Structural dependencies in trophic interaction strengths explain stability in natural food webs

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Abstract

Ongoing biodiversity loss has intensified the need to understand what keeps complex ecological communities stable. Theory predicts that complexity destabilises communities when the strength of interactions is randomly distributed. In natural food webs, however, shared biological traits such as biomass, energy conversion efficiency and specific predation rate link various interaction strengths to one another, creating structural dependencies among them. We retained or broke these dependencies to identify how they affect stability in a three-species intraguild predation module, assess their relevance to Lake Constance food webs and test how their effects vary with complexity in bioenergetic models. Across all three systems, retaining all dependencies produced the greatest reduction in the destabilising effects of interspecific interactions. In the three-species module, retaining structural dependencies brought opposing trophic feedbacks closer in strength, contributing to greater relative stability. It also gave the closest match to empirical stability estimates for Lake Constance, even without enforcing energy balance. Such stabilising effect from interspecific interactions increased with species richness and connectance. Our findings show how non-random patterns in interaction strengths that emerge from species traits can explain stability in real food webs.

Keywords

Species traits, dependencies among interaction strength, food web stability; complexity-stability debate

1. INTRODUCTION

Understanding how complex ecological communities maintain stability remains a central problem in ecology. Early theory proposed that diversity could enhance stability by providing alternative pathways through which ecological processes are maintained when individual populations fluctuate [1]. May [2], by contrast, showed that randomly assembled communities become less likely to be locally stable as species richness, connectance, and the variability of interaction strengths increase. This contrast established the diversity-stability debate and raised a fundamental question: which forms of biological organisation allow complex communities to remain stable?

Subsequent work has shown that local stability, the capacity of a community to return towards equilibrium after a small disturbance, depends on how interaction strengths are distributed and organised in community structure. The interaction strengths are commonly quantified by the off-diagonal elements of the Jacobian matrix, which measure how changes in one species' biomass affect another species' biomass growth rate at equilibrium [3]. Empirical food webs commonly contain many weak interactions and relatively few strong ones, a pattern that can promote stability [4–9]. Organisations among these strengths also matter. Within consumer-resource pairs, reciprocal effects have opposite signs, and correlations between their strengths influence stability [10,11]. Within trophic feedback loops, a closed pathway of species interactions through the Jacobian matrix, the placement of weak interactions in long loops can limit destabilising feedbacks [12–14]. Retaining these forms of organisation can help explain why empirically parameterised food webs do not necessarily exhibit the negative complexity-stability relationship predicted for random communities [15].

A mechanistic understanding of food web stability requires explaining how relationships among interaction strengths arise from the underlying biology. Random-matrix approaches examine how the distributions and organisation of interaction strengths influence stability, describing these properties directly at the level of matrix elements [2,10,16,17]. In mechanistic food web models, Jacobian elements instead follow from assumptions embedded in the equations for population dynamics and depend on biological quantities such as interaction coefficients, species abundance/biomasses, metabolic rates, and conversion efficiencies [3,9]. Several elements can therefore depend on the same trait. The same interaction coefficient can contribute to both reciprocal interaction strengths within a consumer-resource pair, and a species' biomass can scale several interaction strengths acting on that species. When conversion efficiency is specified at the consumer level, the same efficiency also contributes to the positive effects of all its resources on its growth (**Figure 1**). We call these relationships structural dependencies, which arise from shared biological quantities even when those quantities are sampled independently.

Structural dependency can influence stability by linking interactions and trophic feedback pathways through shared biological quantities. Previous studies have shown how trophic fluxes, biomasses, efficiencies, and network structure generate stabilising arrangements of realised interaction strengths [9,13]. Energetic analyses have further shown how the need to balance energy gains and losses constrains interaction strengths within trophic feedback loops and across food webs [18,19]. However,

interaction strengths in these systems reflect both the shared biological quantities and energetic constraints, making the contribution of sharing to stability difficult to isolate. Structural dependency concerns whether the same quantity contributes to several Jacobian elements, whereas energetic constraints restrict which combinations of quantities are feasible. Whether sharing biological quantities itself has a stabilising effect therefore remains unclear.

In this study, we investigate the role of structural dependency in food web stability (**Figure 1**). We aim to address three questions: (1) How does sharing biological quantities alter trophic feedbacks? (2) Do these effects help to explain and understand the stability of empirical food webs? and (3) How does the effect of structural dependency change with food web complexity and with empirical versus theoretical representations of complex communities? To answer these questions, we combine a mathematical analysis of a three-species intraguild predation module with analyses of the empirical Lake Constance food webs and analyses of model food webs of varying complexity. Together, these analyses test whether the sharing of biological quantities constrains destabilising trophic feedbacks and contributes to the stability of complex ecological communities.

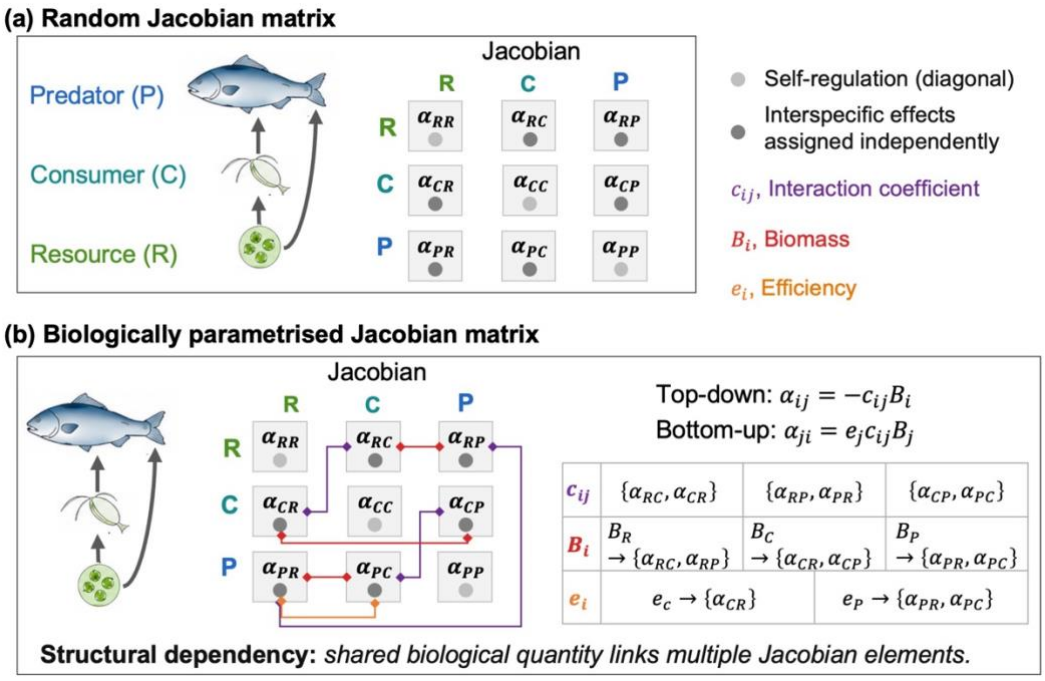


Figure 1. (**a**) Random Jacobian matrix for an intraguild predation module, with interspecific effects assigned independently and self-regulation on the diagonal. (**b**) Biologically parameterised Jacobian matrix, where shared interaction coefficients (c_{ij}), biomasses (B_i), and efficiencies (e_i) link multiple Jacobian elements. Purple, red, and orange links indicate dependencies generated by shared interaction coefficients, biomasses, and efficiencies, respectively.

