

Research



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Community ecology

Constraints and variation in food web link-species space

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Predicting food web structure in future climates is a pressing goal of ecology. These predictions may be impossible without a solid understanding of the factors that structure current food webs. The most fundamental aspect of food web structure—the relationship between the number of links and species—is still poorly understood. Some species interactions may be physically or physiologically ‘forbidden’—like consumption by non-consumer species—with possible consequences for food web structure. We show that accounting for these ‘forbidden interactions’ constrains the feasible link-species space, in tight agreement with empirical data. Rather than following one particular scaling relationship, food webs are distributed throughout this space according to shared biotic and abiotic features. Our study provides new insights into the long-standing question of which factors determine this fundamental aspect of food web structure.

1. Introduction

Anticipating food web responses to environmental change is a pressing issue [1–4]. Yet, doing so is challenging owing to the inherent complexity of food web structure and dynamics [5,6]. Failure to account for the many underlying mechanisms—biotic and abiotic—that constrain food webs makes predicting possible future responses difficult. Gaining the fundamental understanding upon which to ground predictive models should thus be a major focus of food web ecology [7,8], but progress has proceeded slowly owing to a lack of highly resolved food web data that span across environmental conditions [9].

Despite these limitations, ecologists have uncovered many fundamental laws governing food web structure [1,10–22]. For example, larger ecosystems harbour more diverse communities with more trophic levels [23]—although the number of trophic levels is lower than expected owing to the inefficient transfer of energy and matter [24,25]. More fundamentally, the number of feeding interactions, or links (L), increases—unsurprisingly—with the number of species (S) [26,27]. Competing hypotheses have been proposed to explain this foundational pattern, yet it remains poorly understood [28], suggesting a striking lack of understanding of the most fundamental factors constraining food web structure.

According to Martinez’s *constant connectance hypothesis*, L increases in proportion to the total possible number of species interactions, S^2 [29]. The *minimal connectance* model represents the extreme scenario where species are connected to at least one other species, resulting in L increasing as $S - 1$ [29]. Last, the recent *flexible links* model unifies these two extremes, thus making scaling predictions within those boundaries [28]. Tests of these hypotheses suggest that the actual scaling lies somewhere in between the estimated scaling exponent of 1 predicted by *minimal connectance*, and 2, for the *constant connectance hypothesis* [28–30]. As a result, food webs should occur on a continuum, somewhere between minimally connected food webs and fully interconnected ones

