

LETTER

Allometric scaling enhances stability in complex food webs

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Abstract

Classic local stability theory predicts that complex ecological networks are unstable and are unlikely to persist despite empiricists' abundant documentation of such complexity in nature. This contradiction has puzzled biologists for decades. While some have explored how stability may be achieved in small modules of a few interacting species, rigorous demonstrations of how large complex and ecologically realistic networks dynamically persist remain scarce and inadequately understood. Here, we help fill this void by combining structural models of complex food webs with nonlinear bioenergetic models of population dynamics parameterized by biological rates that are allometrically scaled to populations' average body masses. Increasing predator–prey body mass ratios increase population persistence up to a saturation level that is reached by invertebrate and ectotherm vertebrate predators when being 10 or 100 times larger than their prey respectively. These values are corroborated by empirical predator–prey body mass ratios from a global data base. Moreover, negative effects of diversity (i.e. species richness) on stability (i.e. population persistence) become neutral or positive relationships at these empirical ratios. These results demonstrate that the predator–prey body mass ratios found in nature may be key to enabling persistence of populations in complex food webs and stabilizing the diversity of natural ecosystems.

Keywords

Diversity–stability, interaction strength, metabolic theory, networks, population dynamics, predation, predator–prey, trophic interactions.

Ecology Letters (2006) 9: 1228–1236

INTRODUCTION

Most natural communities comprise nearly innumerable numbers of species and trophic interactions creating complex networks of organisms critically dependent on one another for food (Dunne 2006). The question of how all these diverse and highly interdependent food webs continue to persist stimulated decades of productive research (McCann 2000; Dunne *et al.* 2005). Early in this history, Elton (1958) and MacArthur (1955) argued that diversity and its attendant complexity stabilize large food webs by reducing dependence of consumers on individual resources in richer ecosystems. May (1972) showed how mathematically unlikely this explanation is, which presented ecologists with a deep scientific conundrum. Researchers addressing this problem (see McCann 2000; Montoya *et al.* 2006 for reviews) illustrated how interdependent issues of body size (Yodzis & Innes 1992; Jonsson & Ebenman 1998;

Emmerson & Raffaelli 2004), interaction strength (Paine 1980; De Ruiter *et al.* 1995; McCann *et al.* 1998; Neutel *et al.* 2002; Berlow *et al.* 2004; Brose *et al.* 2005b), predator switching (Post *et al.* 2000; Brose *et al.* 2003; Kondoh 2003) and food web structure (Dunne 2006; Martinez *et al.* 2006) including omnivory (McCann & Hastings 1997; Vandermeer 2006) might explain the stability and persistence of complex food webs.

With the exception of recent work on nonlinear models of complex food webs (Brose *et al.* 2005b; Martinez *et al.* 2006), these explanations were limited by ecologically unrealistic assumptions such as very few species and network configurations (usually < 10), populations close to or at equilibrium, and non-saturating consumers who accelerate feeding despite excessive resources. Several or all these assumptions are violated in virtually all natural ecosystems. In particular, the fundamental and newly rejuvenated issue of body mass effects on population

dynamics (Savage *et al.* 2004; Weitz & Levin 2006) has yet to be investigated in more realistically complex networks.

The concept of ecological stability has moved beyond its early and remarkably durable incarnation of linear stability near population equilibrium (May 1972; McCann 2000), an approach that continues to yield ecological insights (e.g. Emmerson & Raffaelli 2004). These analytical methods were supplemented by computer simulations based on nonlinear approaches (e.g. Hastings & Powell 1991; Yodzis & Innes 1992), which allowed closer comparison with empirical population cycles (e.g. Kendall *et al.* 1998), coefficients of variation (CV) and the reciprocal of CV, which measures dynamic stability (e.g. Tilman *et al.* 2006). The concept of stability has also been scaled up to the community level in terms of low CV of total community biomass as well as permanence (Law & Morton 1996) and persistence (Brose *et al.* 2003; Martinez *et al.* 2006) of species within a community. Interestingly, community stability has been found to be inversely related to species' population stability among plants competing for common nutrients (Tilman 1999).

