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# Food web complexity underlies biodiversity effects on ecosystem functioning

https://doi.org/10.1038/s41586-026-10710-5

Received: 25 March 2025

Accepted: 26 May 2026

Published online: 1 July 2026

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Biodiversity change has elicited widespread concern over the consequences for functions and services provided by ecosystems[1–3]. Despite extensive evidence for a positive effect of biodiversity on ecosystem functioning within a single trophic level[4,5], how this biodiversity effect varies with multi-trophic food web structure remains unresolved[6] even though most ecosystems contain two to six trophic levels[7]. We investigate how food web complexity modulates biodiversity–ecosystem functioning relationships in nature by quantifying energy fluxes as proxies for two principal ecosystem functions[8]—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 (that is, maximum trophic level[9]) and trophic complementarity of predators in more taxonomically diverse food webs. Furthermore, predator trophic complementarity[10,11] increased predation fluxes in all freshwater ecosystem types. These findings highlight the threat of trophic downgrading to critical ecosystem functions (for example, biological control and maintenance of biodiversity and ecosystem stability) provided by predators[12,13], which are typically most vulnerable to anthropogenic disturbances[14,15]. 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 biodiversity–ecosystem function relationships.

Humans have vastly altered the diversity of life across the planet[1,3]. Virtually no ecosystem has escaped the influence of anthropogenic activities, which have not only caused global declines in biodiversity[16] but also widespread shifts in the composition of species assemblages[17,18]. These changes have motivated thousands of experimental studies aimed at documenting the positive influence of biodiversity on ecosystem functioning[6]. 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[6]. 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[8]. As most ecosystems comprise two to six trophic levels[7] that each perform unique functions and can respond differently to environmental change[6,8], 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

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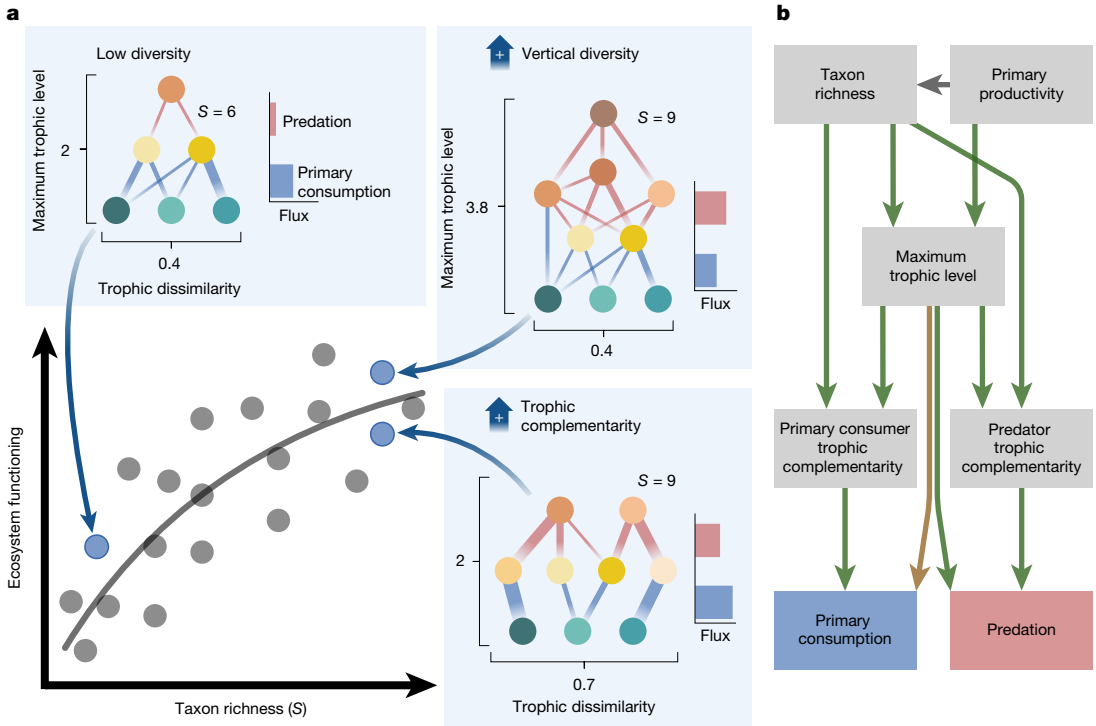


**Fig. 1 | The hypothetical role of food web complexity in mediating biodiversity effects on ecosystem functioning. a**, Ecosystem functioning (primary consumption and predation) should increase with taxon richness in food webs, which is expected to correlate positively with several dimensions of food 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 (positive arrows) in vertical diversity and trophic complementarity compared with a reference low-diversity food web (upper left panel) illustrate how these two mechanisms could contribute independently 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, which enhance primary consumption and predation fluxes in food webs directly and indirectly. Variation in taxon richness and food web complexity is expected to arise as a result of environmental gradients such as primary productivity. Arrows denote hypothesized positive (green), negative (brown) and non-linear (grey) effects. Figure created in BioRender; Barnes, A. https://biorender.com/whu6btx (2026).

a generalized understanding of BEF relationships across trophic levels and ecosystem types[6]. Thus, to translate findings from experimental BEF research to real ecosystems[4,19–21], it is imperative that we embrace the complexity of natural food webs by extending experimental and observational BEF research into the multi-trophic realm.