2. METHODS

2.1 Biological parameterisation of food web Jacobian matrices

We described species biomass dynamics using a consumer-resource Lotka-Volterra model:

$$\frac{dB_i}{dt} = B_i\left(b_i + \sum_{j\in R_i} e_i c_{ji} B_j - \sum_{k\in C_i} c_{ik} B_k\right), \quad (1)$$

where B_i is the biomass of species i; b_i is its intrinsic per capita rate, positive for biomass growth in producers and negative for mortality in consumers [9]; R_i and C_i are its sets of resources and consumers, respectively. The interaction coefficient c_{ji} describes the consumption of resource j by consumer i, and e_i is the conversion efficiency of consumer i.

At equilibrium, local dynamics of an *n*-species community are described by the Jacobian matrix, whose elements $\alpha_{ij} = \frac{\partial(\mathrm{d}B_i/\mathrm{d}t)}{\partial B_j}$ quantify how a small change in the biomass of species j affects the biomass growth rate of species i [3]. For consumer j feeding on resource i, the reciprocal off-diagonal elements are

$$\alpha_{ij} = -c_{ij} B_i \quad (2)$$

$$\alpha_{ji} = e_j c_{ij} B_j \quad (3)$$

where α_{ij} represents the top-down effect of consumer j on resource i, and α_{ji} represents the bottom-up effect of resource i on consumer j.

2.2 Structural dependencies in biologically parameterised Jacobian matrix

The biological parameterisation in Eqs. 2-3 generates three forms of structural dependency among the off-diagonal Jacobian elements, i.e., interspecific interaction strengths (**Figure 1**). First, a dependency based on the interaction coefficient c_{ij} occurs because it determines both the top-down ($-c_{ij}B_i$) and bottom-up ($e_j c_{ij} B_j$) interaction strengths associated with a consumer-resource interaction. Second, a dependency based on biomass B_i occurs because it scales all off-diagonal interaction strengths in row i of the Jacobian, which describe how the biomass growth rate of species i responds to changes in the biomasses of other species. Therefore, interaction strengths associated with different resources and consumers of species i share the same biomass term B_i. Third, a dependency based on conversion efficiency e_i occurs because it is shared across the positive effects of all resources consumed by species i. Thus, when a consumer feeds on multiple resources, the corresponding bottom-up interaction strengths are linked by a common conversion efficiency.

To isolate the effects of structural dependency, we constructed randomised Jacobians in which repeated occurrences of the same biological quantity either shared a common value or were assigned independently. When a dependency was retained, a value was sampled once for each corresponding interaction coefficient, species biomass, or conversion efficiency and reused wherever that quantity

occurred in the Jacobian. When a dependency was removed, a separate value was sampled independently for every occurrence. We considered five scenarios: full dependency, retaining all three forms; feeding-coefficient dependency only; biomass dependency only; conversion-efficiency dependency only; and no dependency, retaining none. **Figure S1** uses a three-species intraguild predation module to show which biological quantities share a sampled value across Jacobian entries and which are sampled independently in each scenario. Within each analysis, all scenarios used the same trophic topology, predator-prey sign structure, and sampling distributions or empirical parameter pools, differing only in how sampled values were reused.

We first combined analytical and numerical analyses of a three-species intraguild predation (IGP) module to determine how structural dependencies alter reciprocal consumer-resource feedbacks, the balance between opposing three-species feedback loops, and relative stability (Section 2.3). We then used empirical Lake Constance food webs to test whether these effects extend to whole networks and whether retaining structural dependencies reduces the difference in relative stability between randomised and empirical Jacobians (Section 2.4). Finally, we used model food webs at steady-state equilibrium to examine how the effects of structural dependency vary with species richness, connectance, and maximum trophic level (Section 2.5). In all three analyses, diagonal elements were set to zero to isolate the contribution of interspecific trophic interactions [18,19]. We quantified local stability using the real part of the dominant eigenvalue $\mathrm{Re}(\lambda_{max})$ of these zero-diagonal Jacobians, with lower values indicating greater relative stability [18,19]. For model food webs, we additionally analysed full Jacobians to assess whether the effects persisted when diagonal terms were included.

2.3 Mechanistic analysis of a three-species intraguild predation module

We used a three-species IGP module to determine whether structural dependencies increase relative stability by constraining trophic feedbacks. We first established the analytical relationship between trophic feedback structure and relative stability, then used numerical experiments to examine how retaining or removing dependencies changes the feedback combinations that occur.

2.3.1 Analytical relationship between trophic feedbacks and relative stability

The module comprised a resource (R), an intermediate consumer (C), and a top predator (P), where C consumes R, and P consumes both R and C. The Jacobian matrix of this module can be written as:

$$\boldsymbol{J} = \begin{bmatrix} 0 & -\gamma_{RC} & -\gamma_{RP} \\ \gamma_{CR} & 0 & -\gamma_{CP} \\ \gamma_{PR} & \gamma_{PC} & 0 \end{bmatrix} \quad (4)$$

where $\gamma_{ij} = |\alpha_{ij}| > 0$ denotes the magnitude of the effect of species *j* on species *i*. This notation distinguishes positive interaction magnitudes from the signed Jacobian elements in Eqs. 2-3. The characteristic equation, $det(\lambda \boldsymbol{I} - \boldsymbol{J}) = 0$, is

$$\lambda^3 + T_1\lambda + T_0 = 0 \quad (5)$$

where $T_1 = \gamma_{12}\gamma_{21} + \gamma_{13}\gamma_{31} + \gamma_{23}\gamma_{32}$, and $T_0 = \gamma_{21}\gamma_{32}\gamma_{13} - \gamma_{12}\gamma_{23}\gamma_{31}$. The coefficient T_1 sums the magnitudes of the three reciprocal consumer-resource feedback loops, whereas T_0 measures the balance between the two opposing three-species loops. Consequently, T_1 is positive, whereas T_0 can be positive, negative, or zero depending on the relative strengths of the two opposing loops. Representing modules in $T_1 - T_0$ space therefore relates their feedback structure to the two coefficients that determine their eigenvalues.