Here, we focus on the effects of predator–prey body mass ratios on the nonlinear dynamics of complex food webs that avoid many of the limitations of earlier analyses. We explore the consequences of increasing predator–prey body mass ratios – spanning from predators that are 100 times smaller than their prey to those that are 10^5 times larger – for population stability and persistence in complex food webs. Our simulations are replicated across three structural food web models, three levels of initial network diversity (20, 30 and 40 species), three functional responses (Holling types II and III, and Beddington–DeAngelis predator interference), and two metabolic categories of species (invertebrates and ectotherm vertebrates) that have different allometric coefficients. We focus on community stability in terms of probability that the community will retain all its species and population stability in terms of the variation of species' abundances over time. The simulation results are compared with empirical predator–prey body mass ratios.

MATERIALS AND METHODS

Food web structure

The predator–prey interaction structure (who eats whom) of our food webs follows the modified cascade (Cohen *et al.* 1990; Williams & Martinez 2000), niche (Williams & Martinez 2000) or nested-hierarchy model (Cattin *et al.* 2004). These stochastic models are based on algorithms that arrange a specific number of links among a specific number of species based on species richness and connectance as input parameters. Their predicted food web structures have been successfully tested against empirical data (Williams &

Martinez 2000; Cattin *et al.* 2004; Stouffer *et al.* 2005). In general, the number of basal species – primary producers without prey – varies substantially and systematically with species richness, and the food web model used. For example, the niche and nested-hierarchy models yield systematically more basal species than the modified cascade model, which causes a lower potential energetic supply to all species in the cascade model food webs. While this has important consequences for species' persistence (Williams & Martinez 2004b), the present study aims to test for differences in stability depending on the species richness in the food web while holding the energetic input from basal species constant. Thus, we reduce confounding effects of variable potential energy supply by selecting the particular subsets of food webs generated by the structural models that contain five basal species. Moreover, we used constant values for food web connectance (0.15) to avoid potentially confounding effects of varying complexity (Williams & Martinez 2004b). However, additional simulations (not reported here) suggest that the results presented here are qualitatively identical with different connectance values (e.g. 0.1 and 0.2) or with fewer basal species.

Population dynamics

The population dynamics within these food webs follow a consumer–resource model (Yodzis & Innes 1992) that we updated with new allometric coefficients (Brown *et al.* 2004) and extended to multispecies systems (Williams & Martinez 2004b), where

$$B_i' = r_i(M_i)G_iB_i - \sum_{j=\text{consumers}} \frac{x_j(M_j)y_jB_jF_{ji}(B)}{e_{ji}f_{ji}} \quad (1a)$$

$$B_i' = -x_i(M_i)B_i + \sum_{j=\text{resources}} x_j(M_j)y_jB_jF_{ij}(B) - \sum_{j=\text{consumers}} \frac{x_j(M_j)y_jB_jF_{ji}(B)}{e_{ji}f_{ji}} \quad (1b)$$

describe changes in relative biomass densities of primary producer (eqn 1a) and consumer species (eqn 1b). In these equations, B_i is the biomass density of population i , r_i is i 's mass-specific maximum growth rate, M_i is the body mass of individuals within population i , G_i is i 's logistic net growth rate where $G_i = 1 - (B_i/K)$ and K is i 's carrying capacity, x_j is j 's mass-specific metabolic rate, y_j is j 's maximum consumption rate relative to its metabolic rate, e_{ij} is i 's assimilation efficiency when consuming population j . Note that the fraction of the biomass removed from the resource population that is actually eaten, f_{ji} , is set to unity and thus effectively disappears from eqns 1a and b, which often characterizes filter feeders and gape-limited consumers. The

functional response, F_{ij} , describes the realized fraction of i 's maximum rate of consumption achieved when consuming species j :

$$F_{ij} = \frac{\omega_{ij} B_j^b}{B_0^b + c_i B_i B_0^b + \sum_{k=\text{resources}} \omega_{ik} B_k^b}, \quad (2)$$

where ω_{ij} is i 's relative consumption rate when consuming j , B_0 is the half-saturation density, b is the Hill coefficient (Real 1977) and c quantifies predator interference. The predator interference term in the denominator quantifies the degree to which individuals within population i interfere with one another's consumption activities, which reduces i 's per capita consumption if $c > 0$ (Beddington 1975; DeAngelis *et al.* 1975; Skalski & Gilliam 2001). We used uniform relative consumption rates for consumers with n resources ($\omega_{ij} = 1/n$, $B_0 = 0.5$) and varied the F_{ij} between type II ($b = 1$, $c = 0$), type III ($b = 2$, $c = 0$) and predator interference ($b = 1$, $c = 1$). The biological rates of production, R , metabolism, X , and maximum consumption, Y , follow negative-quarter power-law relationships with the species' body masses (Enquist *et al.* 1999; Brown *et al.* 2004):