Numerous conceptual reviews highlight the importance of multi-trophic interactions for modulating BEF relationships[6,8,22–26], which has been supported by theoretical investigations of model food webs describing the influence of food web structure on ecosystem functioning[9,11,26,27]. Such models demonstrate the impact of food web structure on the relationship between biodiversity and total biomass at different trophic levels[26] and suggest that changes in food web structure alter several functions such as biomass production and resource use[27]. Despite the large amount of theory, remarkably few empirical investigations exist and have worked only with simplified food webs[28,29] (fewer than 20 taxa) and/or are restricted to specific ecosystems (for example, refs. 28–31). Consequently, despite these important past contributions, our understanding of the BEF relationship in naturally complex food webs remains predominantly conceptual and lacks generality[4].

A principal challenge has been to determine which food web properties capture the underlying mechanisms that modulate BEF relationships in multi-trophic systems[25]. Two main mechanisms have emerged from theoretical research: vertical diversity[9] and trophic complementarity[10,11] (Fig. 1a). The 'vertical diversity hypothesis'[9] proposes that primary productivity should be associated positively with the maximum trophic level of food webs due to increased predation pressure and top-down effects on primary consumption[32]. Ecosystem productivity has long been thought to directly constrain vertical diversity[33–36], such that increased availability of basal resources supplies sufficient energy to sustain higher trophic levels. However, this constraint is probably weakened with decreasing ecosystem size[33] and increasing disturbance frequency, both of which inhibit biomass accumulation of more sensitive top-predator species[14,15,37]. 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 (ecosystem functioning) at each trophic level[11]. Trophic complementarity in food webs is most probably constrained by taxonomic diversity[10,11] as variability in consumer-resource interactions depends on the diversity of consumer types[38] and resource heterogeneity[39]. Thus, unlike vertical diversity, the dependence of trophic complementarity on ecosystem productivity, size and disturbance should be mainly indirect[40,41]. As anthropogenic activities alter ecosystem productivity and size through the introduction of new ecological disturbances[3], humans are not only driving changes in taxonomic diversity but also in the food web complexity that probably underpins the functioning and stability of ecosystems. However, the relative importance of multi-trophic mechanisms for maintaining ecosystem functioning in real, complex food webs remains untested, posing a principal limitation for understanding and predicting ecosystem-scale consequences of biodiversity change[12].

Here we analyse contributions of vertical diversity and trophic complementarity to the relationship between taxon richness and multi-trophic ecosystem functioning (that is, functions carried out simultaneously by different trophic levels) (Fig. 1) in 318 highly resolved,

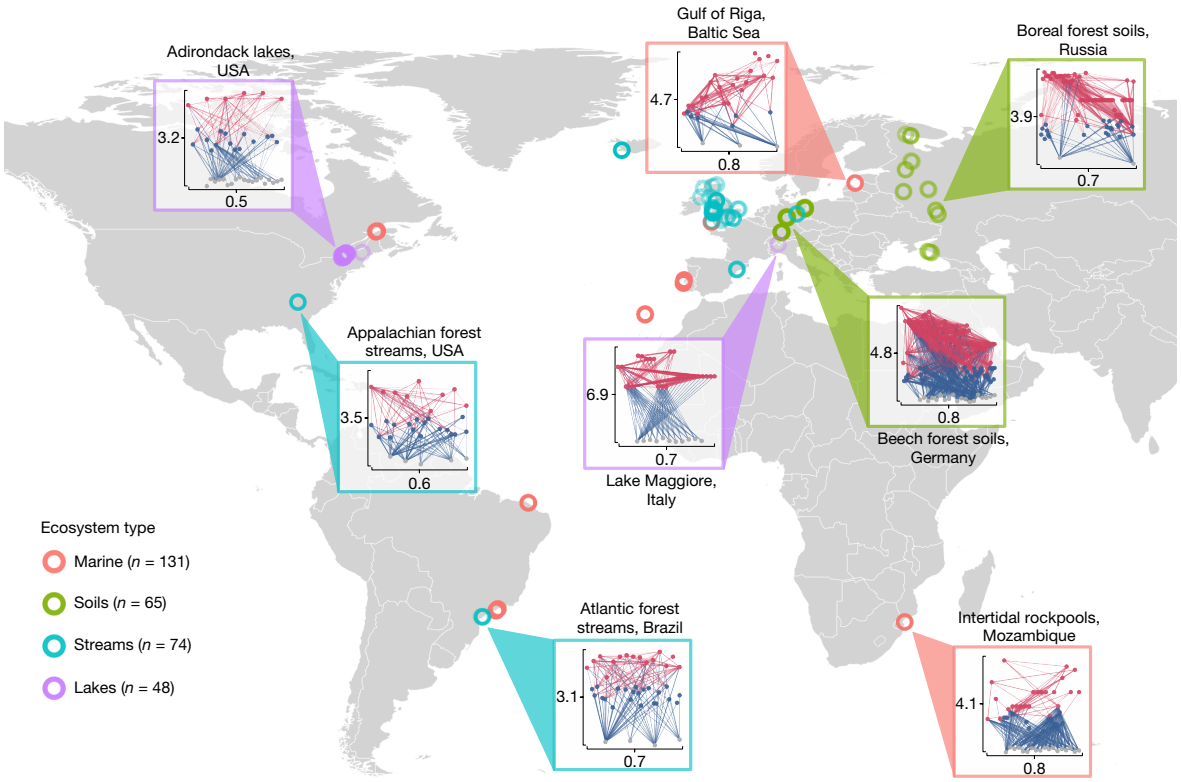


**Fig. 2 | Geographic distribution of the 318 food webs across four main ecosystem types.** Example food webs are shown in zoomed insets, with vertical axes to denote maximum trophic level and horizontal axes to denote mean trophic complementarity (as in hypothetical food webs shown in Fig. 1a). Trophic complementarity ranges between 0 and 1, where a value of 1 indicates 100% dissimilar interactions among consumers (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 created in BioRender; Barnes, A. https://biorender.com/51al0po (2026).