We used Cardano's method to establish the analytical relationship between T_1, T_0, and the eigenvalues (**Appendix S1**). We calculated Re(λ_{max}) across an illustrative grid spanning T_1 from 0 to 2 and T_0 from −2 to 2. The resulting landscape linked feedback combinations to relative stability and provided a reference for interpreting the distributions of simulated modules under different dependency scenarios.

2.3.2 Numerical evaluation of structural dependencies

We parameterised the IGP module using the biological formulation in Eqs. 2-3, giving

$$\boldsymbol{J} = \begin{bmatrix} 0 & -c_{RC}B_R & -c_{RP}B_R \\ e_C c_{RC} B_C & 0 & -c_{CP}B_C \\ e_P c_{RP} B_P & e_P c_{CP} B_P & 0 \end{bmatrix} \quad (6)$$

where c_{RC}, c_{RP}, and c_{CP} are the interaction coefficients for C consuming R, P consuming R, and P consuming C, respectively; B_R, B_C, and B_P are species biomasses; and e_C and e_P are consumer conversion efficiencies.

Substituting these terms into expressions for T_1 and T_0 gives

$$T_1 = c_{RC}B_R \cdot e_C c_{RC} B_C + c_{RP}B_R \cdot e_P c_{RP} B_P + c_{CP}B_C \cdot e_P c_{CP} B_P \quad (7)$$

$$T_0 = e_C c_{RC} B_C \cdot e_P c_{CP} B_P \cdot c_{RP} B_R - c_{RC}B_R \cdot c_{CP}B_C \cdot e_P c_{RP} B_P \quad (8).$$

Each occurrence of a quantity in a different Jacobian element was assigned a separate sampled value unless the corresponding dependency was retained. Under full dependency, all occurrences of the same biological quantity shared a common value, allowing the expressions to be simplified to:

$$T_1 = e_C c_{RC}^2 B_R B_C + e_P c_{RP}^2 B_R B_P + e_P c_{CP}^2 B_C B_P \quad (9)$$

$$T_0 = e_P c_{RC} c_{RP} c_{CP} B_R B_C B_P (e_C - 1) \quad (10).$$

To evaluate the effects of retaining or removing these dependencies on the stability of the IGP modules, we generated 10000 parameter sets under each of the five scenarios defined in Section 2.2. Interaction coefficients, species biomasses, and conversion efficiencies were sampled from U(0,1), with values assigned and reused according to each scenario. For each resulting Jacobian, we used the assigned biological quantities to calculate T_1 and T_0 using Eqs. 7-8, then obtained its eigenvalues by solving the characteristic equation numerically (Eq. 5). We mapped the simulated modules in $T_1 - T_0$ space together with their Re(λ_{max}) values and compared their distributions among scenarios, which

allowed us to determine how structural dependencies constrain feedback combinations and how these constraints relate to differences in relative stability.

2.4 Structural dependency and relative stability in Lake Constance food webs

We tested whether the effects identified in three-species modules extended to empirical food webs using 59 seasonally resolved quantitative food webs from Lake Constance spanning 1987–1993 [19]. These food webs were previously mass-balanced and parameterised to represent empirical energy flow through the planktonic community. They shared the same species pool and trophic topology, while species biomasses, interaction coefficients and energy fluxes varied among seasons and years.

For each food web, we constructed an empirical Jacobian matrix from its empirical interaction coefficients, species biomasses, and conversion efficiencies following Eqs. 2-3. These empirical Jacobians therefore preserve both the structural dependencies among Jacobian elements and the mass-balanced energetic organisation of the original food webs. As in our analysis of the IGP modules, diagonal elements were set to zero, and relative stability was quantified as $\mathrm{Re}(\lambda_{max})$, with lower values indicating greater relative stability.

We applied the five dependency scenarios defined in Section 2.2 by resampling interaction coefficients, biomasses, and conversion efficiencies separately from their respective empirical pools within each food web. Trophic topology and predator-prey sign structure remained unchanged, while the scenarios differed in how sampled values were reused across Jacobian elements. Full-dependency randomisation retained all three forms of sharing but still altered the empirical assignment of values to species and feeding links; mass balance was not enforced after randomisation. Thus, comparisons among scenarios evaluated the effects of structural dependency under common sampling conditions, whereas comparisons with the empirical Jacobian assessed deviations from the original parameter arrangement.

For each seasonal food web and dependency scenario, we generated 1000 randomised Jacobians and calculated $\mathrm{Re}(\lambda_{max})$ for each realisation. To quantify the deviation of each dependency scenario from the corresponding empirical Jacobian, we calculated a standardised effect size (*SES*)

$$SES_s = \frac{\overline{\mathrm{Re}(\lambda_{\max})_s} - \mathrm{Re}(\lambda_{\max})_{\mathrm{ref}}}{\sigma_s} \tag{11}$$

where $\overline{\mathrm{Re}(\lambda_{\max})_s}$ and σ_s are the mean and standard deviation across the 1000 randomisations for scenario s, and $\mathrm{Re}(\lambda_{\max})_{\mathrm{ref}}$ is the value of the corresponding empirical Jacobian. Positive values indicate that the randomised scenario has a higher $\mathrm{Re}(\lambda_{max})$ than the empirical food web.

2.5 Structural dependency across food web complexity gradients

Food web complexity may alter how structural dependencies link trophic feedback pathways. We therefore used synthetic food webs to examine how dependency effects vary with species richness, connectance, and trophic structure, and whether these effects persist when diagonal terms from the underlying population dynamics are included.

2.5.1 Generation of food webs at stable equilibria

We generated candidate food webs using the niche model across initial species richness of 10–150 and connectance of 0.03–0.40. Species body masses were assigned according to trophic position, assuming a predator–prey body-mass ratio of 10 [20,21]. Biomass dynamics were simulated using an allometrically parameterised bioenergetic model implemented in *EcologicalNetworksDynamics.jl* [21], with a linear functional response consistent with the interaction formulation used in the preceding analyses.

For a producer species i:

$$\frac{dB_i}{dt} = r_i B_i \left(1 - \frac{B_i}{K_i}\right) - B_i \sum_{k \in C_i} c_{ik} B_k \quad (12)$$

and for a consumer species i,

$$\frac{dB_i}{dt} = B_i \left(\sum_{j \in R_i} e_i \, c_{ji} B_j - \sum_{k \in C_i} c_{ik} B_k - x_i\right) \quad (13)$$

where r_i and K_i are the intrinsic growth rate and carrying capacity of producer i; x_i is the metabolic rate of consumer i; and e_i is the assimilation efficiency of consumer i. c_{ji} is the interaction coefficient of consumer i on resource j, which was given by $c_{ji} = w_{ji} a_i$, where the overall consumption coefficient a_i was sampled from U(0.1, 5), while prey-specific diet weights w_{ji} were sampled randomly and normalised to sum to one across its resources. Producer growth, carrying capacity, and consumer metabolic rates were scaled with body mass following the parameterisation of Miele et al [22]. Assimilation efficiency was set to 0.45 for herbivory and 0.85 for carnivory [21].