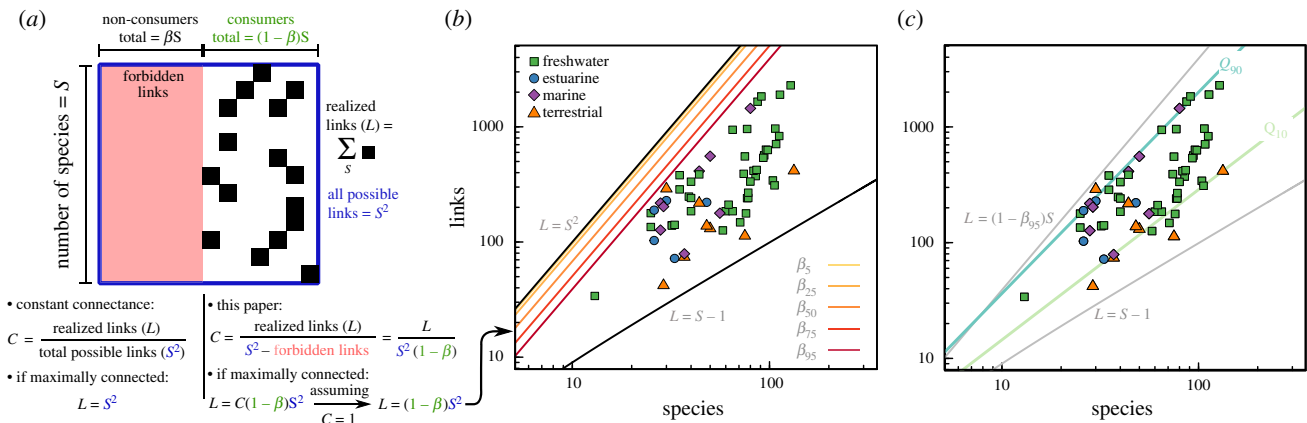


Figure 1. (a) Adjacency matrix with black squares representing links (1s) and blanks representing the absence of links (0s). Forbidden links are shown in pink shading. (b) L – S space, where solid lines represent limits imposed by *constant connectance* and *minimal connectance*, while coloured lines represent how the presence of non-consumers (forbidden links) may reduce the upper boundary of that space. (c) Quantile regression showing the 0.1 and 0.9 quantile regressions in colour. Upper limit as predicted by our results, and lower limit as predicted by minimal connectance.

[29]. This fact rejects the notion of a one-size-fits-all scaling between L and S , but this point has received little attention.

The number and quality of available food webs makes it possible to revisit this classic debate. Furthermore, rapidly changing environmental conditions are expected to alter multiple aspects of food web structure [3,7,8,31], some of which may influence, or be influenced by, the relationship between L and S , like the proportion of apex and basal species [3] and the arrangement of feeding interactions across trophic levels (e.g. degree of omnivory, maximum trophic level, modularity) [7,8,31]. Food webs in different ecosystem types and latitudes are also likely to respond to these changes differentially [8,32]. It is therefore more important than ever to understand how these biotic and abiotic factors determine the relationship between L and S in food webs.

Additionally, we now know that phenotypic and physiological mismatches between consumers and their resources can lead to ‘forbidden interactions’ [16,33–36]. Perhaps the most fundamental type of forbidden interaction occurs in organisms that do not rely on the consumption of others to meet their energetic demands (i.e. autotrophs, chemotrophs), but it may also be common among organisms for whom predation is physically or physiologically impossible (e.g. biomechanical mismatches like gape-limitation in aquatic systems [25,37]). Yet, hypotheses that aim to explain the L – S relationship usually do not account for forbidden interactions, despite their potential influence on food web structure [38–40].

Here, we bridge these gaps by exploring how forbidden interactions, in particular those between non-consumers and other species, may constrain the L – S relationship. We use empirical food webs from across the globe to show that (i) rather than following a single log–linear relationship, food webs occupy a well-defined feasible space within the L – S plane with boundaries that can be predicted from theory, and (ii) food webs closer—or farther away—from those boundaries, share common biotic and abiotic features.

2. Methods

(a) L – S scaling and forbidden interactions

Food webs are represented by an adjacency matrix where 1 indicates that a species in the i -th row is consumed by one in the j -th column and 0 indicates the absence of a link (figure 1a).

Following standard practices [10,16,29,41–48] all links are directed. Directed connectance (C)—the classic metric of linkage density—is calculated as the ratio between realized links (the sum of all 1s in the adjacency matrix) and the total possible number of links (the square of the number of species, S^2) (figure 1a). The constant connectance hypothesis assumes that C is constant across food webs, thus $L = CS^2$, with a maximum of $L = S^2$ when $C = 1$. Minimal connectance requires that $L = S - 1$ so that every species has at least one connection to another species.

In all food webs, there should be a fraction of species that do not consume any other species for several possible reasons. If we consider a fraction β of non-consumer species, then the total number of non-consumers is βS , while that of consumers is $(1 - \beta)S$ (figure 1a). By ignoring non-consumers, classic directed connectance overestimates the maximum possible number of links within food webs. To resolve this, we calculate connectance as the fraction of realized links (L) divided by all possible links (S^2) from which the number of forbidden links due to non-consumers (βS^2) has been subtracted (or $S^2 - \beta S^2$, figure 1a). This results in a new expression for connectance: $C = L / (S^2(1 - \beta))$, which is larger than classic connectance for $\beta > 0$. Rearranging and taking logarithms yields $\log(L) = \log(C(1 - \beta)) + 2 \log(S)$, where $\log(C(1 - \beta))$ is the intercept. Assuming $C = 1$, we can find an upper boundary for L in L – S space that depends on $1 - \beta$ (figure 1a). Because $C = 1$ sets the upper limit given the constant connectance hypothesis, this new upper limit should be interpreted as the magnitude by which forbidden interactions lower the theoretical limit predicted by constant connectance, which can be estimated by quantifying β from data.