$$R_p = a_r M_p^{-0.25}, \quad (3a),$$

$$X_C = a_x M_C^{-0.25}, \quad (3b),$$

$$Y_C = a_y M_C^{-0.25}, \quad (3c),$$

where a_r , a_x and a_y are allometric constants and the subscripts C and P indicate consumer and producer parameters respectively (Yodzis & Innes 1992). The time scale of the system is defined by setting the mass-specific growth rate of the basal population to unity. Then, the mass-specific metabolic rates of all species are normalized by the time scale, and the maximum consumption rates are normalized by the metabolic rates:

$$r_i = 1, \quad (4a)$$

$$x_i = \frac{X_C}{R_p} = \frac{a_x}{a_r} \left(\frac{M_C}{M_p} \right)^{-0.25}, \quad (4b)$$

$$y_i = \frac{Y_C}{X_C} = \frac{a_y}{a_x}. \quad (4c)$$

Substituting the terms on the right in eqns 4a–c in for the terms on the left into eqns 1a and b yields a population dynamic model with allometrically scaled parameters. In food webs with constant predator–prey body mass ratios, Z , the body masses of predators increase ($Z > 1$) or decrease

($Z < 1$) with increasing trophic levels, T by:

$$M_C = Z^T. \quad (5)$$

Accordingly, the body masses of all predators, M_C , are expressed relative to the body mass of the basal species. This makes the results presented here independent of the body mass of the basal species. We updated the allometric constants, a_r , a_x and a_y , of the original model (Yodzis & Innes 1992) with new more extensive allometric data (Brown *et al.* 2004), which yields the following constants: $y_j = 4$ for ectotherm vertebrates and $y_j = 8$ for invertebrate predators; $e_{ij} = 0.85$ for carnivores and $e_{ij} = 0.45$ for herbivores; $K = 1$; $a_r = 1$; $a_x = 0.314$ for invertebrates and $a_x = 0.88$ for ectotherm vertebrates.

Simulations and dependent variables

We used a full factorial design with 100 replicates for each of the 432 combinations of the independent variables (three structural food web models, three functional responses, two metabolic categories, three levels of diversity and eight body mass ratios whose logs are evenly spaced from 10^{-2} to 10^5), which yields a total of 43 200 replicate runs. We started every individual simulation with a food web stochastically generated by a specific model initialized with uniformly random population densities in terms of biomass density ($0.05 < B_i < 1$) and recorded the number of persistent populations ($B_i > 10^{-30}$) at the end of the time series ($t = 2000$). Most extinctions occur within the first 200 time steps and transient dynamics of the persistent populations settle down by $t = 1000$. Thus, we quantified the CV of the biomass densities for each of the persistent populations between $t = 1000$ and $t = 2000$. Analyses of the dynamics of non-persistent populations were prevented by their short time series. Note that: (i) simulations with longer time series ($t = 5000$) yield qualitatively similar results with a slightly lower proportional persistence; and (ii) different extinction thresholds produce qualitatively the same results at different levels of persistence (lower extinction thresholds increase the persistence). We measured food web stability by proportional persistence (i.e. species richness persisting at the end of the simulation divided by initial species richness) and measured population stability as the negative of the average over the CV of the persistent populations' densities.

Empirical data

We used data on predator and herbivore body mass ratios from an empirical data base on consumer–resource body mass ratios from terrestrial, freshwater and marine communities of five continents (Brose *et al.* 2005c). The Grand Caricaie food web was sampled several times at different locations. To avoid pseudo-replication, we only included

one of the samples (ScCont2). Note that this sample does not systematically deviate from the other samples of the Grand Caricaie food web.

RESULTS

Most populations in our simulations exhibited chaotic or limit cycle dynamics, and few populations reached equilibrium. Population stability during simulations – measured as the average negative CV across all persistent populations' densities – is strongly influenced by all two-way interaction terms that include body size ratios (Table 1). For each of these two-way interaction terms, population stability is lowest at intermediate predator–prey body mass ratios around 10^2 which represents predators that are 100 times larger than their prey (Fig. 1). This result holds across food webs that differ in functional responses (Fig. 1a), species' diversity (Fig. 1b), metabolic types (Fig. 1c) and structural network models (Fig. 1d). Each data point in Fig. 1 (and also in Fig. 2) presents one combination of a body mass ratio and one independent variable (functional response, diversity, metabolic type or network type), while the other three independent variables vary. The narrow confidence intervals are caused by the high number of replicates included in each of these data points (see legend of Fig. 1).

