Food web stability and connectance predicted from body-size constraints on trophic topology, self-regulation, and total consumption

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**Food web stability and connectance predicted from body-size
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29 other appropriate open access repository) and the data DOI will be included at the end of the
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ABSTRACT

Understanding why food webs thrive or collapse is a major challenge that has been mostly studied in terms of consumer-resource interaction strengths or the topology of the interaction network. Yet the biological basis and relative importance of these properties are hotly debated. Here, we construct a model that incorporates body-mass constraints on key factors that influence food webs: the likelihood and strength of interactions, self-regulation, and total consumption rates. Our model predicts stability and connectance in real food webs ranging widely in species diversity (29-163 species) and trophic connectance (113-1086 interactions). Despite their absence in most research, we found that realistic self-regulation and consumption rate constraints are not only required to accurately predict stability but have stronger impacts than the more-frequently-studied interaction strengths. Our results demonstrate that food web stability is simultaneously impacted by multiple food web properties—all of which are naturally constrained by species masses.

INTRODUCTION

From vast grasslands in northern Europe to lush tropical forests in southeast Asia, nature has created food webs of different sizes, structures, and complexity. Scientists have long worked to gain a better understanding of which properties of food webs determine their persistence and stability (Elton 1927; May 1973; Emmerson & Raffaelli 2004; Stouffer & Bascompte 2011; Tang & Allesina 2014; Allesina *et al.* 2015). Traditionally, ecologists argued that complex food webs are more stable than simple food webs because of redundancy and robustness (Odum 1953; MacArthur 1955; Paine 1966). Then Robert May showed that larger and more complex systems

are less stable for the simplest scenario of random species interactions (May 1972). Such conflicting views have given rise to the “stability-complexity” debate in food web theory (Landi *et al.* 2018).

Theorists frequently explore how trophic interaction strengths and food web topology—connectance, modularity, nestedness, etc.—each affect food web stability. The consensus is that both play crucial roles (Brose *et al.* 2006; Grilli *et al.* 2016). Specifically, several studies showed that modularity is positively correlated with food web stability (Stouffer & Bascompte 2011; Grilli *et al.* 2016), which is based on the reasoning that a disturbance within a subgroup is less likely to propagate to the rest of the food web when modularity is high. In contrast, trophic interaction strength has been shown to negatively correlate with food web stability (Emmerson & Raffaelli 2004; Jacquet *et al.* 2016; Dougoud *et al.* 2018) because weaker interactions reduce oscillations in consumer-resource abundances (McCann *et al.* 1998).

Previously, researchers have often studied food web topology and interaction strength independently. For instance, when studying the effect of food web topology on stability, researchers often sample consumer-resource interaction strengths randomly from a distribution with zero mean and a variance of one (May 1972; Grilli *et al.* 2016; but see Allesina *et al.* 2015 for empirically-based and size-informed distributions). This stands in contrast to real systems for which it is empirically and theoretically well-known that trophic interaction strengths are correlated with and bounded by metabolic rate, attack rate, handling time, etc. (Pawar *et al.* 2012). In addition, when studying the effect of interaction strength on stability, trophic links are typically placed randomly within the food web (May 1972; Tang *et al.* 2014), ignoring the fact

that real webs have non-random topology and are structurally anti-symmetric (Chawanya & Tokita 2002, Allesina *et al.* 2015). To circumvent this, food web topology is sometimes estimated from empirical data such that there is no topology generating mechanism in the model (Emmerson & Raffaelli 2004; Allesina *et al.* 2015). Other times, interaction strength is studied within small trophic modules that only consist of 3 to 4 species (McCann *et al.* 1998), thus neglecting the larger food web structure.

Indeed, isolating individual factors can make them easier to study. However, such an approach often misses important interactions or correlations among factors that are present in real systems. Consequently, a model that describes nature—by accurately inferring food web stability—most likely needs to incorporate ecologically informed topology, trophic interaction strengths, and any other ecologically relevant factors that impact stability. It has been challenging to sensibly link models and theory outputs with empirical food webs, partly because of the lack of a natural or parsimonious way to link all of the dominant factors within a single model. Here, we argue that species body mass may remedy this issue.

Species body mass has been previously used as a constraint on both trophic interaction strength and food web topology (Cohen *et al.* 1993; McCann *et al.* 1998; Neubert *et al.* 2000; Brose 2010; Pawar *et al.* 2012, 2019; Allesina *et al.* 2015). Trophic interaction strength is generally defined as the rate at which a consumer feeds on a resource (Brose *et al.* 2006; Pawar *et al.* 2012, 2019; Mittelbach & McGill 2019). It thus depends on the densities of consumers and resources as well as consumer traits such as search rate, attack rate, and handling time. Several studies have shown that these traits scale allometrically with the body masses of consumers and

resources (Gillooly *et al.* 2001; Brose *et al.* 2006; Brose 2010; Pawar *et al.* 2012; Rall *et al.* 2012).