(b) Empirical food webs and data analyses

The 65 food webs used are described elsewhere [16,45] and were taken from the Interaction Web Database (<https://www.nceas.ucsb.edu/interactionweb/>), the GlobalWeb food web database (<https://www.globalwebdb.com/>) and the R package *cheddar* [49]. The data span all continents, encompass terrestrial, marine, estuarine and freshwater ecosystems, and average 64 species and 427 interactions (details in electronic supplementary material, appendix S1). Data and code can be found in Dryad [50] or at https://github.com/JPGibert/FWs_LS_feasibility_space.

Because the fraction of non-consumers, β , may be over- or underestimated in empirical data, we determined a series of possible upper boundaries to L – S space of increasing likelihood based on the quantiles of the empirical distribution of β across all food webs. The ‘true’ upper boundary corresponds to the maximum possible β in nature, but owing to sampling error,

Table 1. Regression summary of a multiple linear model estimating the effects of biotic and abiotic variables on species richness in empirical food webs. Increasing values of variance inflation factors (VIFs) indicate increasing levels of collinearity associated with each predictor variable. R^2_{adj} , adjusted R^2 ; n.a., not applicable.

	variable	estimate (<i>b</i>)	s.e.	<i>p</i> -value	VIF
$R^2 = 0.882$	intercept	2.45	0.019	$<10^{-15}$	n.a.
$R^2_{adj} = 0.867$	species richness	0.334	0.02	$<10^{-15}$	1.36
$p < 10^{-15}$	omnivory	0.181	0.023	$<10^{-10}$	1.711
	modularity	-0.131	0.023	$<10^{-6}$	1.853
	latitude	0.053	0.02	0.011	1.403
	fraction top predators	-0.081	0.022	0.001	1.703
	habitat	-0.042	0.066	0.526	1.655
	top preds \times habitat	0.129	0.053	0.018	1.75

our upper boundary estimated based on the 0.95 quantile represents our best estimate of this boundary. We also tested for the existence of statistical boundaries in the L - S plane through a quantile regression with L as response and S as predictor using the R package *quantreg* [51]. Quantile regressions indicate the existence of boundaries in the distribution of stochastic variables [52].

Last, we assessed whether food webs that occur closer or farther away from these boundaries share common biotic and abiotic features. To do so we fitted a multiple linear regression that includes descriptors of food web structure. Biotic factors included the prevalence of omnivory (i.e. the fraction of species that feed on multiple trophic levels [53]), the maximum number of trophic levels (calculated as in [54]), the fraction of basal and top species and modularity (i.e. the existence of groups of species that more likely interact with other species within their group [55]). Abiotic factors included ecosystem type (aquatic or terrestrial) and absolute latitude. We used the \log_{10} of all numerical variables except for absolute latitude and the fraction of basal species. We considered the interaction between ecosystem type and the fraction of top predators (model selection is presented in electronic supplementary material, appendix S2). To control for multicollinearity, we included variance inflation factors (VIFs) for all predictors using R package *car* [56] (VIF > 5 indicates strong collinearity). Owing to moderate collinearity, maximum trophic level and the fraction of basal species were dropped from the main model (see the full model in electronic supplementary material, appendix S2).

3. Results

Values of β ranged from 0.013 to 0.73 with a mean of 0.32 ± 0.03 . The 5th, 25th, 50th, 75th and 95th percentiles of the distribution of β -values set boundaries to L - S space that are lower than the boundary set by constant connectance and above which no food web in our dataset occurs (figure 1b). The lower boundary of this feasible space is still set by the $L = S - 1$ relationship (figure 1b) and all food webs fall within the limits of this space (figure 1b). The existence of a feasible space was corroborated by a significant quantile regression (figure 1c).