Following an initial burn-in simulation, species with biomass below 10^{-12} and species disconnected from the remaining trophic network were removed. The remaining community was simulated again to steady-state equilibrium. We retained communities in which all remaining species persisted and confirmed local asymptotic stability by requiring $\mathrm{Re}(\lambda_{max}) < 0$ for the full dynamical-system Jacobian. The final dataset comprised 700 food webs, with 100 in each of seven realised-richness bins: 6-10, 11-15, 16-20, 21-25, 26-30, 31-35, and 36-40 species. Realised connectance ranged from 0.03 to 0.35. The realised topology, equilibrium biomasses, and biological parameters of each food web provided the reference state for the dependency analyses.

2.5.2 Randomisation and analysis of dependency effects

For each food web, we constructed two Jacobian representations. The interspecific Jacobian followed Eqs. 2-3, with diagonal elements set to zero, allowing direct comparison with the preceding analyses. The full Jacobian was derived from Eqs. 12-13 and included diagonal contributions from trophic interactions, producer density dependence, and metabolic losses. Comparing these representations assessed whether dependency effects on interspecific interactions persisted when diagonal terms were included.

We applied the five dependency scenarios defined in Section 2.2 separately to both representations, retaining trophic topology and predator-prey sign structure. For the interspecific Jacobian, randomisation affected only off-diagonal trophic terms. The full Jacobian was decomposed as $\boldsymbol{J}_{ODE} = \boldsymbol{J}_{inter} + \boldsymbol{D}_{int} + \boldsymbol{D}_{bg}$, where $\boldsymbol{J}_{inter}$ contains interspecific trophic effects, $\boldsymbol{D}_{int}$ contains interaction-derived diagonal effects, and $\boldsymbol{D}_{bg}$ contains the remaining diagonal effects arising from producer density dependence and metabolic losses. We recalculated $\boldsymbol{J}_{inter}$ and $\boldsymbol{D}_{int}$ from the randomised interaction coefficients, biomasses, and conversion efficiencies, while retaining $\boldsymbol{D}_{bg}$ from the corresponding equilibrium food web. The equilibrium and local stability criteria were applied to the original communities; the randomised matrices were used to evaluate changes in their Jacobian structure.

For each food web, scenario, and Jacobian representation, we generated 1000 randomised matrices and calculated $\mathrm{Re}(\lambda_{max})$. Deviations from the original Jacobians were quantified using the standardised effect size in Eq. 11, with the original interspecific or full Jacobian serving as the corresponding reference. Positive SES values indicate that randomisation reduced relative stability, whereas negative values indicate an increase.

We further quantified the stabilising effect attributable specifically to full structural dependency by comparing the full-dependency and no-dependency scenarios within each food web:

$$E_{\mathrm{dep}} = \frac{\overline{\mathrm{Re}(\lambda_{\mathrm{max}})_{\mathrm{no}}} - \overline{\mathrm{Re}(\lambda_{\mathrm{max}})_{\mathrm{full}}}}{\sigma_{no}} \tag{14}$$

where σ_{no} is the standard deviation of $\mathrm{Re}(\lambda_{max})$ under the no-dependency scenario. Positive E_{dep} indicates that retaining dependency increases relative stability, whereas negative values indicate a destabilising effect.

2.6 Statistical analysis

To determine how different forms of structural dependency influence relative stability, we compared $\mathrm{Re}(\lambda_{max})$ among dependency scenarios in the IGP modules using one-way ANOVA. For Lake Constance food webs, SES was analysed using a linear mixed-effects model with dependency scenario as a fixed effect and food web identity as a random intercept. For model food webs, SES was analysed using linear mixed-effects models with richness bin, dependency scenario, and their interaction as fixed effects and food web identity as a random intercept. Separate models were fitted for the interspecific and full Jacobians. Mixed models for both datasets were fitted using lme4 and lmerTest [23,24]. Fixed effects were evaluated using Type III F-tests with Satterthwaite degrees of freedom [24], with sum-to-zero contrasts for factors in the interaction models. Pairwise scenario comparisons used estimated marginal means with Tukey adjustment [25].

Food web complexity may modify the stabilising contribution of structural dependency by changing the number and arrangement of trophic feedback pathways. We therefore examined relationships between E_{dep} and food web complexity using multiple linear regression, with species richness, connectance, and maximum trophic level included together as predictors. Separate regressions were

fitted for the interspecific and full Jacobians using the *lm* function. Richness and connectance were natural-log transformed, and all predictors were centred and scaled to unit variance.

All statistical analyses were conducted in R version 4.5.1 [26].

3. RESULTS

3.1 Structural dependencies increase relative stability by constraining trophic feedbacks

Structural dependencies increased relative stability in the IGP module by restricting the combinations of reciprocal and three-species feedbacks (**Figure 2**). The analytical landscape showed that Re(λ_{max}) was lowest near $T_0 = 0$, where the opposing three-species feedback loops were closely balanced, and this low Re(λ_{max}) region broadened as T_1 increased (**Figure 2a**). Thus, stronger reciprocal consumer-resource feedbacks moderated the destabilising contribution of an imbalance between the three-species loops. Re(λ_{max}) increased as $|T_0|/|T_1|$ increased, with a steeper increase when $T_0 < 0$ (**Figure 2a**).

The dependency scenarios generated different distributions of independently parameterised replicates of the same IGP module within this landscape (**Figure 2b-f**). Under full dependency, T_0 was restricted to negative values and concentrated near zero, placing most replicates within the region of low Re(λ_{max}) (**Figure 2b**). Breaking structural dependencies broadened the distribution of feedback combinations and increased Re(λ_{max}) (**Figure 2c-g**). Among scenarios retaining only one dependency, interaction-coefficient dependency produced the lowest Re(λ_{max}), whereas biomass and conversion-efficiency dependencies produced smaller reductions relative to no dependency (**Figure 2g**). Without structural dependencies, replicates occupied the broadest range of T_0 values and generated the highest Re(λ_{max}), particularly where T_1 was small and $|T_0|$ was large (**Figure 2f-g**). Together, these patterns suggest that structural dependency increases relative stability by concentrating modules near the region where opposing three-species feedback loops are closely balanced.