Implementing ecologically realistic body-size constraints on trophic topology, however, is more subtle. There have been several advances over the last few decades, including the cascade model that was an early attempt to include how size constrains topology in food webs (Cohen *et al.* 1993). A core assumption of the cascade model is equiprobability (Neubert *et al.* 2000)—consumers only interact with smaller resources and there is an equal probability of any single smaller species being used as a resource. However, empirical studies have shown that consumers prefer resources of specific sizes and that trophic interactions are limited by slower movement and longer reactive distances of consumers when consumer-resource body size-ratios (resource mass/consumer mass) are large. Conversely, small size-ratios limit a consumer's ability to detect and catch small prey (Thiebaut & Dickie 1993; Hansen *et al.* 1994; Brose *et al.* 2008; Brose 2010). Thus, a much more ecologically-informed constraint for a food web model is to use recent results to implement an interaction likelihood that is hump-shaped with respect to consumer-resource size-ratios (Petchey *et al.* 2008; Brose 2010; Pawar *et al.* 2019).

Although mass constraints on topology and interaction strength have been much studied in food web stability analysis, there has been little work to investigate or include realistic species-mass constraints on two other key food web properties: 1) self-regulation and 2) total per-capita consumption rate (hereafter referred to as just total consumption rate).

There is substantial evidence from empirical studies that species across a wide range of taxa and trophic levels commonly experience self-regulation (Woiwod & Hanski 1992; Brook & Bradshaw 2006), and more specifically, the existence of a limiting population abundance (or biomass) density, called the carrying capacity and determined by competition for resources. Although the mathematics of stability analysis makes it clear that the self-regulation—corresponding to negative diagonal elements in an interaction matrix—has a strong stabilizing effect on food web dynamics (Haydon 1994; Barabás *et al.* 2017), previous studies often either ignored self-regulation altogether (Grilli *et al.* 2016) or set all species’ self-regulation to the same constant value regardless of body mass (May 1972, Allesina *et al.* 2015). (But see Barabás *et al.* 2017 for an exploration of how varying self-regulation can impact stability). Based on the Lotka-Voterra model, however, self-regulation is typically the ratio of a species growth rate to its carrying capacity, both of which scale with species body mass (Damuth 1981; Savage *et al.* 2004; Bernhardt *et al.* 2018; Yeakel & Redner 2018). Including these body-size constraints leads to a large range—as big as a few orders of magnitude—in the strength of self-regulation, and consequently, to a large range in the diagonal elements of the interaction matrix that in turn substantially shift the average of the eigenvalues. We show that including these effects majorly influences how species body sizes affect the overall stability of food webs.

Another seldom-studied body-size constraint is an upper limit on a consumer population’s total energy intake (total consumption rate). This constraint must exist because consumers cannot consume infinite resources and the upper limit depends on factors that impact a population’s diet, such as resource abundance, attack probability, capture success rate (Manly 1974 & Chesson 1978, 1983), predation risk (Ho *et al.* 2019), and gape-limitation (Hairston & Hairston 1993). All

these factors can in turn be determined by species body masses combined with consumer-resource (C-R) mass-ratios (Pawar *et al.* 2012). These constraints in turn limit the total number of resource links for each consumer species and thus ultimately govern the connectance and stability of whole food webs (May 1972; Dune & Williams 2009).

Most models have not included how self-regulation changes with body size and have not imposed a constraint on total consumption per consumers (such a constraint considers *all* potential consumer-resource links, which is very different from the density dependence of the type II functional response that applies only at the level of a single consumer-resource pair at a time). We argue that these omissions have likely led to misestimation or misunderstanding of the extent to which food web stability and connectance are governed by species sizes.

Here, we construct a comprehensive “Allometrically Regulated Trophic” (ART) model based on the generalized Lotka-Volterra (GLV) framework (Supplementary Information (SI) section 1.2) in which realistic values for key network properties—trophic interaction strength distributions, food web modularity, connectance, and eigenvalue stability analysis—emerge naturally from species masses and consumer-resource mass-ratio via their effects on four key factors: interaction likelihood, interaction strength, self-regulation, and consumption rate. Our novel framework can be used to predict and compare real food web properties based only on species masses. In so doing, we clarify the origins and pervasiveness of the food web complexity-stability relationships. Furthermore, by investigating alternative models that include or omit these body-size constraints, we disentangle the individual and combined effects of interaction strengths and network topology on food web stability and connectance.

MATERIALS AND METHODS

Allometrically Regulated Trophic Model (ART Model)

Here, we detail the steps and procedures of our Allometrically Regulated Trophic (ART) model. We construct food webs using empirically informed mass-based constraints on species composition and consumer-resource interactions (see SI section 1, 2 & Fig. S3 for more details).

Our algorithm for constructing these food webs proceeds according to the following steps:

Step 0. Select species: To start building the food web, n species are chosen with masses

$m_1, m_2, \dots, m_n$ sampled from the logarithm of a normal distribution with mean μ_m and variance σ_m^2 . The mean and variance values are calculated using the data pooled together from all our empirical webs (SI 1.1).