A model with S as the sole predictor of L accounted for 50% of observed variance within the feasible space, while a model including other biotic and abiotic variables accounted for 87% (adj. $R^2 = 0.867$; table 1). Biotic and abiotic variables thus account for all but 13% of the variation observed within the feasible space. Indeed, food webs with a higher

prevalence of omnivory also were ones with more links ($b = 0.181 \pm 0.023$, $p < 10^{-10}$; figure 2a), while modular food webs had fewer links ($b = -0.131 \pm 0.023$, $p < 10^{-6}$; figure 2b). Food webs with more top predators had fewer links in aquatic ecosystems ($b = -0.081 \pm 0.022$, $p = 0.001$; figure 2d), but more links in terrestrial ecosystems (interaction term = 0.129 ± 0.053 , $p = 0.018$; figure 2e). Among abiotic factors, food webs closer to the upper boundary also were farther away from the equator ($b = 0.053 \pm 0.02$, $p = 0.011$; figure 2c), while ecosystem type did not influence the number of links (terrestrial intercept relative to aquatic = 0.042 ± 0.066 , $p = 0.526$; figure 2f). Multicollinearity precluded us from assessing whether food webs closer or farther away from the upper boundary were also similar in terms of the fraction of basal species and the number of trophic levels (VIF(no. trophic levels) = 4.67, VIF(basal spp.) = 4.14; electronic supplementary material, appendix S2).

4. Discussion

Understanding how biotic and abiotic factors influence food web structure is a prerequisite to forecasting environmentally induced changes to food webs. Despite a century of research since Elton's seminal work [57], we still do not fully understand what determines why some food webs have more interactions than others of similar richness. We show theoretically (figure 1a), empirically (figure 1b) and statistically (figure 1c), that accounting for forbidden interactions sets an upper boundary to the feasible link-species space within which all analysed food webs occur. We also show that food webs that are closer or farther away from this upper boundary share biotic and abiotic features (figure 2), suggesting underlying rules governing how food webs are structured in nature. These results amend our understanding of the processes controlling food web structure and emphasize the importance of interactions that cannot occur in nature as a factor structuring food webs [36,39].

A recent study examined several possible L - S scaling relationships, with a 'flexible links' model accurately predicting this scaling as well as the distribution of values in L - S space [28]. Despite this important advance, the flexible links model does not predict an upper limit to the feasible L - S plane, nor does it attribute residual variation to underlying ecological factors. We show that food webs do not occur within feasible L - S space at random. Instead, food webs

