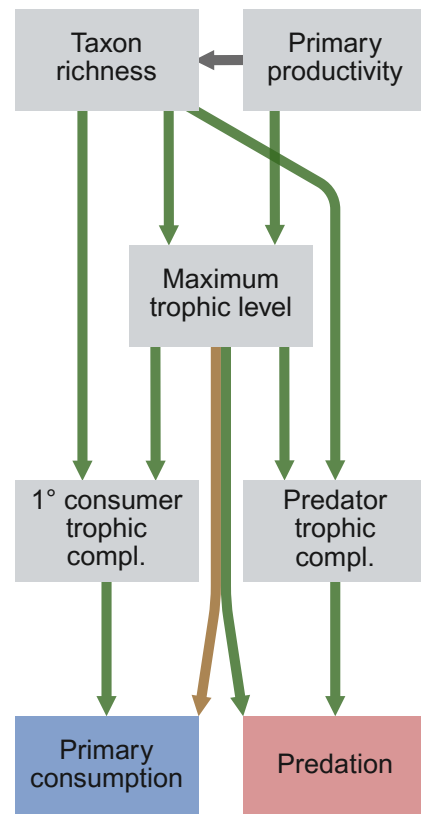
(b) Structural equation model (Fisher's  $C_8 = 4.3$ ,  $P = 0.83$ ) testing the indirect effect of taxon richness on total energy flux via maximum trophic level and total trophic complementarity across all organisms in food webs. Fitted trend line and associated 95% CI in (a) is taken from the linear mixed effects model with food web study (dataset) nested within ecosystem type set as a random intercept. Points are coloured according to ecosystem type purely as a visual aid to illustrate cross-ecosystem differences in taxon richness and total energy flux. Arrow widths in (b) are scaled to standardised path coefficients to indicate relative effect sizes (with path coefficient values given next to each arrow). Green arrows indicate positive relationships, while grey arrow denote quadratic relationships with arrows weighted according to Cohen's  $f^2$  (see methods).  $R^2$  values give the estimated proportion of variance explained, based on conditional pseudo- $R^2$  from the linear mixed effects models.

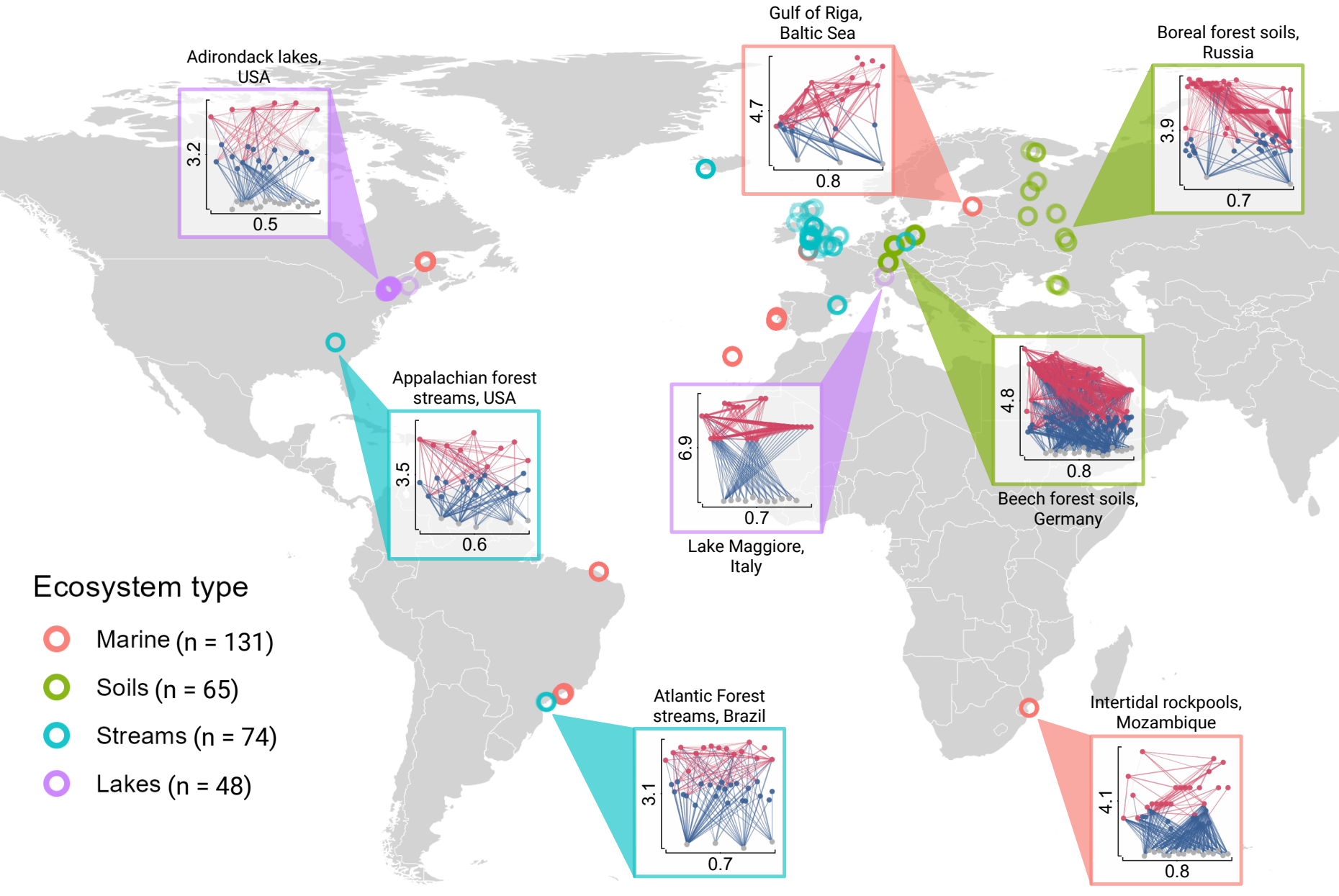
**Extended Data Figure 2. Little evidence for the importance of other dimensions of food**