Step 1. Generate food web links (C-R interactions): For the n species chosen in step 0, there are potential trophic links between every species pair, corresponding to $n(n-1)$ potential C-R interactions. For consumer i and resource j , the interaction likelihood is calculated as $\mathcal{L}_{ij} = g(\frac{m_j}{m_i} | \mu_l, \sigma_l^2)$ for all $i \neq j$ (no self-interactions are allowed for this step) where g is the logarithm of a normal probability density function (PDF) of C-R mass-ratios with mean (μ_l) and variance (σ_l^2). The variance is calculated based on the C-R mass-ratio distribution of our combined empirical food webs (SI 1.2). For the stability analysis, N links with the largest likelihood values are selected for each n -species food web. The number of initial links (N) is determined by empirical connectance values (Fig. 4) (this single part differs from our connectance analysis explained below). These links then

become possible C-R interactions in our food web, but note that some of these will later be pruned in step 3 to limit total consumption rate.

Step 2. Determine interaction strengths: For the N selected links, interaction strengths are calculated using metabolic scaling theory with masses of resources and consumers as input parameters (Fig. 1b). Specifically, interaction strength is measured as per-capita (biomass) consumption rate (α) (Pawar *et al.* 2019)

$$\alpha = sARf \quad (1)$$

which is comprised of per-capita search rate (s) (area/time), attack success probability (A), resource biomass density ($R = \text{mass/area}$) (SI 1.2), and a functional response (f) that can be type I, II, or III (Holling 1959; Jeschke *et al.* 2004; Vucic-Pestic *et al.* 2010). We use a type I functional response (i.e., $f = 1$; SI 1.2) for simplicity and because type I and II functional responses produce qualitatively similar results (SI 5.1; Fig. S4). Note that the parameters for α are estimated from data and theory for trophic interactions in two dimensions (Table S1; SI 4.1; Pawar *et al.* 2012). Consequently, we can fully construct a mass-constrained interaction matrix (I) with per-capita consumption rate entries for consumers i and resource j as

$$I_{ij} = e s_{ij} A_{ij} R_j f_{ij} \quad (2)$$

where e is the efficiency (SI 5.2) of converting resources into consumers (note that I_{ij} is defined from the perspective of the consumer, thus e is included). The corresponding interaction matrix entries for resources are $I_{ji} = -s_{ij} A_{ij} R_j f_{ij}$, thus imposing a structural type of anti-symmetry on the food web matrix. *This type of anti-symmetry was not imposed in most previous work but has crucial effects on model results (but see Pimm & Lawton 1977, 1978 as early attempts to grapple with sign anti-symmetry in random food*

web matrices). Note that s_{ij} and A_{ij} depend on the masses and mass-ratios of consumer i and resource j (SI 1.2).

Step 3. Limit total consumption rate: Thus far, our model construction does not limit a consumer's total intake of resources—in terms of space, handling time, appetite, or other factors. This is unrealistic for actual consumers and for food webs. Therefore, we use allometric scaling theory to place realistic limits on total per-capita consumption rates for each species and thus, by definition, the total consumption of an average individual in that species. According to metabolic scaling theory, individuals must consume enough (but not more) to satisfy metabolic demands, thus total per-capita consumption rate has roughly the same mass-dependence constraint as metabolic rate (SI 1.3; Yodzis and Innes 1992; Brown *et al.* 2004; Vasseur and McCann 2005; Pawar *et al.* 2012). For two-dimensional trophic interactions, the total consumption rate is approximately equal to $z_0 m_i^{3/4}$, where z_0 is a normalization constant determined from empirical data (SI 1.3; Pawar *et al.* 2012). Thus, in the ART model, when the total per-capita consumption rate ($T_i = (\sum_{j=1}^n I_{ij})/e$) for each species i exceeds its total consumption rate constraint $T_i > z_0 m_i^{3/4}$ (SI 1.3; Fig. S2), the model “prunes” excessive trophic interactions by randomly setting one trophic link to zero (Fig. 1c) and repeating this process until $T_i \leq z_0 m_i^{3/4}$ for all i . Pruning is randomized to avoid introducing additional biases. Note that because our model is based on GLV, we are able to factor out species abundance and thus can compare and apply the constraint at the individual level instead of the population level (SI 1.2). However, limitation of total consumption rate also applies at the population level and can be obtained by multiplying the equations above by the population size of the consumer, N_i . The resultant equations are $N_i T_i = N_i (z_0 m_i^{3/4})$. When the total consumption

rate for the population is constant, $N_i T_i = \text{constant}$, this leads to the tradeoff that $N_i \propto m_i^{-3/4}$, known as Damuth's rule.