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[8,42], 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[43]. This allows us to quantify two main ecosystem functions in complex food webs: primary consumption (total outflux from primary producers and detritus) and predation (total outflux from consumers; that is, secondary consumption) that exhibit wide-ranging variation across productivity and temperature gradients present in each of the ecosystems (Supplementary Figs. 1 and 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 multi-trophic taxon diversity (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); that is, 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 (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 (maximum trophic level) will increase total predation but reduce primary consumption due to increased top-down control of primary consumers[9,35] (Fig. 1b). We further hypothesize that greater trophic complementarity (dissimilarity of trophic interactions) will enhance both primary consumption and predation due to increased partitioning of resources by consumers[10] (Fig. 1b). By exploring variation in several dimensions of food web complexity that capture a suite of trophic processes (trophic cascades and niche partitioning), we reveal how the multi-trophic structure of ecosystems determines the role of biodiversity in maintaining functions in natural, complex ecosystems.

## Consistent biodiversity–functioning relationships in food webs

The cross-ecosystem analysis revealed consistently positive effects of taxon richness on rates of primary consumption (linear mixed effects model coefficient $\beta = 0.85 \pm$ s.e. 0.11, d.f. = 305; $P < 0.001$) and predation ($\beta = 1.89 \pm$ s.e. 0.20, d.f. = 305; $P < 0.001$) (Fig. 3a). This positive bivariate relationship, between taxon richness and multi-trophic 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 ($\beta = 0.95 \pm$ s.e. 0.10, d.f. = 304; $P < 0.001$) and secondary consumption ($\beta = 1.77 \pm$ s.e. 0.02,

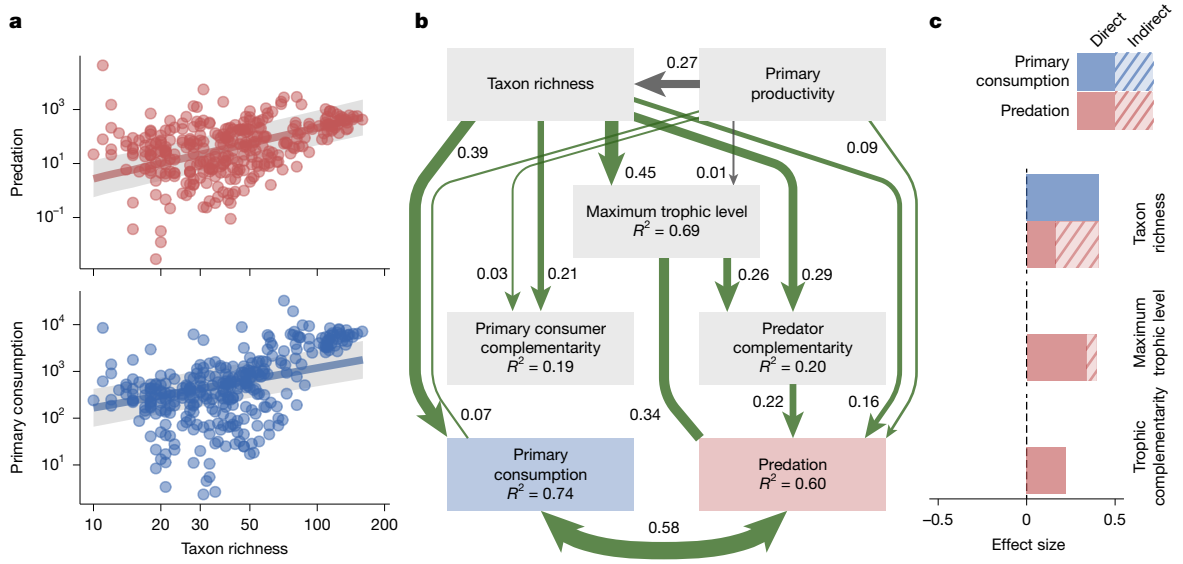


**Fig. 3 | Positive effects of taxon richness on multi-trophic functioning rely on vertical diversity and trophic complementarity. a**, Marginal effects of taxon richness on ecosystem functioning derived from bivariate analyses of all 318 food webs for predation (red) and primary consumption (blue). Predation and primary consumption fluxes are expressed in J day$^{-1}$ m$^{-2}$. Solid trend lines and associated 95% confidence intervals denote statistically significant relationships ($P < 0.05$) derived from the log-transformed linear mixed effects models (LMM) models. **b**,**c**, 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 through maximum trophic level, trophic complementarity of primary consumers and trophic complementarity of predators (**b**) with associated effect plot summarizing direct effects (solid bars) derived from the SEM and indirect effects (hatched bars) mediated by other food web properties (**c**). Arrow widths are scaled to standardized 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 $f^2$ (Methods). Red and blue bars in **c** denote standardized effects of food web properties on predation and primary consumption, respectively. Figure created in BioRender; Barnes, A. https://biorender.com/hpel27h (2026).