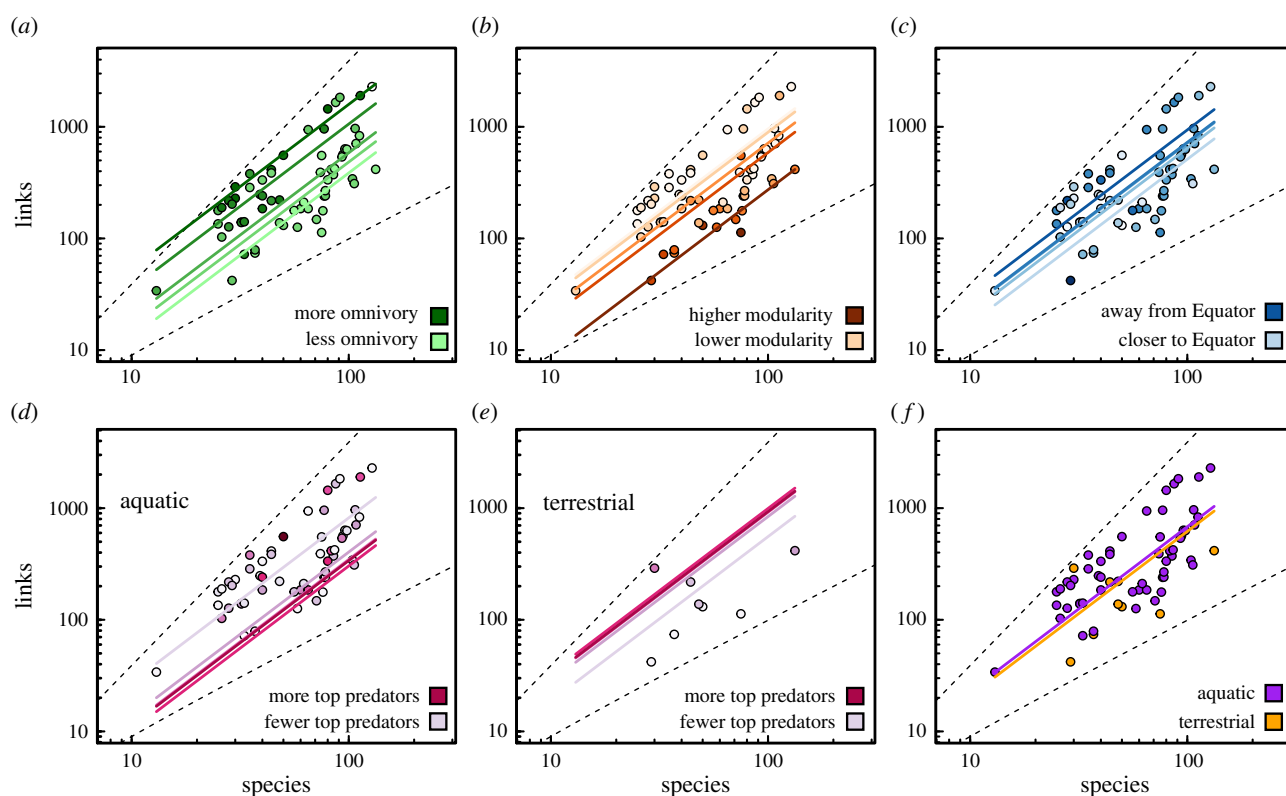


Figure 2. Model predictions showing effects of (a) omnivory, (b) modularity, (c) latitude, (d) fraction of top predators in aquatic ecosystems, and (e) fraction of top predators in terrestrial ecosystems and (f) terrestrial and aquatic ecosystems.

that occupy certain portions of this space also share a combination of biotic and abiotic features like the prevalence of omnivory or the proportion of apex predators (figure 2). We notice, however, that our analysis falls short of assigning causality to these variables, as cause and effect can be difficult to disentangle among structural features. Interestingly, however, and contrary to what was observed in terrestrial food webs, aquatic food webs showed (i) a *negative* correlation between the proportion of apex predators and the total number of links, and (ii) higher overall connectivity. One possible explanation is that, despite being equally productive, aquatic food webs tend to have high consumer biomass relative to terrestrial food webs (i.e. inverted biomass pyramids [58,59]), potentially leading to more omnivory and interactions. In addition to having higher connectivity, aquatic food webs also tended to be less modular, which could reduce stability, thus providing a possible explanation as to why trophic cascades are seemingly more frequent in aquatic systems.

Our findings suggest possible ways in which food webs might change with the climate. Rising temperatures are expected to decrease the proportion of apex predators and increase the proportion of basal species and primary producers [3]. Our results suggest that as the proportion of top predators decreases, aquatic food webs may become more interconnected while terrestrial ecosystems may become less

interconnected (figure 2*d,e*). A simple numerical exploration yields mixed support for this prediction (electronic supplementary material, appendix S3), highlighting an avenue for future research. Latitude had a small but significant effect on the L - S relationship, consistent with previous studies [45,60]. If temperature is partially responsible for the decrease in linkage density with latitude, then food webs could become less interconnected in a warmer world, but more work is needed to understand whether that is the case. Our results stress the need to revisit the fundamental factors that determine food web structure and emphasize the role of forbidden interactions in that endeavour.

Data accessibility. Data and code can be found in Dryad Digital Repository: <https://doi.org/10.5061/dryad.4b8gthtc3> [50].

Authors' contributions. J.P.G. conceived the study. J.P.G. and D.J.W. analysed the data. J.P.G. wrote the first draft and both authors contributed substantially to subsequent versions and revisions. Both authors approved the final version of the manuscript and agreed to be held accountable for the content therein.

Competing interests. We declare we have no competing interests.