Step 4. Assign self-regulation: The strength of self-regulation for any given species can be calculated as the ratio between species growth rate (r) and biomass carrying capacity (K), which is based on the intraspecific competition term of the Lotka-Volterra model. The variables r and K are known to scale with mass as $r \propto m^{-0.25}$ and $K \propto m^{0.25}$ (Peters 1986; Brown *et al.* 2004; Savage *et al.* 2004; Pawar *et al.* 2012; Bernhardt *et al.* 2018). Combining the mass-dependence of these terms yields an expression for the strength of self-regulation: $-(r_0/K_0)m^{-0.5}$, where r_0 and K_0 are the respective normalization constants (Pawar *et al.* 2012). After calculating the potential strength of self-regulation for all species, a percentage of species ($q=70\%$, which is estimated from empirical data (Woiwod & Hanski 1992, Zimmermann *et al.* 2018); SI 1.4) with the highest strength (absolute value) are selected to experience self-regulation and these values are assigned as diagonal terms in the interaction matrix (Fig. 1d). Self-regulation for the remaining species is set to zero because it is considered negligible in magnitude for that interaction and often corresponds to top predators that experience little or no predation or autotrophs with abundant resources.

The final interaction matrix formed from these steps is referred to as $\tilde{I}$. Consequently, our ART food web model creates networks where the directed edges/links between nodes (species) represent mass-based feeding constraints, i.e. diet, and the weights (thicknesses) of these edges represent trophic interaction strengths (Fig. 1).

In short, the ART Model incorporates mass-based effects on interaction likelihood, interaction strength, consumption rate, and self-regulation as four core components. Note that even though all these components are determined by mass, they can be analyzed independently. Hence, a big advantage of the ART Model is that it can easily disentangle effects and interactions among these four potentially important factors. By including or omitting one or more core components, we create five different mass-based food web models (Fig. 2) that represent a range of model classes. In so doing, we can study the individual and combined effects of each component on food web stability:

I. **Random Model (RM):** Species and trophic interactions are chosen completely at random while keeping connectance the same as for the other models below. Each interaction strength is randomly sampled from a uniform distribution with a range constrained by the interaction strengths (Eqn. 2) and calculated in step 3 in order to make it comparable with other models. The diagonal terms of the interaction matrix are all -1, corresponding to strong self-regulation for all species. Note that the RM omits all four core components and is analogous to May's original "Random" Food web model (May 1972).

II. **Base Mass Model (BMM):** This model only includes ART steps 0-2, meaning no mass-dependence on total consumption rate or self-regulation. As above for RM, the diagonal entries for self-regulation in the interaction matrix are all -1.

III. **Base + Self-Regulation Model (BSRM):** This model includes ART steps 0-2 plus self-regulation (step 4) but excludes mass-dependence on total consumption rate (step 3).

IV. **Base + Total Consumption Model (BTCM):** This model includes ART steps 0-3 but completely excludes self-regulation (step 4), meaning all diagonal entries are set to zero. We

set all diagonal entries to zero to eliminate the effects of self-regulation and thus isolate and study the effect of the total consumption rate constraint on stability.

V. **ART Model:** Includes all mass-dependencies in ART steps 0-4 and all core components.

Stability analysis

For each model food web, stability is defined by whether a food web eventually returns to its original state (equilibrium point) of species abundances after perturbation (a change in one or more abundances for any reason). This can be mathematically determined by calculating the eigenvalues of the interaction matrix $\tilde{I}$. When the real parts of the eigenvalues are all negative, this means the perturbed abundances will all exponentially decay back to their original state. When at least one eigenvalue has a real part that is positive—meaning at least one perturbed abundance will exponentially grow and never return to its original state—the system is defined as unstable (May 1972; Otto & Day 2011; Allesina & Tang 2015). Note that the standard Jacobian matrix approach (Strogatz 2018) yields equivalent results to the interaction matrix in our case because the food web dynamics are based on the generalized Lotka-Volterra model (SI 1.2; Allesina & Grilli 2020) and because we are only interested in non-trivial solutions (i.e., abundances are non-zero for all species).

For all models and for each choice of parameters, we compute the proportion of resulting networks that are stable—termed the frequency-of-stability—by simulating 1000 replicate networks, counting the number of cases for which the real part of the eigenvalues are all negative, and dividing this by the total number of replicates (1000).

We study all model formulations across a range of mean consumer-resource mass-ratios (μ_l) for the communities. That is, we vary the average resource mass preferred by consumers—higher μ_l indicates that consumers prefer larger resources. This allows us to predict frequency-of-stability distributions across a range of possible average mass-ratios (μ_l) for all models, determine which values of μ_l lead to the highest stability, and compare the μ_l values with the highest stability to empirical consumer-resource mass-ratio distributions. More specifically, the reasoning is that food webs that are stable and feasible should persist longer in nature, so the consumer-resource mass-ratios associated with these webs should occur with higher frequency (Heckmann *et al.* 2012; Borrelli *et al.* 2015). This is supported by the peak for the mass-ratio distribution that we obtain when we combine consumer-resource mass-ratios from 8 empirical food webs (Fig. 2; Table 1; SI 4.1) and suggests an approximate optimum mass-ratio among empirical food webs that persist in nature. Similarly, for the simulated food webs with high frequency-of-stability, their average mass-ratios (μ_l) have a higher probability to persist. Combining these, our frequency-of-stability distributions, across a range of μ_l , are a useful surrogate to compare with empirical consumer-resource mass-ratio distributions and thus test which candidate models are best matched by real food webs.