d.f. = 304, $P < 0.001$). Across the full range of taxon richness observed in the 318 food webs—from 10 taxa in an eastern Canadian intertidal rock pool to 159 taxa in central German forest soils—we found a predicted increase of 1,875 J day$^{-1}$ m$^{-2}$ in primary consumption (1,297% increase) and of 375 J day$^{-1}$ m$^{-2}$ in predation (7,050% 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 and Supplementary Table 1). These results support our main hypothesis that taxon richness affects ecosystem functioning (predation rates) in food webs directly and indirectly through several 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 (Supplementary Methods and Supplementary Fig. 3).

## Trophic structure shapes biodiversity effects on predation and stability

Our cross-ecosystem food web analyses confirm the prevalent role of vertical diversity and trophic complementarity in maintaining predation rates in food webs[2]. 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. As large-bodied predators are predicted to be the organisms most sensitive to environmental change[14,15,37], biodiversity loss is likely to be characterized by 'trophic downgrading'[12] and trophic niche compression[44] 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 fourfold loss in predation rates under pessimistic scenarios of 50% biodiversity loss by the end of this century[45]. These findings exemplify the potential risk of species loss to the critical ecosystem functions provided by predators, such as natural biological control[46,47], maintenance of biodiversity at lower trophic levels[48,49] and regulation of ecosystem stability[12,50]. 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[33]. 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 and 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 (for example, energy channel asymmetry[50], weak trophic loop weights[51] and trophic omnivory[33,52]) that modulate potentially destabilizing effects of strong top-down control in more diverse, naturally assembled food webs.

We hypothesized 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 constrained more strongly by structural properties of food webs compared with primary consumption such as herbivory and decomposition (but see ecosystem-specific analysis of lake food webs; Fig. 4e). Accordingly, taxon richness appeared to