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References

1. Brose U, Dunne JA, Montoya JM, Petchey OL, Schneider FD, Jacob U. 2012 Climate change in size-structured ecosystems. *Phil. Trans. R. Soc. B* **367**, 2903–2912. (doi:10.1098/rstb.2012.0232)
2. O'Gorman EJ *et al.* 2017 Unexpected changes in community size structure in a natural warming experiment. *Nat. Clim. Change* **7**, 659–663. (doi:10.1038/nclimate3368)
3. Petchey OL, McPhearson PT, Casey TM, Morin PJ. 1999 Environmental warming alters food-web structure and ecosystem function. *Nature* **402**, 69–72. (doi:10.1038/47023)

4. Albouy C, Velez L, Coll M, Colloca F, Le Loc'h F, Mouillot D, Gravel D. 2014 From projected species distribution to food-web structure under climate change. *Glob. Change Biol.* **20**, 730–741. (doi:10.1111/gcb.12467)
5. Bascompte J. 2010 Structure and dynamics of ecological networks. *Science* **329**, 765–766. (doi:10.1126/science.1194255)
6. Stouffer DB, Bascompte J. 2010 Understanding food-web persistence from local to global scales. *Ecol. Lett.* **13**, 154–161. (doi:10.1111/j.1461-0248.2009.01407.x)
7. Takemoto K, Kajihara K. 2016 Human impacts and climate change influence nestedness and modularity in food-web and mutualistic networks. *PLoS ONE* **11**, e0157929. (doi:10.1371/journal.pone.0157929)
8. Takemoto K, Kanamaru S, Feng W. 2014 Climatic seasonality may affect ecological network structure: food webs and mutualistic networks. *Biosystems* **121**, 29–37. (doi:10.1016/j.biosystems.2014.06.002)
9. Polis GA. 1991 Complex trophic interactions in deserts: an empirical critique of food-web theory. *Am. Nat.* **138**, 123–155. (doi:10.1086/285208)
10. Allesina S, Tang S. 2012 Stability criteria for complex ecosystems. *Nature* **483**, 205–208. (doi:10.1038/nature10832)
11. Berlow EL. 1999 Strong effects of weak interactions in ecological communities. *Nature* **398**, 330–334.
12. Brose U, Berlow EL, Martinez ND. 2005 Scaling up keystone effects from simple to complex ecological networks. *Ecol. Lett.* **8**, 1317–1325. (doi:10.1111/j.1461-0248.2005.00838.x)
13. de Roos AM, Persson L, McCauley E. 2003 The influence of size-dependent life-history traits on the structure and dynamics of populations and communities. *Ecol. Lett.* **6**, 473–487. (doi:10.1046/j.1461-0248.2003.00458.x)
14. Pascual M, Dunne JA (eds). 2006 *Ecological networks: linking structure to dynamics in food webs*. Oxford, UK: Oxford University Press.
15. Gibert JP, DeLong JP. 2014 Temperature alters food web body-size structure. *Biol. Lett.* **10**, 20140473. (doi:10.1098/rsbl.2014.0473)
16. Gibert JP, DeLong JP. 2017 Phenotypic variation explains food web structural patterns. *Proc. Natl Acad. Sci. USA* **114**, 11 187–11 192. (doi:10.1073/pnas.1703864114)
17. Gravel D, Poisot T, Albouy C, Velez L, Mouillot D. 2013 Inferring food web structure from predator–prey body size relationships. *Methods Ecol. Evol.* **4**, 1083–1090. (doi:10.1111/2041-210X.12103)
18. McCann KS. 2011 *Food webs*. Princeton, NJ: Princeton University Press.
19. McCann KS, Hastings A, Huxel GR. 1998 Weak trophic interactions and the balance of nature. *Nature* **395**, 794–798. (doi:10.1038/27427)
20. Poisot T, Canard E, Mouillot D, Mouquet N, Gravel D, Jordan F. 2012 The dissimilarity of species interaction networks. *Ecol. Lett.* **15**, 1353–1361. (doi:10.1111/ele.12002)
21. Poisot T, Mouquet N, Gravel D. 2013 Trophic complementarity drives the biodiversity–ecosystem functioning relationship in food webs. *Ecol. Lett.* **16**, 853–861. (doi:10.1111/ele.12118)
22. Gravel D, Canard E, Guichard F, Mouquet N. 2011 Persistence increases with diversity and connectance in trophic metacommunities. *PLoS ONE* **6**, e19374. (doi:10.1371/journal.pone.0019374)
23. Post DM, Pace ML, Hairston Jr NG. 2000 Ecosystem size determines food-chain length in lakes. *Nature* **405**, 1047–1049. (doi:10.1038/35016565)
24. Pimm SL, Lawton JH. 1977 Number of trophic levels in ecological communities. *Nature* **268**, 329–331. (doi:10.1038/268329a0)
25. Arim M, Bozinovic F, Marquet PA. 2007 On the relationship between trophic position, body mass and temperature: reformulating the energy limitation hypothesis. *Oikos* **116**, 1524–1530. (doi:10.1111/j.0030-1299.2007.15768.x)
26. Pimm SL, Lawton JH, Cohen JE. 1991 Food web patterns and their consequences. *Nature* **350**, 669–674. (doi:10.1038/354031a0)
27. Cohen JE, Jonsson T, Carpenter SR. 2003 Ecological community description using the food web, species abundance, and body size. *Proc. Natl Acad. Sci. USA* **100**, 1781–1786. (doi:10.1073/pnas.232715699)
28. MacDonald AAM, Banville F, Poisot T. 2020 Revisiting the links-species scaling relationship in food webs. *Patterns* **1**, 100079. (doi:10.1016/j.patter.2020.100079)