Network properties of model food webs

To compare and contrast models with different assumptions, we also measure the connectance, modularity, and interaction strength for all models while varying mean consumer-resource mass-ratios (μ_l). Connectance is defined as the ratio between the number of observed trophic links and

total possible trophic links ($n(n - 1)$) (SI 3; Delmas *et al.* 2019). Importantly, our connectance analysis differs from the ART model above in that we start with a fully connected food web and then prune based on the total consumption rate (step 3). We do this to avoid any circularity if empirical data on connectance were used as input to our model prediction for connectance. Additionally, for the pruning process, we use a normalization constant z_0 that is estimated from empirical data for abundant resources instead of sparse resources (SI 1.3). For modularity, we set non-zero entries in the interaction matrix to 1 and use a fast algorithm developed by Newman (Newman 2004) that measures the degree of nodes connecting to nodes within the same group/cluster compared to other groups (SI 3). The mean and variance of interaction strength distributions are calculated from all the positive entries of the interaction matrix. The connectance of the ART model is also calculated for different food web sizes.

Empirical data and parameters used for model comparison

For all model configurations and simulations except connectance analysis (Fig. 4), we set food web size (species richness) to 93 species, corresponding to the average size of the 8 empirical food webs for which we have comprehensive data for consumer-resource pairs and species masses (Table 1). Moreover, the initial connectance of all model food webs (size = 93) is approximated from 189 empirical food webs, i.e., 8 food webs with species mass (Table 1) and 181 binary food webs (SI 4.2; Cohen 2010). Note that the binary food webs only contain information on whether a consumer interacts with a resource (1 for interaction and 0 for no interaction). Therefore, these binary webs can only be used for estimating connectance.

Because each species in the 8 food webs with species mass information is identified and distinguished by its body mass and both the species mass and C-R mass-ratio distributions are typically unimodal (Fig. 2&S1), we obtain the mean and variance, μ_m and σ_m^2 , used for sampling species masses from the log-transformed species mass distributions of those 8 food webs (SI 1.1). Similarly, we obtain the variance, σ_l^2 , from the log-transformed consumer-resource mass-ratio distributions of these empirical food webs to determine interaction likelihood (SI 1.1) while varying the mean mass-ratio. Note that all the species masses and C-R mass-ratios are from 2-dimensional (2D) trophic interaction data (SI 4.1). The majority of trophic interactions for our empirical food webs are 2D, consistent with our model choices and parameterization. These empirical food webs include Eastern Weddell Sea, Grand Cariçaie Marsh, Scotch Broom, Skipwith Pond, Broadstone Stream, UK Grassland, Gearagh Woodland, and Estero de Punta Banda (Pawar *et al.* 2019).

For conversion efficiency (e), Lindeman (1942) indicated that the efficiencies range from 0.001 to 0.375 based on the observed energy transfer from one trophic level to the next. But later research showed that e also differs across metabolic groups—herbivore, endotherms, ectotherms, etc. (Peters 1986) and have higher values that range from 0.50 to 0.85 (Peters 1986; Delong *et al.* 2010; Lang *et al.* 2017). Therefore, we simulate the ART model using efficiency ranges from 0.10-0.85 to test the impact of efficiency on food web stability (SI 5.2; Fig. S5).

RESULTS

The ART model—which incorporates mass-based constraints on both interaction strengths and food web topology—produces a frequency distribution for stability that peaks precisely at the mean of the empirical consumer-resource mass-ratio distribution (at $\mu_l \approx -1$, i.e. the resource is about 10 times smaller than the consumer) (Fig. 2). More importantly, the frequency-of-stability decreases faster at higher consumer-resource mass-ratios and more gradually for lower ratios, matching subtle features of the empirical consumer-resource mass-ratio distribution. This is in strong contrast to models that predict equal stability for those consumer-resource mass-ratio values (RM & BMM), and others that do not fully capture the shape of the empirical distribution (BSRM & BTCM). Intriguingly, this demonstrates that mass-dependency in interaction likelihood, total consumption rate, and self-regulation are determining factors that shape the frequency-of-stability distribution.

Additionally, although weak interactions (I_{ij} and I_{ji}) are known to improve stability (Emmerson & Raffaelli 2004; Tang *et al.* 2014) and correspond to real food web data (table 1), the frequency-of-stability of the ART model (Fig. 2) does not negatively correlate with the mean interaction strengths when the logarithm of the mean C-R mass-ratio is greater than -0.5 (Fig. 3b). Furthermore, the ART model correctly predicts poor stability for extreme—both small and large—values of the mean C-R mass-ratios, while mean interaction strength exhibits a more than 4 orders of magnitude difference for those values of the mean C-R mass-ratios (Fig. 3b). Taken together, these results suggest that interaction strength is not the strongest contributor to food web stability.