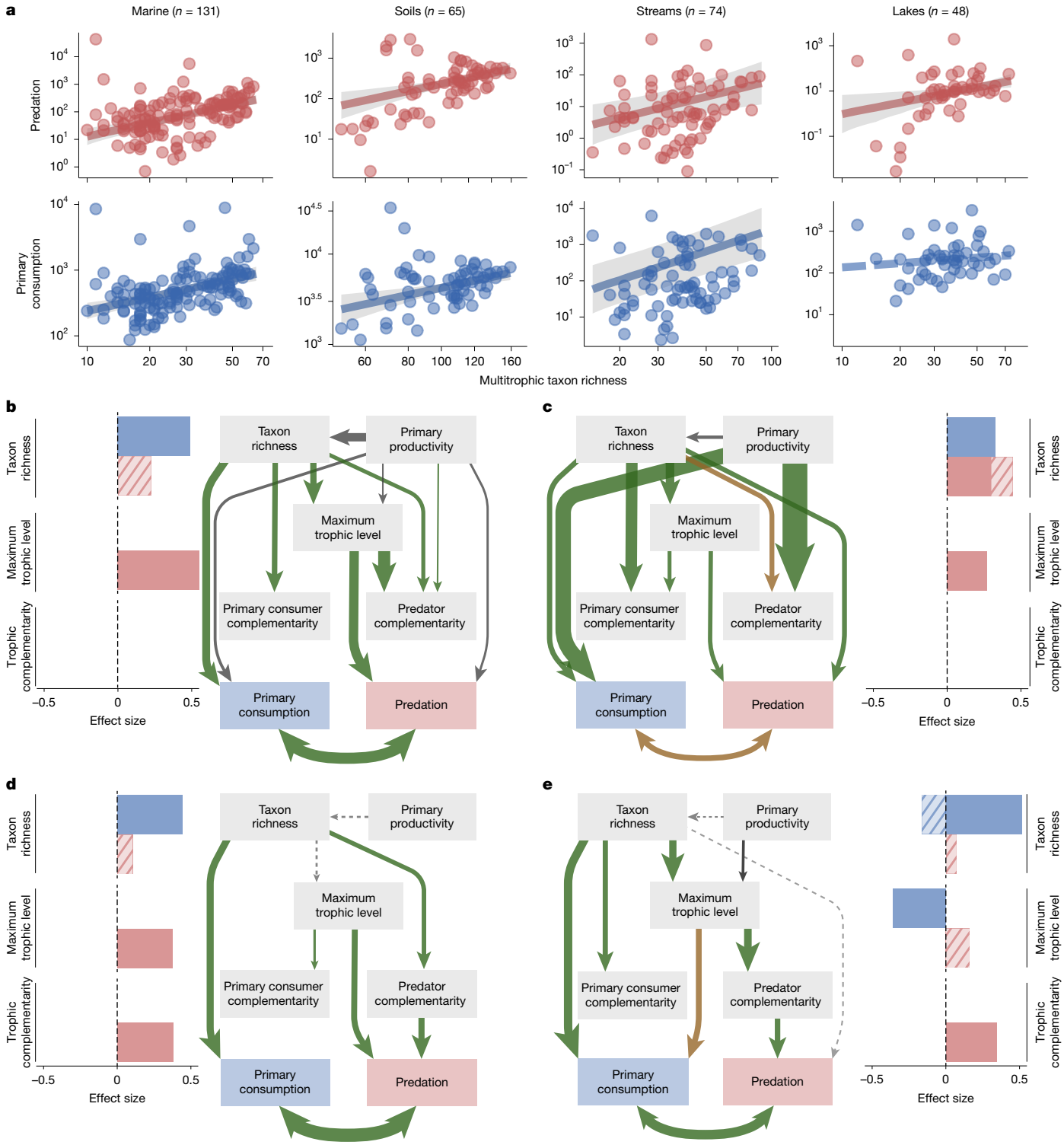


**Fig. 4 | Positive effects of taxon richness on ecosystem functioning are mediated by food web complexity across ecosystems. a**, Marginal effects of taxon richness on ecosystem functioning derived from bivariate analyses across ecosystems (Supplementary Table 5), with associated SEMs (Supplementary Tables 7–10) testing the effects of taxon richness on primary consumption and predation through maximum trophic level, trophic complementarity of primary consumers and trophic complementarity of secondary consumers for marine (**b**; $n = 131$), soil (**c**; $n = 65$), stream (**d**; $n = 74$) and lake (**e**; $n = 48$) food webs. Solid trend lines and associated 95% confidence intervals in **a** denote statistically significant relationships ($P < 0.05$) derived from log-transformed generalized least squares 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 (that is, with the lowest Akaike information criterion (AIC) score following model simplification). Arrow widths are scaled to the standardized 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. Standardized effects of food web properties on predation and primary consumption are denoted by red and blue bars, respectively. The *y*-axes scales vary among panels in **a** to aid visual interpretation of within-ecosystem relationships. Figure created in BioRender; Barnes, A. https://biorender.com/iushr8a (2026).

directly explain variation in primary consumption rates, irrespective of variability in food web complexity (Fig. 3 and Supplementary Table 1). This finding was further supported by our analysis of total food web energy flux (with predation and primary consumption combined), where 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 and Supplementary Table 3). We further assessed whether other food web properties, namely, average trophic omnivory and food web connectance, could have 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 and 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.

## Food-web mechanisms vary across ecosystems amid consistent biodiversity effects

Effects of taxon richness on multi-trophic 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 and 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 multi-trophic BEF mechanisms, such that taxon richness had a net positive effect on all functions across all ecosystem types (Fig. 4b–e and 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 and Supplementary Table 11). Thus, the only statistically non-significant bivariate relationship observed between taxon richness and primary consumption in lakes probably resulted from an indirect negative taxon richness effect through 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, such as some aquatic ecosystems, where trophic cascades may be the strongest[53]. 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 (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 and Supplementary Tables 7–10), with some notable variation in the relative importance of multi-trophic 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 and Supplementary Tables 7, 8 and 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 and 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[54,55], the detection of this effect only in lakes aligns with evidence that trophic cascades can be stronger in lake ecosystems[53]. 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 and Supplementary Tables 9 and 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[56]. 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. By 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 and Supplementary Figs. 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[57]. Ultimately, this variation could give rise to the natural variation in trophic complementarity required to influence significantly the relationships between biodiversity and ecosystem functioning.

## Conclusions

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 multi-trophic 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[58], could further explain biodiversity effects on ecosystem functioning and stability in naturally complex multi-trophic ecosystems, though we found no evidence to support this in our data (Extended Data Fig. 2). Furthermore, environmental gradients that underlie the observed variation in taxonomic richness and food web properties probably create context-dependencies that could weaken or intensify multi-trophic BEF relationships[59]. Although we incorporate geographic variation in environmental temperature and primary productivity in our analyses analytically and statistically, 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 generalized BEF effects in food webs. Most notably, it is possible that

our inability to detect effects of food web complexity (particularly trophic complementarity) on primary consumption resulted from poorer taxonomic resolution of basal resources (phytoplankton, bacteria, and so on) and associated definitions of feeding links. Although this has long been recognized as a widespread constraint in food web ecology, it highlights the critical need for better global standards in food web data generation[60].

Until now, BEF research has been constrained heavily to within trophic levels, lacking explicit consideration of the vast complexity of trophic interactions that shape species assemblages and their influence on the environment[6,8]. 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.

## Online content

Any methods, additional references, Nature Portfolio reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41586-026-10710-5.


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# Methods

### Food web data collation

We compiled 318 food web datasets from 12 studies[56,61–70] 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[57,71]). 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[72]. 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 (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[8,43], we first needed to quantify the energetic losses of each population across the 318 food webs. To do so, we estimated metabolic expenditure (population energetic demands due to metabolism of consumed resources) and assimilation efficiency (the proportion of energy assimilated from consumed resources and allocated to metabolism and biomass production). Individual metabolic rates, $I$, were calculated based on generalized allometric and thermal scaling of organism metabolism[73] using the formula:

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

where $i_0$ is a normalization constant, $M$ is organism body mass and $E/k_BT$ is the Vand't Hoff–Arrhenius relationship described by the activation energy ($E$ = 0.69), Boltzmann's constant ($k_B = 8.62 \times 10^{-5}$) 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 and colleagues[73]. For each food web node (that is, a consumer population in a local food web), we calculated consumer population energy use, $X_j$, as $X_j = I \bullet N_j$ where $N_j$ is the population density of consumer $j$.