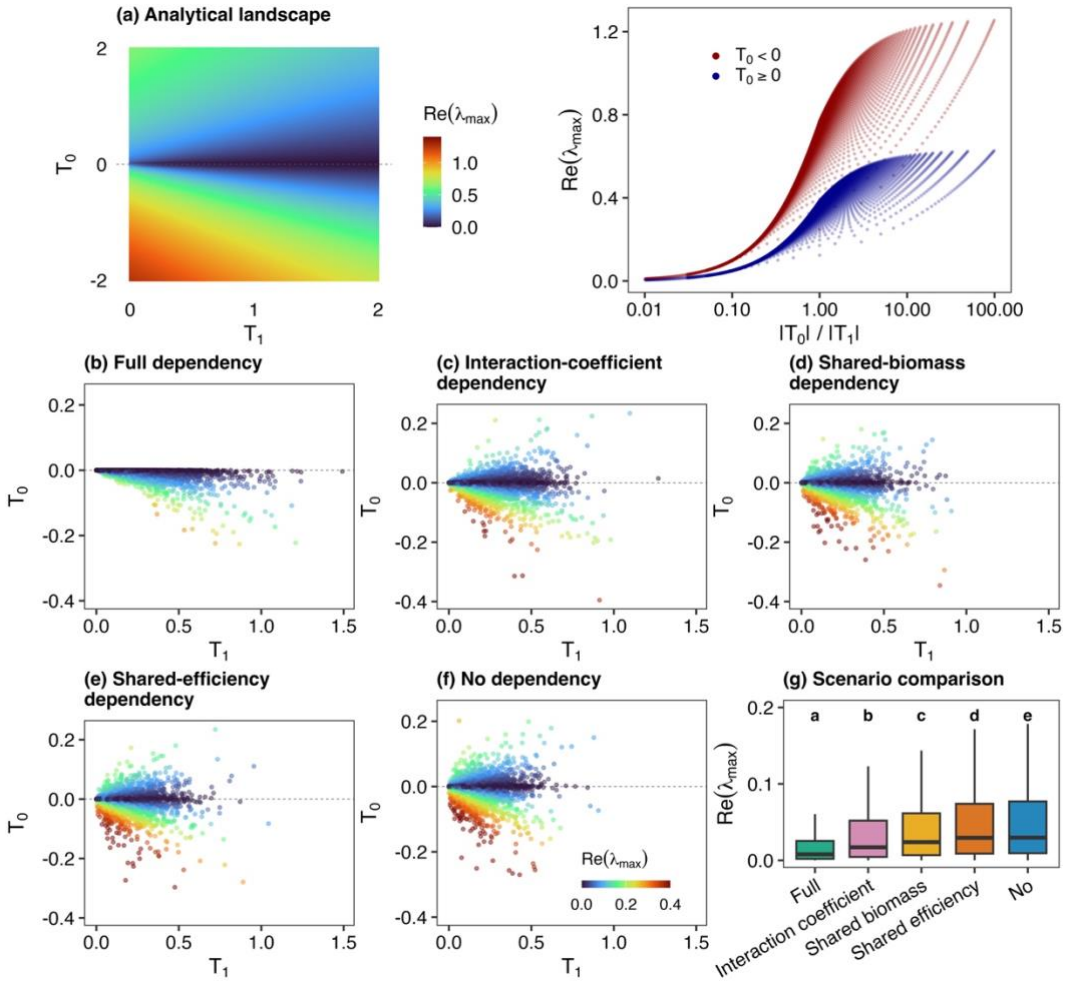


Figure 2. Structural dependencies shift three-species modules across the T_1–T_0 stability landscape. (a) Analytical landscape of the real part of the dominant eigenvalue, Re(λ_{max}), for the characteristic equation $\lambda^3 + T_1\lambda + T_0 = 0$, where T_1 summarises reciprocal consumer–resource feedbacks and T_0 describes the balance between opposing three-species feedback loops. Lower Re(λ_{max}) indicates greater relative stability. The dashed horizontal line indicates $T_0 = 0$. The upper-right panel shows how Re(λ_{max}) changes with the relative loop-feedback imbalance, $|T_0|/|T_1|$, separately for $T_0 < 0$ and $T_0 \geq 0$. (b–f) Distribution of 10000 three-species intraguild predation modules per scenario in T_1–T_0 space under full dependency, feeding-coefficient dependency, shared-biomass dependency, shared-efficiency dependency, and no dependency. Points are coloured by Re(λ_{max}). (g) Compariaions of Re(λ_{max}) across scenarios. Boxes show medians and interquartile ranges, with whiskers extending to the most extreme values within 1.5 interquartile ranges of the box. Scenarios with no letters in common differ significantly according to Tukey-adjusted pairwise comparisons following one-way ANOVA ($p < 0.05$).

3.2 Structural dependencies increase relative stability in Lake Constance food webs

The stabilising pattern identified in the IGP module extended to the Lake Constance food webs. Although Re(λ_{max}) varied seasonally, the ranking of dependency scenarios remained largely consistent across the 1987–1993 time series (**Figure 3a**). Full-dependency randomisations produced the lowest mean Re(λ_{max}), followed by interaction-coefficient dependency and biomass dependency, whereas conversion-efficiency dependency and no dependency produced the highest values. Standardised deviations from the empirical Jacobians differed significantly among scenarios (linear mixed-effects model: $F_{4,232} = 696$, $p < 0.001$). Tukey-adjusted pairwise comparisons distinguished all scenarios except conversion-efficiency dependency and no dependency (**Figure 3b**), indicating that retaining conversion-efficiency dependency alone provided little evidence of a stabilising contribution at the whole-network scale.

Full-dependency randomisations also showed the smallest deviations from the empirical Jacobians (**Figure 3a-b**). Mean randomised Re(λ_{max}) exceeded the corresponding empirical value in all 59 food webs under the four scenarios that broke at least one dependency, compared with 51 of 59 food webs under full dependency.