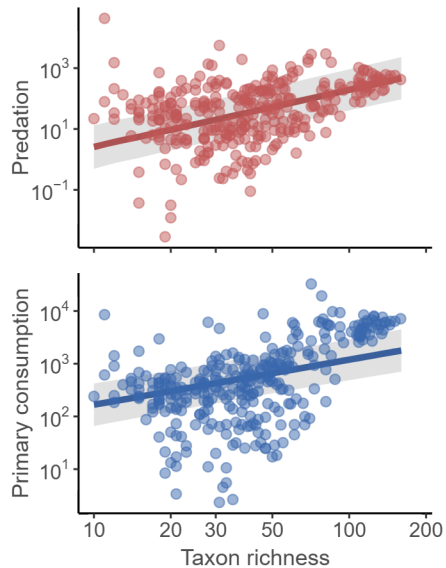
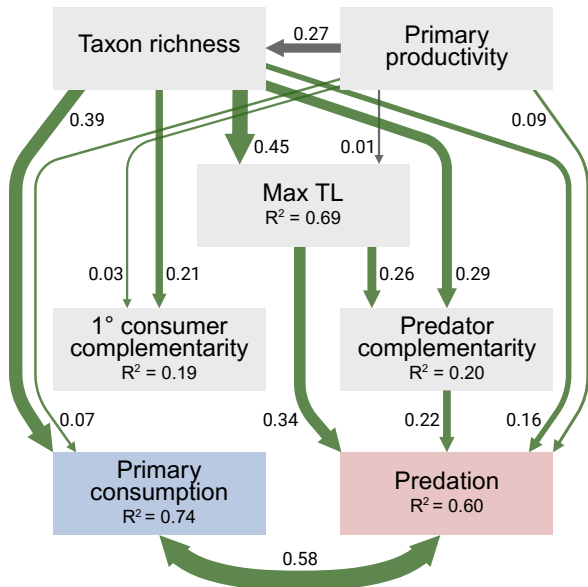
**web complexity for modulating BEF relationships in food webs.** Results from the cross-ecosystem structural equation model (SEM) ( $C_{32} = 38.13$ ,  $P = 0.21$ ) testing the effects of taxon richness on primary consumption and predation via trophic omnivory ('Omnivory'), food web connectance ('connectance'), maximum trophic level ('Max TL'), trophic complementarity of primary consumers ('1° consumer complementarity'), and trophic complementarity of predators ('predator complementarity'). Arrow widths are scaled to standardised path coefficients (numbers adjacent to arrows) from the SEM to indicate relative effect sizes. Green and brown arrows indicate positive and negative relationships,

respectively. Grey arrows indicate the absolute effect size of quadratic relationships whereby non-directional standardized path coefficients are derived from Cohen's  $f^2$ .

**Extended Data Figure 3. Effects of food web taxon richness and complexity on *per capita* predation rates and food web stability.** (a) Marginal effects of taxon richness on *per capita* predation rates (log10 ratio of energy flux to predators per g of prey biomass) and local food web stability (inverse of the real part of the dominant eigenvalue of the Jacobian matrix) . Solid trend lines and associated 95% CI denote statistically significant relationships ( $p < 0.05$ ) derived from the LMM models. (b) Outcomes of the cross-ecosystem structural equation model (SEM) ( $C_{32} = 39.30$ ,  $P = 0.18$ ) testing the effects of taxon richness on *per capita* predation rates and local food web stability via maximum trophic level ('Max TL'), trophic complementarity of primary consumers ('1° consumer complementarity'), and trophic complementarity of predators ('predator complementarity'), with (c) associated effect plot summarising direct effects (solid bars) derived from the SEM and indirect effects (hatched bars) mediated by other food web properties. Arrow widths are scaled to standardised path coefficients (numbers adjacent to arrows) from the SEM to indicate relative effect sizes. Green and brown arrows in (b) indicate positive and negative relationships, respectively. Grey arrows indicate the absolute effect size of quadratic relationships whereby non-directional standardized path coefficients are derived from Cohen's  $f^2$ . Teal and yellow bars in (c) denote standardised effects of food web properties on *per capita* predation and food web stability, respectively. 'Trophic compl.' = trophic complementarity; 'Max TL' = maximum trophic level.

**a****b**



**a****b****c**