To partition energy fluxes from several 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

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

where $\acute{\varepsilon}_0$ is a normalization constant, $E_\varepsilon$ is the activation energy, $k_B$ is Boltzmann's constant, and $T - T_0$ is absolute temperature (K) normalized to 20 °C ($T_0$: 293.15 K)[74]. We specified different $\acute{\varepsilon}_0$ values for the three main resource types, animal (predation), plant (herbivory) and detritus (detritivory), for each trophic interaction within food webs, according to Lang and colleagues[74]. This allowed for several possible assimilation efficiencies per consumer population where they fed on several resource types in a food web (that is, omnivores).

### Quantifying multi-trophic ecosystem functioning using energy fluxes

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

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

where $F_j$ represents the sum of ingoing fluxes to node $j$. This bioenergetic framework[8,51,76] was developed to use readily accessible biological information, allowing the system of equations to be fully defined (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 (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 (the sum of outgoing fluxes from animal populations)[46]. Furthermore, we estimated top-down effects of predators on prey by calculating per capita predation rates ($\mathrm{Pr}_i$) as $\mathrm{Pr}_i = \frac{\sum_j F_{ij}}{N_i}$, where $F_{ij}$ is the energy flux from prey node $i$ to its predators $j$, and $N_i$ is the population density of prey $i$[46]. 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 (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 (that is, prey-averaged trophic level), scaled by relative energy fluxes:

$$\mathrm{TL}_i = 1 + \frac{1}{|P_i|}\sum_j \mathrm{TL}_j \quad (5)$$

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

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

$\mathrm{P}_i$ represents the set of prey of consumer $i$ and $|P_i \cap P_j|$ is the cardinality of the intersection of $\mathrm{P}_i$ and $\mathrm{P}_j$ (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 $1 - \mathrm{TS}_{ij}$. 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 multi-trophic 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[77], 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 (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[78]. 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 (that is, 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 generalized least squares 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 (fewer than three studies, and therefore levels, per ecosystem type).

We applied structural equation modelling with piecewise SEM[79], which uses directed tests of separation[80] to determine the conditional independence of several response and predictor variables in a multi-variate framework. This approach allowed us to determine the direct and indirect effects of taxon richness on primary consumption and predation rates in food webs, using 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 net primary productivity (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 (Fig. 1b). We also 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 (that is, with all ecosystem types combined) and for within-ecosystem SEMs, we used the same model structures described above, using LMMs with study ID included as a random effect (global and stream food web analysis) and generalized least squares models (marine, soil and lake analyses), the inclusion of variance functions where necessary to ensure all assumptions of parametric tests were met. Due to the probably 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 piecewise SEM approach[79], 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 greater than 0.05, this infers that the hypothesized paths are consistent with the data and the SEM cannot be rejected[80]. 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 2 units or more.

From the final minimum adequate SEMs, we then summarized the direct and indirect effects of taxon richness, maximum trophic level and trophic complementarity using the standardized ($z$-transformed) path coefficients from each SEM[79]. 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[81]. Cohen's $f^2$ is defined as

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

Where $R^2_{\text{included}}$ is the conditional $R^2$ from the full model including the linear and non-linear effects of NPP, whereas $R^2_{\text{excluded}}$ 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 standardized path coefficients along identified pathways within each SEM. All analyses were carried out in R version 4.5.0 (ref. 82). All data and code used to produce the results in this study are available at Zenodo (https://doi.org/10.5281/zenodo.17728782)[83].

### Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

## Data availability

All data used in this study are available at Zenodo (https://doi.org/10.5281/zenodo.20130985)[83]. Source data are provided with this paper.

## Code availability

Code for computing food web properties, energy fluxes, stability, NPP and statistical analyses is available at Zenodo (https://doi.org/10.5281/zenodo.20130985)[83].


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**Acknowledgements** This work was initiated from the Food web Structure, Ecosystem functioning and Diversity across ecosystems (FuSED) workshop at the German Centre for Integrative Biodiversity Research (iDiv) Halle–Jena–Leipzig, funded by the German Research Foundation (DFG–FZT 118, 202548816).

**Author contributions** A.D.B., U.B., N.E., D.G.-C., D.P.G., J.H., M.J., E.J.O'G., D.O., D.M.P., B.R., C.V. and B.G. designed the study. A.D.B. assembled the datasets and A.D.B., E.B., B.R. and B.G. conducted the analysis. U.B., M.B., S.L.E., D.P.G., R.O.H., D.I.K., S.K., P.K., M.M., J.-R.M., M.C.N., E.J.O'G., D.O., D.M.P., R.A.S., V.S.S., A.J.T. and C.V. contributed data. All authors contributed to discussions on study design, analysis and interpretation. A.D.B. wrote the manuscript with contributions from all authors.