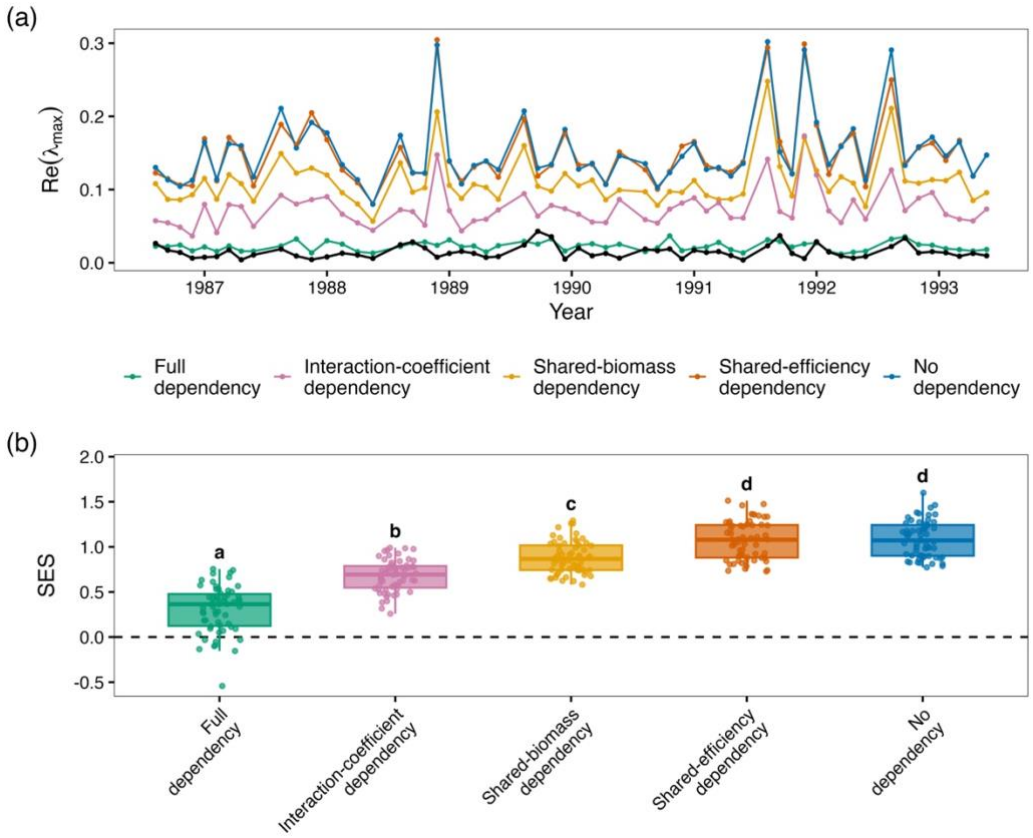


Figure 3. Effects of structural dependency on the relative stability of Lake Constance food webs. (a) Temporal variation in the real part of the dominant eigenvalue, Re(λ_{max}), across 59 seasonally resolved food webs from 1987 to 1993. The black line represents the empirical Jacobian, and coloured lines represent the mean Re(λ_{max}) from 1000 randomised Jacobians per food web under each dependency

scenario. Lower values indicate greater relative stability. (b) Standardised effect sizes (SES) relative to the corresponding empirical Jacobians, calculated as the difference between the randomised mean and empirical Re(λ_{max}), divided by the standard deviation of the randomisations. Positive SES indicates lower relative stability than the empirical food web. Boxes show medians and interquartile ranges, with whiskers extending to the most extreme values within 1.5 interquartile ranges of the box. Scenarios with no letters in common differ significantly in Tukey-adjusted comparisons from a linear mixed-effects model with food web identity as a random intercept ($p < 0.05$).

3.3 Structural dependency has stronger stabilising effects in richer and more connected model food webs

In model food webs at stable equilibria, the separation among dependency scenarios generally increased with species richness (**Figure 4a**). SES differed among scenarios ($F_{4,2760} = 923$, $p < 0.001$) and richness bins ($F_{6,690} = 24$, $p < 0.001$), with a significant interaction indicating that scenario differences varied across richness bins ($F_{24,2760} = 16$, $p < 0.001$). Full dependency produced the lowest SES, followed by interaction-coefficient dependency, with both scenarios distinguished from the others in every richness bin. Biomass dependency produced lower SES than conversion-efficiency dependency and no dependency in bins above 10 species, whereas these three scenarios were not significantly different in the 6–10 species bin. Conversion-efficiency dependency and no dependency were not significantly different within any richness bin.

Multiple linear regression showed that the standardised stabilising effect of full dependency, E_{dep}, increased with species richness (β = 0.71, 95% CI: 0.68-0.74) and connectance (β = 0.59, 95% CI: 0.57−0.62, both $p < 0.001$), whereas maximum trophic level had little independent association (95% CI: −0.01 to 0.01) (**Figure 4b-d**). The regression explained 82.4% of variation in E_{dep} (adjusted $R^2 = 0.82$), indicating that the stabilising contribution of structural dependency was greater in richer and more connected food webs.