While the single effect of body size ratios on food web stability – measured by the fraction of original species that dynamically persist – is 10-fold stronger than any effect of any other independent variable examined, all two-way interaction terms that include body size ratios are also highly

significant (Table 1). Also similar to the population results, the high number of replicates for each fixed mass ratio yields relatively narrow confidence intervals despite variance in the three other independent variables among the replicates (Fig. 2). However, in contrast to population variability, food web stability consistently increases with the predator–prey body mass ratios (Fig. 2) unless food web stability has already reached its maximum of 1 (Fig. 2a). Food webs with type II functional responses are far less stable than those with type III or predator interference (Fig. 2a). Moreover, our results show rapid increases in food web stability between body mass ratios of 10^{-1} and 10^1 in invertebrate food webs and also between body mass ratios of 10^0 and 10^2 in ectotherm vertebrate food webs (Fig. 2c). Food web stability appears to be most sensitive to variation in predator–prey body mass ratio at intermediate ratios saturating at the highest persistence levels at the highest ratios. The inflection point of increasing stability with increasing body mass ratio is substantially lower for invertebrates (10^1) than for ectotherm vertebrates (10^2 , Fig. 2c). This indicates that dynamic persistence of invertebrate predators begins to saturate when they are 10 times larger than their prey species, whereas ectotherm vertebrate predators reach a similar point when they are at least a 100 times larger than their prey species. Our simulations reproduce a classic result (May 1972) that species diversity strongly decreases food web stability when body mass ratios are smaller than 10^1 (Fig. 2b). However, between body mass ratios between 10^1 and 10^2 , these negative diversity–stability relationships are surprisingly inverted into

Table 1 Effects on population and food web stability

Independent variable (d.f.)	Population stability		Food web stability	
	SS $\times 10^6$	<i>P</i> -value	SS	<i>P</i> -value
Network type (2)	1.18	0.000000	0.93	0.000000
Metabolic type (1)	0.97	0.000000	9.00	0.000000
Functional response (2)	287.59	0.000000	284.61	0.000000
Diversity (2)	23.45	0.000000	59.91	0.000000
Body size ratio (7)	210.32	0.000000	2645.89	0.000000
Network \times metabolic type (2)	0.03	0.174761	0.99	0.000000
Network \times functional response (4)	3.44	0.000000	3.54	0.000000
Metabolic type \times functional response (2)	5.43	0.000000	52.01	0.000000
Network type \times diversity (4)	0.17	0.000793	0.06	0.159578
Metabolic type \times diversity (2)	0.08	0.010394	2.33	0.000000
Functional response \times diversity (4)	6.03	0.000000	7.38	0.000000
Network type \times body size ratio (14)	17.23	0.000000	6.07	0.000000
Metabolic type \times body size ratio (7)	22.31	0.000000	156.25	0.000000
Functional response \times body size ratio (14)	54.05	0.000000	102.25	0.000000
Diversity \times body size ratio (14)	41.18	0.000000	153.84	0.000000
Error (43 118)	546.74		543.28	

ANOVA: population stability ($r^2 = 0.559$; $P < 0.001$), food web stability ($r^2 = 0.869$; $P < 0.001$). Higher than second-order interaction terms between the predictors are of minor importance.