Conversely, we find that the mass-dependencies of total consumption rate and self-regulation do play important roles in modulating the stability of food webs, as evidenced by the observation that the frequency-of-stability curves produced by the Random Model (RM) and Base Mass Model (BMM) do not match the empirical mass-ratio distribution. Both RM and BMM generate uniform stability across mass-ratios, whereas the empirical distribution is lognormal (Fig. 2). Note that the stability values produced by BMM are all 1 due to stabilizing effects of strong self-regulation and correlation between trophic interaction pairs (Tang *et al.* 2014; Jacquet *et al.* 2016).

Total consumption rate constraints and self-regulation have divergent effects on food web stability (Fig. 2). Most notably, the frequency-of-stability curve produced without total consumption rate constraints shifts the peak towards extremes—both bigger and smaller—C-R mass-ratios (BSRM) compared with the ART model. For the model with no self-regulation (BTCM), even though the shape of stability does not match the empirical C-R mass-ratio distribution, the peak for stability curve does match the peak of the mass-ratio distribution (Fig. 2). This result indicates that the mass-based total consumption constraint is essential for correctly predicting the location of the peak of food web stability within the consumer-resource mass-ratio space.

Apart from stability, the ART model also more accurately captures empirical trends between connectance (C) and food web size (n) (Fig. 4), compared with phenomenological models. Previously, Schmid-Araya *et al.* (2002) fitted a phenomenological model through extensive empirical data to show that the exponent for connectance should be close to -0.70, i.e.

$C \propto n^{-0.70}$, disagreeing with a linear link-species scaling law, $C \propto n^{-1}$ (Hall & Raffaelli 1993) and the constant connectance hypothesis, $C \propto n^{-2}$ (Martinez 1992). The ART model produces an exponent of -0.76, $C \propto n^{-0.76}$, close to that of Schmid-Araya *et al.* (2002) and outperforming link-species scaling and the constant connectance hypothesis. The ART model thus provides a mechanistic basis for the scaling of food web connectance that closely matches empirical scaling. Note that for the sparse resource case, the ART model produces an exponent of -0.86 (due to stricter pruning), which still outperforms the other hypotheses (SI 1.3).

Finally, we find a high correlation between modularity and stability in the ART model (Fig. 2&3c). This is consistent with previous research suggesting that modularity promotes stability by limiting the likelihood of collapse (Stouffer & Bascompte 2011; Grilli *et al.* 2016).

DISCUSSION

Understanding and separating how different food web properties—such as connectance, modularity, and interaction strengths—relate to the stability of food webs is a central challenge that has puzzled ecologists for decades (Elton 1958; Paine 1966; May 1972; Emmerson & Raffaelli 2004). We argue this has been puzzling largely due to the lack of models that include mechanistic processes that influence food web topology, interaction strengths, self-regulation, and total consumption rates simultaneously.

Therefore, by using species mass as a common currency that connects multiple aspects of food web properties, we create the ART Model that predicts food web stability better than previous

models and all other model configurations (Fig. 2). We demonstrate that the body-mass-dependence of the total consumption rate constraint and self-regulation are fundamental building blocks of food web topology that in turn lead to a more mechanistic and systematic understanding of how food web structure affects stability, while interaction strength plays a relatively minor role (Allesina *et al.* 2015; Fig. 2&3).

Total consumption rate constraints affect food web stability by limiting connectance and optimizing size-ratio based foraging strategies. More concretely, even though the allometrically scaled function (Eq. 1&2) can produce realistic interaction strengths for pairwise consumer-resource interactions, consumers normally feed on multiple resources to maximize their energy intake (Stephens & Krebs 1986). However, according to metabolic theory there is a mass-dependent upper bound for the total energy and rate of intake for each consumer. The ART model enforces the upper bound by omitting trophic links. The effect of total consumption rate constraints on stability is distinguished by comparing with the BTCM. *And interestingly, we find that the stability curve generated by BTCM exhibits a peak, indicating that a food web can be stable without any self-regulation (Fig. 2).* This type of stability and the corresponding peak are achieved mainly by reduced connectance (Fig. 2&3a).

Although the ART model correctly predicts the trend for food web connectance, the absolute values of connectance are a little lower than empirical values (Fig. 4). A possible reason for systematically lower connectance is that the trophic links are collected accumulatively. Meaning that the empirical food web is not a “snapshot” but an overlay of “snapshots”. Another reason is due to the fact that our consumption constraint eliminates trophic links instead of reducing their

strengths. However, other trophic traits, e.g. predation risk (Ho et al. 2019) and scarce resources, can potentially constrain diet choice by weakening the existing trophic links instead of omitting links. Therefore, combining this “weakening” procedure with our “pruning” procedure in future models might further improve estimation of absolute values for connectance.