**Funding** A.D.B. acknowledges support by the Marsden Fund Council from Government funding managed by Royal Society Te Apārangi (grant no. MFP-23-UOW-029). We acknowledge funding by the German Research Foundation (DFG-FOR 5000, Ei 862/29-1) and the Portuguese Foundation for Science and Technology (UIDB/04326/2020, UIDP/04326/2020, LA/P/0101/2020, UIDB/04292/2020, CEECINST/00146/2018/CP1493/CT0007). V.S.S. was supported by NSF/FAPESP grant 2022/01452-1. D.I.K. was supported by the Russian Science Foundation (project no. 25-24-00639). M.B. was funded through BiodivRestore ERA-NET Cofund (grant no. 101003777) and the Federal Ministry of Education and Research Germany (16LW0174K). P.K. was supported by the NERC Pushing the Frontiers grant (NE/Y001184/1). S.K. acknowledges support from (www.coastclim.org), and the Research Council of Finland (grant no. 361049). D.G.-C. was funded by the New Zealand Biological Heritage National Science Challenge and the Austrian Science Fund (grant reference FWF ESPRIT ESP-671). M.C.N. acknowledges the Research Council of Finland University Profiling funding for InterEarth (grant no. 353218). R.A.S. was funded by the Russian Science Foundation, grant no. 23-14-00201. S.L.E. was supported by NSF grants DEB-9207498, DEB-9629268, DEB-0212315 and the USDA Forest Service Northern Research Station. D.M.P. was supported by the British Ecological Society grants SR21\100750 & 4973-6013. A.J.T. was supported by the Canada Research Chairs Programme and a Natural Sciences and Engineering Research Council of Canada Discovery Grant (RGPIN-2023-03977).

**Competing interests** The authors declare no competing interests.

**Additional information**

**Supplementary information** The online version contains supplementary material available at https://doi.org/10.1038/s41586-026-10710-5.