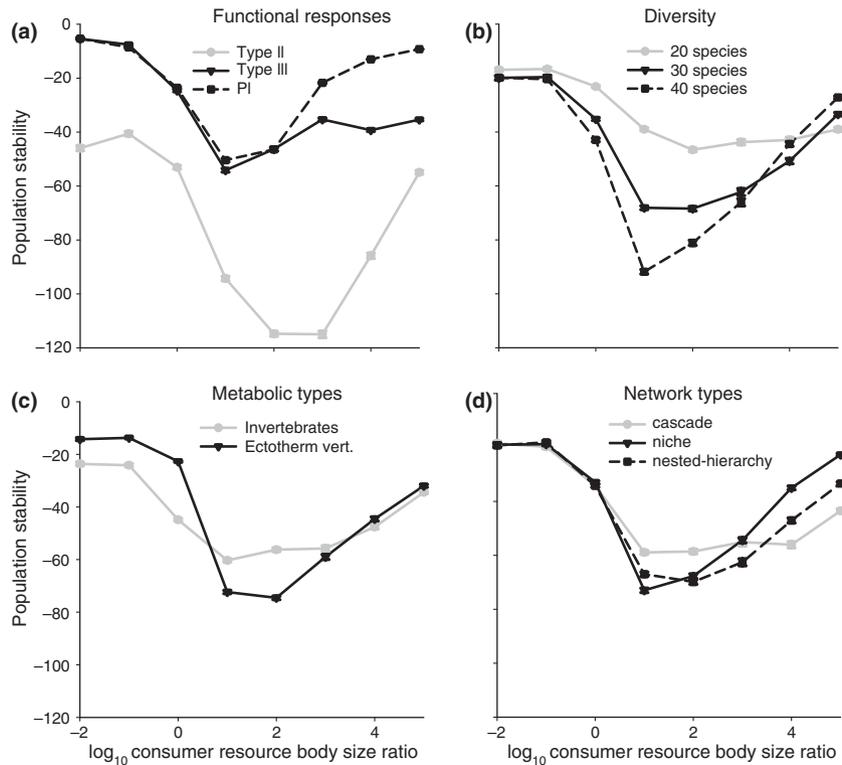


Figure 1 The dependence of population stability (mean and 95% CI) on predator–prey body mass ratios for models of varying: (a) functional responses; (b) initial network diversity; (c) metabolic types of species; and (d) network models. Population stability is the negative coefficient of variation of the persistent species. Note that in each of the panels (a–d) mean values and 95% CI are calculated for one independent variable but averaged across all other independent variables. Accordingly, each data point is averaged over 1800 (panels a, b and d) or 2700 (panel c) replicated runs that vary in all other independent variables. The SD around these mean values never exceeds 60 which is divided by n^{-2} ($1800^{-2} = 42$, $2700^{-2} = 52$) to calculate the very small confidence intervals (< 1.4) around the mean values of these distributions.

positive relationships (Fig. 2b). Increasing species richness increases species' probability of persisting at ratios of 10^2 and above. Overall, variation in predator–prey body mass ratios explained more variation in both population and food web stability than did variation in species diversity, food web structure, metabolic type or functional responses (Table 1).

Among the empirical data, the median among the 3887 invertebrate feeding interactions are predators that are 14 times heavier than their prey. The median among the 1501 ectotherm vertebrate feeding interactions are predators that are 398 times heavier than their prey (Fig. 3). Similar results are obtained when comparing prey of similarly sized invertebrate and ectotherm vertebrate predators – indicating that the trends reported here do not just reflect the higher body masses of ectotherm vertebrates. These body mass ratios are only slightly higher than the simulation inflection points for both invertebrates (empirical average = $10^{1.15}$, simulation inflection point = 10^1) and ectotherm vertebrates (empirical average = $10^{2.6}$, simulation inflection point = 10^2).

DISCUSSION

Our model simulations demonstrate that increasing predator–prey body mass ratios in complex model food webs: (i) increase food web stability (i.e. population persistence); and (ii) can convert negative into positive diversity–stability relationships. Moreover, the body mass ratios that are necessary for high food web stability are consistent with empirical data. Our approach assumes: (i) negative-quarter power-law scaling of biological rates with body masses; (ii) constant body mass ratios of all predator–prey interactions within individual food webs; and (iii) similar metabolic types of predators within individual food webs. Note that constant body mass ratios within individual food webs yield a continuous spectrum of body masses that increase with the trophic levels (see eqn 5), which is consistent with empirical data (Cohen *et al.* 1993; Jennings *et al.* 2001). While natural communities deviate from these assumptions (e.g. body mass ratios and metabolic types vary within food webs), our model hypothesizes the consequences of systematic vari-