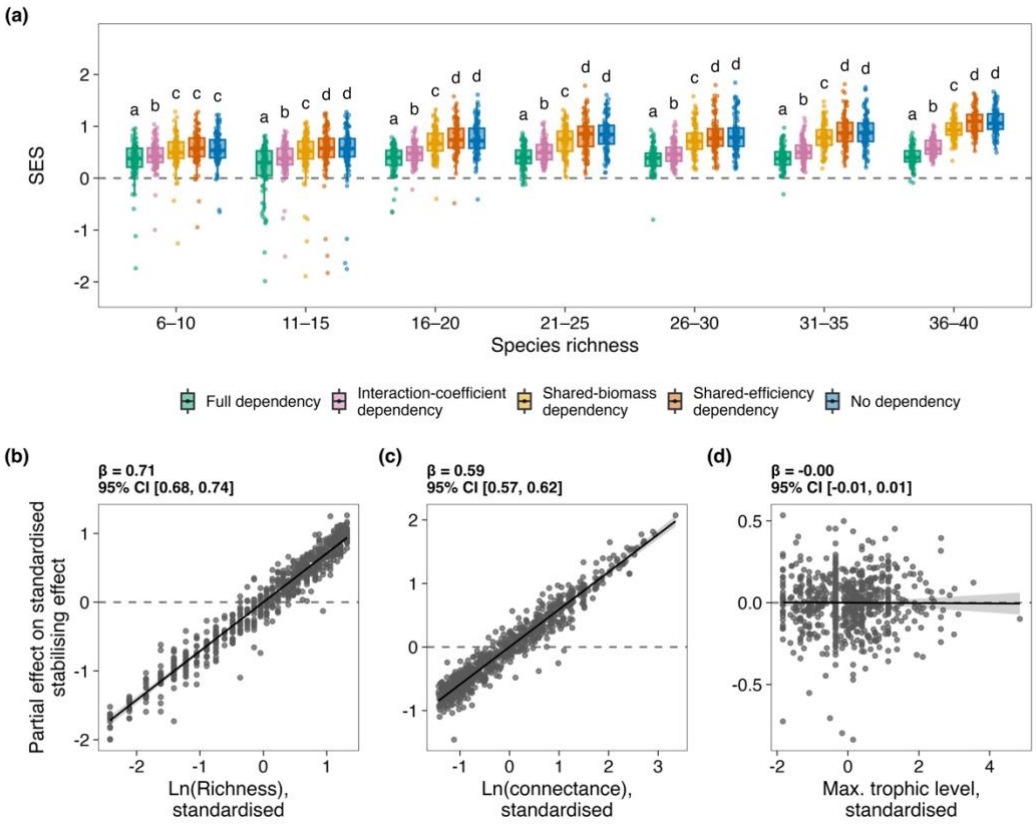


Figure 4. Structural dependency and relative stability across complexity gradients in model food webs. (a) Standardised effect size (SES) of Re(λ_{max}) under each dependency scenario relative to the original equilibrium interspecific Jacobian across richness bins. Positive SES indicates that mean Re(λ_{max}) across randomisations exceeds the corresponding reference value, indicating lower relative stability. Boxes show medians and interquartile ranges, with whiskers extending to the most extreme values within 1.5 interquartile ranges of the box. Scenarios with no letters in common differ significantly within a richness bin according to Tukey-adjusted comparisons from the linear mixed-effects model ($p < 0.05$). (b-d) Partial relationships between the stabilising effect of full dependency, E_{dep}, and richness, connectance, and maximum trophic level, estimated using multiple linear regression. E_{dep} is the mean Re(λ_{max}) under no dependency minus that under full dependency, divided by the standard deviation under no dependency. Richness and connectance were natural-log transformed, and all predictors were standardised. Points show partial residuals, lines show fitted partial relationships, and shading indicates 95% confidence intervals. All Jacobians had zero diagonal elements.

3.4 Complexity-dependent effects of structural dependency are attenuated in full Jacobians

When diagonal terms were included, differences among dependency scenarios persisted, but the strong increase in scenario separation with richness observed for interspecific Jacobians was no longer evident (**Figure 5a**). SES differed among scenarios ($F_{4,2772} = 250$, $p < 0.001$), and a significant scenario ×

richness-bin interaction indicated that their differences varied across richness bins ($F_{24,2772}$ = 13, p < 0.001). The main effect of richness bin was not significant ($F_{6,693}$ = 1.6, p = 0.138). Full dependency generally produced the lowest SES, although its pairwise differences from other scenarios varied among richness bins.

In a multiple linear regression including species richness, connectance, and maximum trophic level, E_{dep} showed weak negative associations with richness (β = −0.017, 95% CI: −0.033 to −0.001, p = 0.041) and connectance (β = −0.033, 95% CI: −0.048 to −0.018, p < 0.001; **Figure 5b-c**). Maximum trophic level showed no detectable association (β = −0.004, 95% CI: −0.013–0.004, p = 0.306; **Figure 5d**). The regression explained only 4.2% of variation in E_{dep} (adjusted R^2 = 0.038), compared with 82.4% for interspecific Jacobians. Full structural dependency therefore generally remained stabilising when diagonal terms were included, but its stabilising effect no longer increased with species richness or connectance.

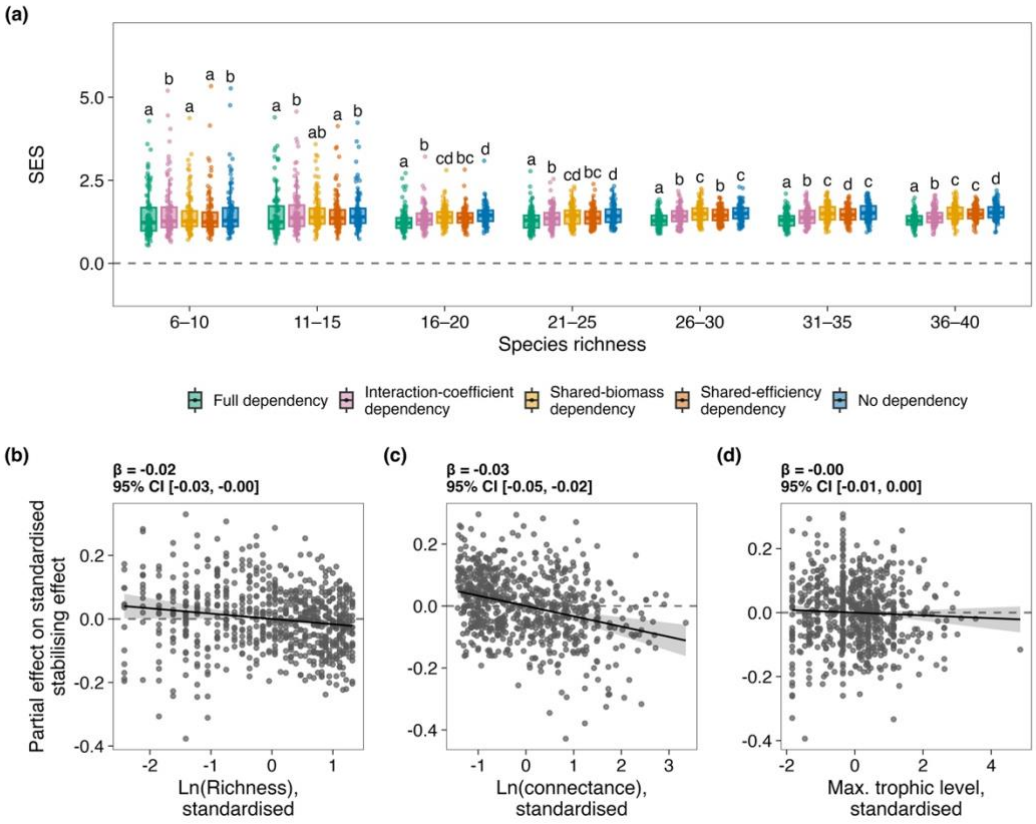


Figure 5. Effects of structural dependency on full Jacobians. (a) Standardised effect size (SES) of Re(λ_{max}) relative to the original equilibrium full Jacobian across species-richness bins. (b-d) Partial relationships between E_{dep} and species richness, connectance, and maximum trophic level. Full Jacobians included diagonal terms derived from the population dynamics. Definitions, predictor transformations, statistical comparisons, and plotting conventions follow **Figure 4**.

4. DISCUSSION

Our study identifies structural dependency among the strength of species interactions as a stabilising mechanism in food webs. We show that the interaction strengths among species are made up of biological quatities related to their traits. This makes that the interaction strengths are linked in various ways to one another. And that this creates patterns in interaction strengths explain food web stability. This we found in the IGP module, Lake Constance food webs and bioenergetic model communities spanning a gradient of complexity, even when distinct quantities were sampled independently. Mechanistically, shared quantities link the strengths of multiple interactions, restricting how opposing trophic feedback pathways vary relative to one another. The stabilising contribution of these dependencies increased strongly with species richness and connectance when interspecific interactions were considered alone. Including diagonal terms generally retained the stabilising benefit of structural dependency but removed its strong positive relationship with complexity.