Although it is recognized that self-regulation can strongly influence food web stability, studies often ignore the body-mass-dependence of self-regulation that leads to systematic variation in self-regulation. Consequently, when constructing an interaction matrix, researchers often set the diagonal terms (self-regulation terms) to either all zeros or all negative ones (but see Barabás *et al.* 2017). The former case can be useful if only interested in how trophic interaction strengths or correlations affect stability because setting diagonal terms to zero eliminates additional effects from self-regulation (Tang *et al.* 2014). However, this ignores the stabilizing effect of self-regulation and underestimates food web stability. The other common choice—setting diagonal terms all to -1—imposes strong homogeneous regulation and can artificially inflate or underestimate baseline stability in the system (May 1972).

From an ecological standpoint, it is unrealistic to assume that none of the species experience self-regulation in a food web. In nature, species often experience some form of self-regulation through intraspecific competition (Brook & Bradshaw 2006). By excluding the total consumption rate constraint, the BSRM produces two peaks around consumer-resource mass-ratios close to -5.0 and 3.5. Although those stability peaks do not match the peak for the empirical consumer-resource mass-ratio distribution, the stability decreases away from preferred consumer-resource mass-ratios, indicating that when facing self-regulation, a predator that

consumes smaller or larger resources (compared with itself) has a higher probability to survive and persist.

The closest precursor for comparison to our ART model is the seminal work by Allesina *et al.* (2015) who developed food webs with trophic interactions that were structured by the cascade and niche models. This approach led to approximately skew-symmetric community matrices that are structurally similar to those produced by our ART model. Moreover, Allesina *et al.* (2015) used empirically-informed interaction strengths, thus tying the model to data, again similar to our ART model approach. Importantly, our model differs from that of Allesina *et al.* (2015) in terms of interaction structure because we also add empirically-informed species interaction likelihoods drawn from a *lognormal* distribution. Our likelihoods differ from the cascade and niche models by having an optimal consumer-resource mass-ratio and thus being much less uniform in terms of the probability of trophic interaction. Even more fundamentally, the ART model differs from that of Allesina *et al.* (2015) in that we include a total consumption rate constraint and a self-regulation that varies with species body size. These differences lead to important new insights for the ART model, including the novel and correct prediction of connectance, while echoing some of the qualitative conclusions in Allesina *et al.* (2015) in relation to how ecological structuring of the interaction matrices might deviate from and alter the conclusions of Random Matrix Theory (RMT).

Based on our results, we argue that Random Matrix Theory (RMT) is an interesting theoretical baseline but differs from empirical food webs in fundamental ways that alter conclusions about system stability. RMT assumes that networks are large and highly connected with random values

occupying non-zero entries, producing an eigenvalue spectrum that is bounded by a circle (May 1972&1973; Allesina & Tang 2015) and with a well-defined boundary set by food web size and interaction strength. In contrast, empirical food webs are normally small and sparsely connected (compared to large values used in RMT) with trophic interactions that exhibit directional (energy/mass flow from resource to consumer) and non-random (constrained by species mass) patterns (Landi *et al.* 2018). Intriguingly, we find that a more realistic interaction matrix that is small, sparse, and non-random produces an eigenvalue spectrum with a shape closer to a diamond (Allesina & Grilli 2020). The potential effects of this diamond-shaped eigenvalue spectrum on stability remain an open question and should be investigated in future research.

When looking at the predicted eigenvalue spectra for empirical food webs, the real parts of leading eigenvalues are close to or even exceed zero (SI 5.3; Fig. S6), meaning that these empirical food webs are not stable in the strict sense or may oscillate between stable and unstable states. Such observations further suggest that we should shift from looking for absolute stability to studying the frequency-of-stability and comparing other alternative metrics of stability (Pettersson *et al.* 2019).

Throughout this project we tested our model with real data wherever possible. We used consumer-resource body mass-ratio distributions from 8 well-measured empirical food webs as a basis to predict food web stability. These predictions can be improved in the future by incorporating more and larger food web datasets that include information about trophic links as well as species masses. Future research should utilize more advanced tracking technologies (Dell

et al. 2014) and collect more comprehensive food web population abundance time-series data to test model predictions.

In conclusion, we created a novel food web model termed ART that is solely driven by species masses and that links all core food web characteristics—topology, interaction strength, total consumption rate, and self-regulation. Because of its flexibility and simple parameterization, the ART model allows us to create sub-models and analyze how multiple ecological constraints impact stability either alone or in combination. In doing so, we found that trophic interaction strength distributions have a relatively weak impact on food web stability compared with the energetic constraints of consumer consumption and species self-regulation. Finally, our ART model correctly matches empirical patterns such as the frequency of stable consumer-resource mass-ratios and the connectance.

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FIGURES

Figure 1

Figure 1. Food web constructed by the ART Model. Generally, food webs consist of resource and consumer species as nodes. (a) Each trophic link/edge in the food web is assigned an interaction likelihood value (link color), which is a Gaussian function of log consumer-resource mass-ratios. (b) For each selected trophic link, the interaction strength (link width), i.e. consumption rate, is calculated using metabolic theory. (c) The total consumption rate constraint is imposed when the sum of all resource consumption rates (sum of all weighted trophic links) exceeds the maximum consumption rate for a given consumer. (d) Some species experience self-regulation, the probability and strength of which both depend on mass. Note that topology is determined by interaction likelihood and diet while consumption rates and self-regulation together shape the interaction strength distribution.