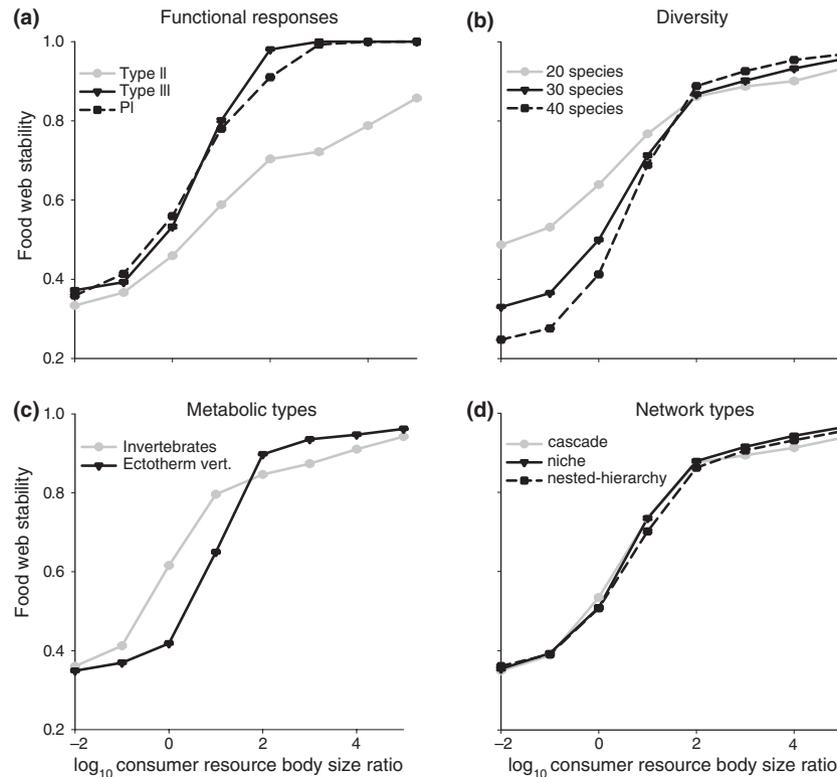


Figure 2 The dependence of food web stability (mean and 95% CI) on predator–prey body mass ratios for models of varying: (a) functional responses; (b) initial network diversity; (c) metabolic types of species; and (d) network models. Food web stability is the fraction of persistent species in the food web. Note in Fig. 1 legend also applies to this figure.

ation in average body mass ratios in an empirically well-informed and consistent manner. Given these and other related results, where replacing only one of two type II responses with a type III response stabilizes a tri-trophic food chain as well as replacing both with type III responses (Williams & Martinez 2004b), we speculate that fewer links incorporating high body mass ratios could stabilize food webs with more links incorporating lower body mass ratios. Exploring system-specific deviations from our assumptions would be important tests of the generality of our quantitative results and the validity of our speculations. However, additional simulations (results not shown) indicate that our results are qualitatively unaffected as long as the mass-specific biological rates scale negatively with the species body masses – independent of the exact exponent.

The median empirical body mass ratios coincide with both, the inflection point of food web stability and also near minimum population stability among our simulations. We propose the following explanation for this behaviour: the proportion of persistent species for a given diversity level increases with body mass ratios until species richness begins to saturate at the inflection points (Fig. 2). Simultaneously, increases in the numbers of coupled populations decreases population stability (Fig. 1). Above the inflection points, the

stability benefit of increasing body mass ratios only slightly increases species richness (Fig. 2) but more strongly dampens population oscillations (Fig. 1). This dampening may only be possible if not opposed by increases in the number of coupled populations. The opposing forces of dampened population oscillations and increasing population coupling with increasing body mass ratios help explain the curiously incongruent behaviour of population and food web stability in our simulations.

An important implication of our results is that natural food webs may gain stability (i.e. population persistence) by their intrinsic body mass structure. Increasing predator–prey body mass ratios decrease the predators' relative per unit biomass rates of metabolism and consumption (Yodzis & Innes 1992). Simulated species removal experiments have demonstrated that low consumption rates are strongly correlated to low direct per unit biomass interaction strengths between predators and their prey (Brose *et al.* 2005b). Per unit biomass interaction strengths decrease with body mass ratios (Brose *et al.* 2005b), whereas per capita interaction strengths increase with body mass ratios (Emmerson & Raffaelli 2004), because consumption rates scale negatively and positively with body mass ratios when expressed per unit biomass or per capita respectively (Yodzis & Innes 1992).