29. Martinez ND. 1992 Constant connectance in community food webs. *Am. Nat.* **139**, 1208–1218.
30. Schmid-Araya JM, Schmid PB, Robertson A, Winterbottom J, Gjerlov C, Hildrew AG. 2002 Connectance in stream food webs. *J. Anim. Ecol.* **71**, 1056–1062. (doi:10.1046/j.1365-2656.2002.00668.x)
31. Jeppesen E *et al.* 2010 Impacts of climate warming on lake fish community structure and potential effects on ecosystem function. *Hydrobiologia* **646**, 73–90. (doi:10.1007/s10750-010-0171-5)
32. Antão LH, Bates AE, Blowes SA, Waldock C, Supp SR, Magurran AE, Dornelas M, Schipper AM. 2020 Temperature-related biodiversity change across temperate marine and terrestrial systems. *Nat. Ecol. Evol.* **4**, 927–933. (doi:10.1038/s41559-020-1185-7)
33. Barbour MA, Fortuna MA, Bascompte J, Nicholson JR, Julkunen-Tiitto R, Jules ES, Crutsinger GM. 2016 Genetic specificity of a plant–insect food web: implications for linking genetic variation to network complexity. *Proc. Natl Acad. Sci. USA* **113**, 2128–2133. (doi:10.1073/pnas.1513633113)
34. Gibert JP, Brassil CE. 2014 Individual phenotypic variation reduces interaction strengths in a consumer–resource system. *Ecol. Evol.* **4**, 3703–3713. (doi:10.1002/ece3.1212)
35. Dehling DM, Jordano P, Schaefer HM, Böhning-Gaese K, Scheuling M. 2016 Morphology predicts species' functional roles and their degree of specialization in plant–frugivore interactions. *Proc. R. Soc. B* **283**, 20152444. (doi:10.1098/rspb.2015.2444)
36. Olesen JM, Bascompte J, Dupont YL, Elberling H, Rasmussen C, Jordano P. 2011 Missing and forbidden links in mutualistic networks. *Proc. R. Soc. B* **278**, 725–732. (doi:10.1098/rspb.2010.1371)
37. Hairston Jr NG, Hairston Sr NG. 1993 Cause-effect relationships in energy flow, trophic structure, and interspecific interactions. *Am. Nat.* **142**, 379–411. (doi:10.1086/285546)
38. Allesina S, Alonso D, Pascual M. 2008 A general model for food web structure. *Science* **320**, 658–661. (doi:10.1126/science.1156269)
39. Strona G, Veech JA. 2017 Forbidden versus permitted interactions: disentangling processes from patterns in ecological network analysis. *Ecol. Evol.* **7**, 5476–5481. (doi:10.1002/ece3.3102)
40. Pires MM, Guimarães Jr PR. 2012 Interaction intimacy organizes networks of antagonistic interactions in different ways. *J. R. Soc. Interface* **10**, 20120649. (doi:10.1098/rsif.2012.0649)
41. Allesina S, Pascual M. 2007 Network structure, predator–prey modules, and stability in large food webs. *Theor. Ecol.* **1**, 55–64. (doi:10.1007/s12080-007-0007-8)
42. Dunne JA, Labandeira CC, Williams RJ. 2014 Highly resolved early Eocene food webs show development of modern trophic structure after the end-Cretaceous extinction. *Proc. R. Soc. B* **281**, 20133280. (doi:10.1098/rspb.2013.3280)
43. Dunne JA, Williams RJ, Martinez ND. 2002 Network structure and biodiversity loss in food webs: robustness increases with connectance. *Ecol. Lett.* **5**, 558–567. (doi:10.1046/j.1461-0248.2002.00354.x)
44. Dunne JA, Williams RJ, Martinez ND, Wood RA, Erwin DH. 2008 Compilation and network analyses of Cambrian food webs. *PLoS Biol.* **6**, e102. (doi:10.1371/journal.pbio.0060102)
45. Gibert JP. 2019 Temperature directly and indirectly influences food web structure. *Scient. Rep.* **9**, 5312. (doi:10.1038/s41598-019-41783-0)
46. Williams RJ, Berlow EL, Dunne JA, Barabási A-L, Martinez ND. 2002 Two degrees of separation in complex food webs. *Proc. Natl Acad. Sci. USA* **99**, 12 913–12 916. (doi:10.1073/pnas.192448799)
47. Williams RJ, Martinez ND. 2000 Simple rules yield complex food webs. *Nature* **404**, 180–183. (doi:10.1038/35004572)
48. Williams RJ, Purves DW. 2011 The probabilistic niche model reveals substantial variation in the niche structure of empirical food webs. *Ecology* **92**, 1849–1857. (doi:10.1890/11-0200.1)
49. Hudson LN *et al.* 2013 Cheddar: analysis and visualisation of ecological communities in R. *Methods Ecol. Evol.* **4**, 99–104. (doi:10.1111/2041-210X.12005)
50. Gibert JP. 2021 Data from: Constraints and variation in food web link-species space. Dryad Digital Repository. (doi:10.5061/dryad.4b8gthtc3)
51. Koenker R. 2018 quantreg: Quantile regression. R package version 5.35. See <https://cran.r-project.org/web/packages/quantreg/index.html>.
52. Cade BS, Noon BR. 2003 A gentle introduction to quantile regression for ecologists. *Front. Ecol. Environ.* **1**, 412–420. (doi:10.1890/1540-9295(2003)001[0412:AGITQR]2.0.CO;2)
53. Williams RJ, Martinez ND. 2004 Limits to trophic levels and omnivory in complex food webs: theory and data. *Am. Nat.* **163**, 458–468. (doi:10.1086/381964)