4.1 Structural dependency as a biological constraint on trophic feedbacks

Structural dependencies determine how interaction strengths vary together. In the IGP module, each three-species feedback loop traces top-down and bottom-up effects through all three species and back to the starting species. The products of these effects have opposite signs. One loop reinforces the initial change in biomass, and the other counteracts it. Under full dependency, the two loop products share the same biological factors, with one product also including the intermediate consumer's conversion efficiency (Eq. 8). Their common factors therefore scale both loop strengths together, limiting their independent variation. In our simulations, retaining dependencies concentrated T_0 near zero, while larger T_1 reduced the destabilising effect of a given imbalance. This links shared biological quantities to the balance between three-species and reciprocal consumer-resource feedbacks previously associated with food web stability [14].

The comparatively strong stabilising effect of interaction-coefficient dependency confirms the importance of coupling reciprocal consumer–resource interactions for food web stability [11,15]. Our analysis provides a biological explanation for this result. The same interaction coefficient contributes to both interaction strengths within a pair, so it enters their feedback product as a squared term (Eq. 7). Under our sampling design, sharing the coefficient increases the mean magnitude of reciprocal negative feedback, helping explain its stronger stabilising effect. A species' biomass scales the strengths of interactions acting on that species, helping explain variation among rows of empirical Jacobians [27]. Theoretical work has also shown that equilibrium abundances can influence how quickly communities return to equilibrium [28]. A consumer's conversion efficiency links the positive effects of its resources on its growth. These links provide a biological context for theoretical findings that statistical dependencies beyond reciprocal pairs can affect stability [29,30]. Our results show that shared quantities can reduce destabilisation by constraining how interaction strengths vary together within feedback loops. Structural dependency thus complements the stabilising role of weak links [6,12,31] by constraining how interaction strengths vary together, without necessarily weakening individual interactions.

4.2 Complexity and diagonal terms shape the stabilising effects of structural dependency

The increasing benefit of structural dependency in richer and more connected model food webs offers a conditional perspective on the complexity-stability relationship. In randomly assembled community matrices, increasing richness and connectance can increase the destabilising contribution of interspecific interactions [2]. Empirical studies show that this relationship depends on how interactions are organised [15]. For example, stability estimates for soil food webs were positively associated with connectance when feeding fluxes were used to weight trophic links [32]. Our results identify another way in which the organisation of interactions can matter. The standardised benefit of retaining structural dependency increased with richness and connectance when we considered interspecific interactions alone. One possible explanation is that more connected food webs allow each biomass or consumer efficiency to occur in more Jacobian elements, coupling more interactions and feedback pathways. Breaking these dependencies would then uncouple more interaction strengths and feedback pathways.

A stronger effect of dependency in the more complex webs was absent in full Jacobians, although full dependency generally remained stabilising. Previous work shows that variation among diagonal elements can change the dominant eigenvalue even when their mean is held constant [27]. The prevalence of self-regulation and its distribution across trophic levels can also influence stability and its relationship with connectance [33]. A common, fixed negative diagonal would shift all eigenvalues equally and preserve differences among dependency scenarios. Our full Jacobians instead contained species-specific diagonal terms, including interaction-derived terms recalculated from the randomised biological quantities. Their heterogeneity and trophic patterning (**Figure S2**) may alter which feedback combinations determine the dominant eigenvalue. The weaker complexity dependence therefore cannot be explained simply by adding a uniform amount of self-regulation. Because E_{dep} is standardised using the standard deviation of no-dependency randomisations within each representation, identifying the processes responsible for this change also requires examining unstandardised effects and randomisation variances.

4.3 Accounting for structural dependency in Jacobian-based stability analyses

We propose constructing biologically informed Jacobian ensembles by sampling the underlying biological quantities rather than assigning independent random values to individual matrix elements. This approach builds on mechanistic and generalised food web models that express Jacobian elements in terms of biological processes [34]. Reusing each sampled biological quantity wherever it occurs preserves structural dependency, even when distinct biological quantities are sampled independently. This approach retains relationships imposed by the biological formulation that independent sampling of Jacobian elements would omit. Selectively breaking these dependencies, while retaining topology, sign structure and sampling distributions, then allows their contributions to relative stability to be evaluated.

Preserving structural dependency alone does not ensure that a randomised Jacobian corresponds to a feasible equilibrium, which requires all species to have positive biomasses at a steady state [35,36]. Although our original model communities were obtained at stable equilibria, the randomised matrices were not required to satisfy equilibrium conditions. These comparisons therefore quantify how changes in structural dependency alter Jacobian eigenvalues, without establishing whether the resulting matrices describe dynamically feasible communities. Future work could impose equilibrium constraints during dependency manipulations and examine nonlinear functional responses and alternative forms of density dependence, testing whether the stabilising effects persist under these additional biological conditions.

4.4 Distinguishing structural dependency from energetic constraints in natural food webs

Structural dependencies and energetic constraints represent related but distinct forms of food web organisation. Structural dependencies arise when several Jacobian elements share the same biological quantity, whereas energetic constraints restrict the combinations of quantities compatible with biomass production and energy flows. In empirical or energetically constrained food web models, these processes are usually incorporated together, so realised interaction strength patterns can reflect both parameter sharing and restrictions on parameter values [9,18,19,37].

Our randomisations tested the contribution of structural dependency while disrupting the original assignment of biological values to species and feeding links. Retaining dependencies reduced the destabilising contribution of interspecific interactions even when community energy balance was not enforced. In Lake Constance, full-dependency randomisations also produced relative stability close to that of the empirical Jacobians, suggesting that structural dependency explains part of the empirical pattern. However, conversion efficiencies below one, parameter distributions and trophic topology retained some energetic influences. Further work could separate these effects by retaining structural dependencies while comparing parameter combinations with and without energy balance constraints. This would help distinguish the stabilising effects of parameter sharing from those of energetic organisation and clarify how the two interact in natural food webs.

Data and code accessibility

All data and analysis scripts required to reproduce this study are archived on Zenodo (https://doi.org/10.5281/zenodo.24116561) and are also available on GitHub (https://github.com/Xxiao-Li/FW_Jacobian_dependency).

Declaration of AI use

AI-assisted technologies were used to improve readability and language of the study.

Authors' contributions

X.L.: conceptualization, formal analysis, investigation, methodology, software, visualization, writing—original draft, writing—review and editing; E.F.: methodology, validation, writing—review and editing; U.G.: methodology, writing—review and editing; A.P.B.: methodology, investigation, writing—review and editing; P.C.R.: conceptualization, methodology, validation, visualization, writing—review and editing.

Conflict of interest declaration

We declare we have no competing interests.

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