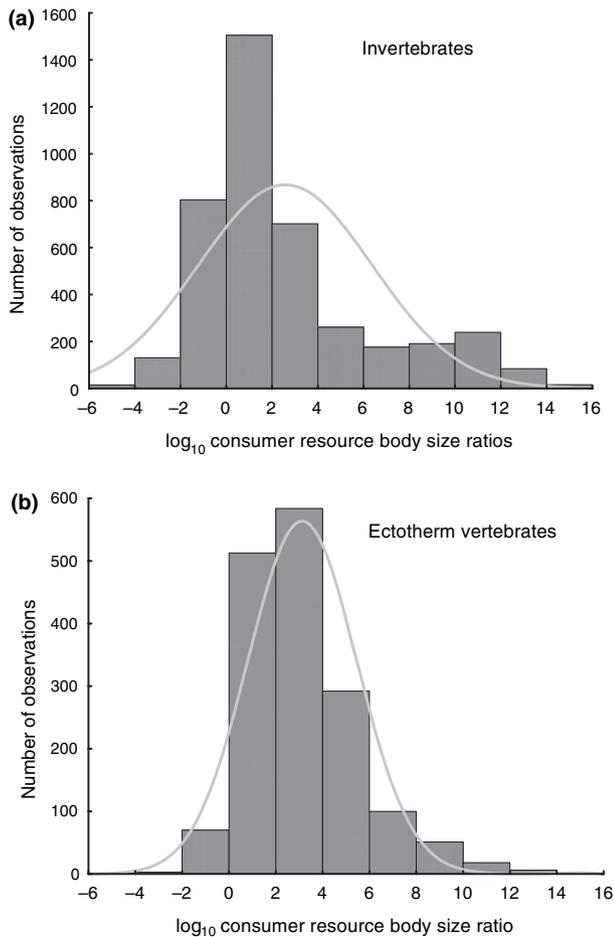


Figure 3 Frequency distribution of empirical \log_{10} predator–prey body mass ratios for (a) invertebrates ($n = 3887$) and (b) ectotherm vertebrates ($n = 1501$). The red lines represent the best fit to a log-normal distribution. Both data sets significantly differ from log-normal distributions (Kolmogorov–Smirnov $P < 0.001$), and central tendencies are thus characterized by the median (invertebrates: $10^{1.15}$, ectotherm vertebrates: $10^{2.6}$). The differences in \log_{10} body mass ratios between the metabolic groups are highly significant (Mann–Whitney U -test, $P < 0.001$).

Therefore, the positive correlation between body mass ratios and food web stability appears to be due to a reduction in direct interaction strengths on a per unit biomass basis. Despite fundamental differences in definitions of interaction strength and stability, this explanation is consistent with the classical linear stability theory argument that lowered average interaction strengths will increase food web stability (May 1972). More recent linear stability analyses also suggest that empirically informed body mass interaction strength relationships influence the stability both of food chains in general (Jonsson & Ebenman 1998) and the food web of the Ythan Estuary (Emmerson & Raffaelli 2004) in particular. In the same vein, our results generalize these conclusions across more realistic food web models with widely varying structural

and dynamical parameters. Our systematic variation of predator–prey body mass ratios offers a mechanistic understanding how the high ratios in natural communities lower metabolic and consumption rates and help explain how and why natural per unit biomass interaction strengths are lower than in random networks (May 1972).

Our analyses focus on formal ‘predators’ while excluding other consumer types, such as parasites, parasitoids, terrestrial herbivores, social insects and group hunters, that are often smaller than their resource species (Brose *et al.* 2005c, in press). Dynamical persistence of these consumer types may depend on reducing interaction strength by other factors such as the dampening forces of weak interactions (McCann *et al.* 1998; Neutel *et al.* 2002; Vandermeer 2006) or spatially discrete distributions of species causing a reduced co-occurrence of predators and their prey (Brose *et al.* 2004; McCann *et al.* 2005) and lower spatially averaged consumption rates (Bergstrom *et al.* 2006) and interaction strengths (Berlow 1999). Moreover, the stabilizing effect of large-bodied predators demonstrated here may be enhanced when they loosely couple spatially segregated food webs (McCann *et al.* 2005).