54. Martinez ND. 1991 Artifacts or attributes? Effects of resolution on the Little Rock Lake. *Ecol. Monogr.* **61**, 367–392 (doi:10.2307/2937047)
55. Newman MEJ. 2006 Finding community structure in networks using the eigenvectors of matrices. *Phys. Rev. E Stat. Nonlin. Soft Matter* **74**, 036104. (doi:10.1103/PhysRevE.74.036104)
56. Weisberg FJ. 2019 *An R companion to applied regression*, 3rd edn. Thousand Oaks, CA: Sage.
57. Elton CS. 1927 *Animal ecology*. New York, NY: Macmillan Co.
58. Bar-On YM, Phillips R, Milo R. 2018 The biomass distribution on Earth. *Proc. Natl Acad. Sci. USA* **115**, 6506–6511. (doi:10.1073/pnas.1711842115)
59. Schramski JR, Dell AI, Grady JM, Sibly RM, Brown JH. 2015 Metabolic theory predicts whole-ecosystem properties. *Proc. Natl Acad. Sci. USA* **112**, 2617–2622. (doi:10.1073/pnas.1423502112)
60. Cirtwill AR, Stouffer DB, Romanuk TN. 2015 Latitudinal gradients in biotic niche breadth vary across ecosystem types. *Proc. R. Soc. B* **282**, 20151589. (doi:10.1098/rspb.2015.1589)