Figure 2

Figure 2. Stability results produced by our food web models compared with the empirical frequency of consumer-resource body mass-ratios. The empirical mass-ratio distribution was obtained from 8 well-documented food web datasets (Pawar *et al.* 2019). The frequency of stable food webs is shown for a variety of models. For the Random Model (RM), a fixed number of trophic links were selected randomly from a species pool with lognormally distributed masses. The Base Mass Model (BMM) is similar to RM except a fixed number of links were selected based on consumer-resource mass-ratio. Models with total consumption constraint (BTCM) are built upon BMM by limiting the number of trophic links for each consumer species according to a mass-dependent consumption rate constraint. Models with self-regulation (BSRM) are based on BMM as well by imposing a mass-based negative intraspecific self-regulation on a subset of species (70%). Note that 70% is an average percentage of species experiencing self-regulation based on empirical data (SI 1.4). The ART model includes all features (steps 0-4 in main text). Note that the ART model produces a frequency-of-stability that closely matches the empirical mass-ratio frequency.

Figure 3

Figure 3. Key network properties—(a) mean connectance (unitless, ranges 0-1), (b) $\log_{10}(\text{mean interaction strength (kg s}^{-1}\text{)})$, and (c) modularity (unitless, ranges 0-1)—shown across a range of consumer-resource mass-ratios for the ART food web model. For interaction strength, the negative values are omitted since all trophic pairs are perfectly correlated and the positive value equals the positive value times the conversion efficiency constant. All food web metrics represent averages across 1000 replicate model simulations. And the error bars represent the standard deviation for each data point. Furthermore, the vertical dashed line (where mass-ratio = -0.5) indicates the C-R mass-ratio where stability peaks for the ART model.

Figure 4

Figure 4. Log-log plot for model and empirical food web connectance versus food web sizes. The light orange points are connectance data of 181 food webs from ECOWeB1.1 compiled by Cohen (2010). The grey points are connectance data of 8 food webs used in our paper. The orange line represents the best fitted line for all empirical data (189 food webs) with slope $a = -0.69 \pm 0.08$. The light purple error bars represent the standard deviation of $\log(\text{connectance})$ produced by our ART model (over 200 run/food web size) over 20 different food web sizes. The dark purple line represents the best fitted line for model connectance with slope $a = -0.76 \pm 0.009$. The green dotted line represents the best fitted line over data for linear scaling hypothesis with slope = -1. And the blue dotted line represents the best fitted line over data for constant connectance hypothesis with slope = -2. This demonstrates that the ART model correctly predicts that connectance scales log-linearly with food web sizes with a scaling exponent close to -0.70, which to our knowledge is the first model to predict this. Notably, the model predicts connectance values that are generally lower than the empirical data. This is possibly because empirical trophic links are accumulative and the consumption constraint eliminates links instead of weakening them.

Table 1. Topological and allometric measurements for 8 empirical food webs. The *Size* column shows the number of trophic species in corresponding food webs. The *Connectance* column measures the density of consumer-resource interactions (links) within food webs, i.e. number of observed links divided by the total possible number of links. The $\log_{10}(\text{mass})$ columns show the observed mean (μ) and variance (σ^2) for $\log_{10}$ transformed species masses (kg). The $\log_{10}(m_R/m_C)$ columns show the observed mean (μ) and variance (σ^2) for $\log_{10}$ transformed consumer-resource mass-ratios. The *Interaction Strength* columns measure the mean (μ) and variance (σ^2) of the distributions of consumers' consumption rates (kg s^{-1}).

Food webs	Topology		$\log_{10}(\text{mass})$		$\log_{10}(\frac{m_R}{m_C})$		<i>Interaction Strength</i>	
	<i>Size</i>	<i>Connectance</i>	μ	σ^2	μ	σ^2	μ	σ^2
Eastern Weddell Sea	153	0.0261	-2.85	5.13	-2.08	7.48	5.35E-05	3.24E-08
Grand Cariçai Marsh	90	0.1133	-5.42	2.74	-0.68	2.61	6.51E-07	8.17E-11
Scotch Broom	147	0.0322	-5.49	1.46	-0.14	3.23	1.22E-08	1.28E-15
Skipwith Pond	33	0.4848	-5.01	1.32	-0.81	0.89	2.69E-08	1.22E-15
Broadstone Stream	29	0.3200	-6.85	1.04	-1.07	1.35	5.75E-10	9.73E-19
UK Grasslands	61	0.0608	-5.00	2.10	0.56	2.31	2.11E-09	8.04E-18
Gearagh Woodland	113	0.0580	-5.31	4.46	-0.17	5.05	2.79E-09	5.88E-17
Estero de Punta Banda	119	0.1534	-2.58	6.67	-2.28	6.63	9.44E-06	4.72E-10

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