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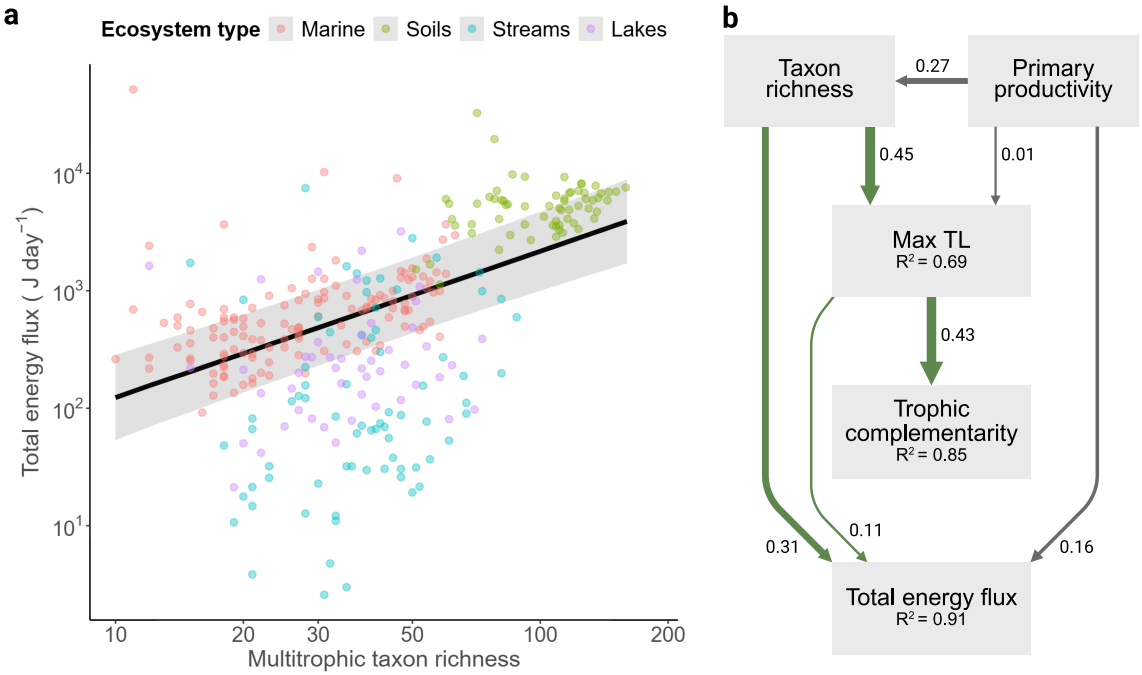
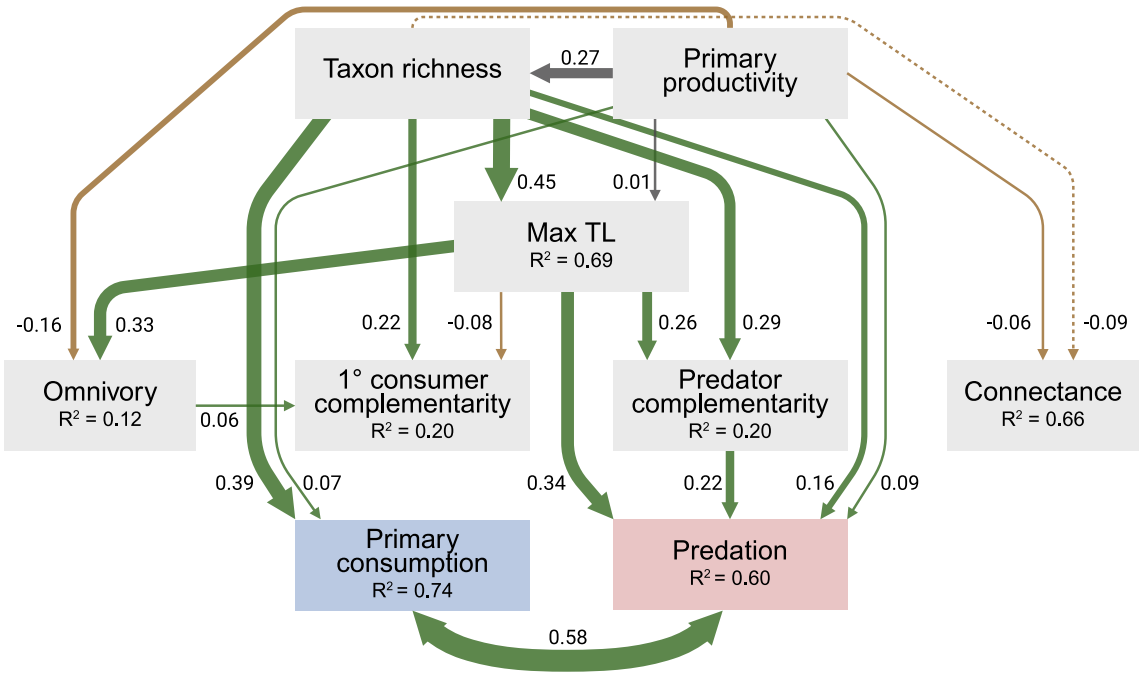
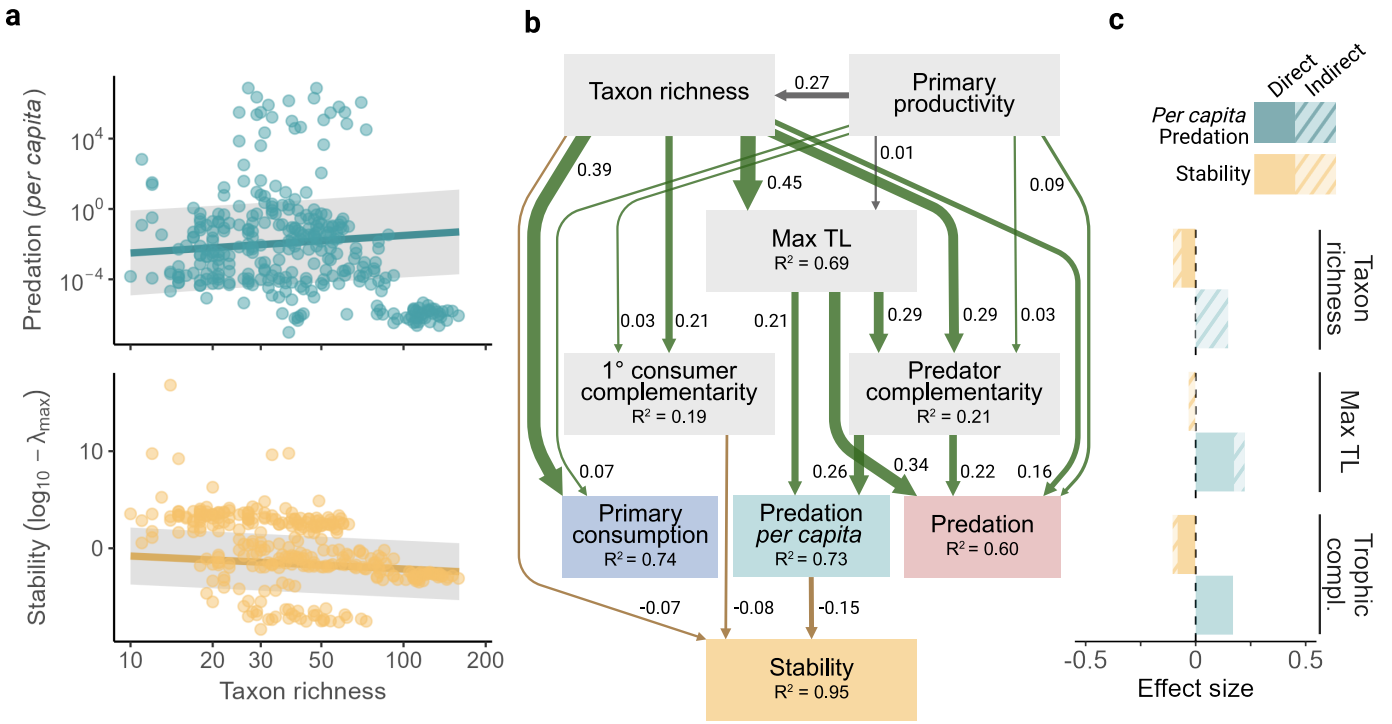
**Peer review information** *Nature* thanks J. Emmett Duffy and the other, anonymous, reviewer(s) for their contribution to the peer review of this work. Peer reviewer reports are available.




**Extended Data Fig. 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 ($\beta = 1.24 \pm$ SE 0.14, df = 305, $p < 0.001$). (b) Structural equation model (Fisher's $C_s = 4.3$, $P = 0.83$) 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. Figure created in BioRender; Barnes, A. https://biorender.com/3v93kyd (2026).




**Extended Data Fig. 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 $f^2$. Figure created in BioRender; Barnes, A. https://biorender.com/3v93kyd (2026).




**Extended Data Fig. 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. Figure created in BioRender; Barnes, A. https://biorender.com/0scvc75 (2026).