In our models, ectotherm vertebrates gain their highest persistence at higher body mass ratios than invertebrate predators. Consistently, ectotherm vertebrate predators have higher allometric coefficients, a_z (eqn 1), than invertebrates (Yodzis & Innes 1992; Brown *et al.* 2004), which makes vertebrate mass-specific metabolic and consumption rates higher. This difference in rates suggests that per unit biomass interaction strengths of invertebrates are generally lower than those of similarly sized ectotherm vertebrates, which leads to persistence increases of invertebrates at lower body mass ratios. Other explanations for the high predator–prey mass ratios found in nature, such as increased hunting, killing and handling capacities of predator species that are larger than their resources have not yet, to our knowledge, explained the different ratios of invertebrate and ectotherm vertebrate predators. In contrast to this, our model results appear to uniquely explain both the: (i) general increase in food web stability with increasing body mass ratios; and (ii) differences in body mass ratios between the two metabolic types. Nevertheless, increasing body mass decreases individual growth, assimilation efficiency and developmental rates (Brown *et al.* 2004). As our modelling approach does not include these factors, our results can only qualitatively suggest that average body mass ratios in nature should be higher than the observed inflection points. However, because the persistence benefits of increasing body masses as well as these excluded factors are selective forces at the species level, there is likely to be a tradeoff between the factors. Such a tradeoff may help explain why the medians of empirical body mass ratios are just above the inflection points for saturation levels of dynamical

persistence. Additionally, our food webs roughly span four to five trophic levels. Body mass ratios higher than 10^2 suggest that the top predators are more than 8–10 orders of magnitude larger than the basal species, which rarely occurs in natural food webs (Brose *et al.* 2005c, 2006).

The inversion of strongly negative to neutral or slightly positive diversity–stability relationships with increasing predator–prey body mass ratios (Fig. 2b) helps reconcile a long-standing debate between theoretical and empirical ecologists (McCann 2000; Dunne *et al.* 2005). Theoreticians employing linear stability analyses of random interaction matrices that implicitly distribute body masses randomly report negative diversity–stability relationships (May 1972). Similarly, we also find that mean body mass ratios of unity which would result from random body mass distributions yield negative diversity–stability relationships (Fig. 2). However, average body mass ratios in natural systems that are well above unity (Fig. 3) yield neutral or positive diversity–stability relationships in our simulations (Fig. 2) as expected by empiricists studying naturally diverse ecosystems.

We have not explored the effects of altering the other component of May's stability criterion, connectance (May 1972), although based on other explorations of this component (Martinez *et al.* 2006), we expect varying connectance would provide qualitatively similar results. However, our exploration of varying the topology between that provided by different structural models (Figs 1d and 2d) only weakly supports the greater food web stability of niche-model networks found previously (Martinez *et al.* 2006). This is due to the very narrow constraint of restricting our analyses to only food webs with five basal species. Removing this constraint leads to higher basal species richness in niche and nested-hierarchy model food webs than in cascade model food webs, which causes a lower food web stability of the latter model.

Allometrically linking metabolic and consumption rates to body mass hierarchies in natural food webs decreases the per unit biomass consumption with increasing body masses and trophic levels. Additionally, inverse relationships between body masses and abundances create food webs in which strong energetic flows are found in vertical food chains across multiple trophic levels. In contrast, weaker energetic flows characterize interactions between species of similar trophic levels, body mass and abundance (i.e. omnivorous and intraguild predation links). This is consistent with: (i) empirical patterns of consumption strength in natural food webs (Williams & Martinez 2004a; Bascompte *et al.* 2005); (ii) the concentration of weak links in long vertical loops and strong links in short chains (De Ruiter *et al.* 1995; Neutel *et al.* 2002); and (iii) the stabilizing effects of peripheral weak interactions on food chains of strong interactions (McCann *et al.* 1998; Emmerson & Yearsley 2004; Vandermeer 2006). Thus, consistent

with much ecological theory and data, our results describe how the interaction strength distributions that emerge naturally from body size structures can stabilize complex food webs. This description provides an improved foundation to generally explore how additional ecological realities such as shared resource consumption by plants (Brose *et al.* 2005a) and variability of body size ratios (Brose *et al.* 2005c), metabolic types (Brose *et al.* 2005c) and functional responses (Williams & Martinez 2004b) within food webs affect the functioning and stability of complex food webs.

ACKNOWLEDGEMENTS

Comments by Eric L. Berlow, Sonja Otto, Björn C. Rall, Owen Petchey, Jennifer Dunne, Tomas Jonsson, Bo Ebenman and Stefan Scheu helped improve the manuscript. U.B. is an Emmy-Noether fellow of the German Research Foundation (BR 2315/1-1,2). This research was also supported by US National Science Foundation grants DBI-0234980 from the Biological Databases and Informatics program and ITR-0326460 from the Information Technology Research Program to N.D.M.

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Editor, Michael Hochberg

Manuscript received 18 July 2006

First decision made 17 August 2006

Manuscript accepted 31 August 2006