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LETTER

Body masses, functional responses and predator–prey stability

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Abstract

The stability of ecological communities depends strongly on quantitative characteristics of population interactions (type-II vs. type-III functional responses) and the distribution of body masses across species. Until now, these two aspects have almost exclusively been treated separately leaving a substantial gap in our general understanding of food webs. We analysed a large data set of arthropod feeding rates and found that all functional-response parameters depend on the body masses of predator and prey. Thus, we propose generalised functional responses which predict gradual shifts from type-II predation of small predators on equally sized prey to type-III functional-responses of large predators on small prey. Models including these generalised functional responses predict population dynamics and persistence only depending on predator and prey body masses, and we show that these predictions are strongly supported by empirical data on forest soil food webs. These results help unravelling systematic relationships between quantitative population interactions and large-scale community patterns.

Keywords

Allometric scaling, body size, consumer-resource, ecological modelling, feeding rate, food webs, interaction strength, metabolic theory.

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INTRODUCTION

The stability of populations, communities and ecosystem functions depends critically on the strengths, distributions and characteristics of the interactions connecting species in complex food webs (McCann *et al.* 1998; Neutel *et al.* 2002; Rooney *et al.* 2006). Traditionally, consumer–resource interactions have been categorised according to their functional response as hyperbolic (type-II) or sigmoid (type-III) increases in the consumer's *per capita* feeding rate with the resource density (Holling 1959; Murdoch & Oaten 1975; Sarnelle & Wilson 2008). Historically, the quest for type-III functional responses has been fuelled by their severe consequences for population dynamics: they promote stable equilibria by accelerating predation risk at low resource densities which prevents unstable population oscillations (Murdoch & Oaten 1975; Williams & Martinez 2004; Fryxell *et al.* 2007; Rall *et al.* 2008). Despite their dynamical importance, however, characterising these functional-response types for each of the myriads of interactions in natural communities by tedious individual experiments is unfeasible thus rendering a generalised understanding of natural population dynamics virtually or nearly impossible.

An alternative approach employs body masses and their *allometric* relationships with ecologically important traits of species and their interactions (Peters 1983; Brown *et al.* 2004; Brose 2010). This allometric approach predicts the biological rates of populations such as respiration, consumption and growth by population-averaged body masses (Peters 1983; Brown *et al.* 2004) that are often available for consumer-resource pairs (Digel *et al.* 2011; Riede *et al.* 2011). Moreover, this constrains the universe of possible combinations of biological rates into those that are probable given that they all scale with species' body masses (Brose 2010). In this vein, systematic scaling relationships of the functional-response parameters handling time and capture rate (see Methods for detailed functional-response models) have been documented (Wahlström *et al.* 2000; Aljetlawi *et al.* 2004; Vonesh & Bolker 2005; Vucic-Pestic *et al.* 2010b; McCoy *et al.* 2011; Rall *et al.* 2011). Recently, it was shown that predatory beetles exhibited type-II or type-III functional responses when feeding on a small or a large prey species, respectively (Vucic-Pestic *et al.* 2010b), but this pattern has not been generalised across different predator and prey species. Allometric scaling of handling time and capture rate (also known as attack rate, see Methods) were included in population dynamic models demonstrating that variance in body masses has profound effects on population dynamics (Yodzis & Innes 1992; Weitz & Levin 2006; Otto *et al.* 2007) and food-web persistence (Loeuille & Loreau 2005; Brose *et al.* 2006; Rall *et al.* 2008; Heckmann *et al.* 2012). However, as none of these models addressed relationships between body masses and functional-response types, they could not explain the radical dynamic shifts associated with differences between these types (e.g. Williams & Martinez 2004; Brose *et al.* 2006; Rall *et al.* 2008).

We investigated how allometric scaling models can be integrated into functional-response types. These generalised allometric functional responses go beyond traditional functional-response types by including a body mass dependency for the capture exponent causing a gradual transition between hyperbolic and sigmoid functional responses. After parameterising allometric functional-response models employing data of terrestrial arthropod consumer–resource interactions, we show in dynamical analyses that allometric scaling of the capture exponent causes severe differences in population dynamics. In consequence, this model predicts a more realistic domain of

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stable coexistence for consumer-resource pairs than previous models, as we show by comparing the match with body-mass data from an entirely independent data base on natural food webs.

MATERIAL AND METHODS

Functional responses

The functional-response model framework established by Holling (1959) has been used in a plethora of studies (reviewed in Rall *et al.* 2012), where the per capita consumption rate of the predator, F, depends on the density of the prey, N:

$$F = \frac{aN}{1 + abN}, \tag{1}$$

with the handling time, b [s], needed to kill, ingest and digest a prey individual (Jeschke *et al.* 2002) and the capture rate, a [$m^2\ s^{-1}$], as a measure of the predator's hunting efficiency (originally termed 'rate of successful search'; Holling 1959). The capture rate was also termed 'attack rate' in other studies, a term that we consider as deprecated because of its ambiguity in excluding or including unsuccessful attempts of attack (Koen-Alonso 2007). This model framework is suitable for a wide range of consumer–resource interactions but as our experimental work was exclusively based on terrestrial invertebrate predators and their prey we will subsequently adhere to the terminology of predators and prey. Several functional-response studies have addressed allometric scaling and showed that capture rates follow hump-shaped relationships with predator–prey body-mass ratios while handling times decrease with increasing predator body mass and increase with prey body mass which can be explained by functional morphological constraints and allometric arguments based on metabolic theory (Wahlström *et al.* 2000; Aljetlawi *et al.* 2004; Vonesh & Bolker 2005; Vucic-Pestic *et al.* 2010b; McCoy *et al.* 2011; Rall *et al.* 2011; more references in Brose 2010).

The type-II functional response with a constant capture rate (eqn 1) can be modified to account for capture rates that vary with prey density, $a = bN^q$ (Williams & Martinez 2004; Rall *et al.* 2008; Vucic-Pestic *et al.* 2010b), which yields type-III functional responses:

$$F = \frac{bN^{1+q}}{1 + bbN^{1+q}}, \tag{2}$$

where b is a capture coefficient (sometimes also referred to as search coefficient), and q is a scaling exponent (hereafter: capture exponent) that converts hyperbolic type-II ($q = 0$) into sigmoid type-III ($q > 0$) functional responses. Subsequently, we aim to demonstrate that the inclusion of allometric dependencies for the capture coefficient, b, and capture exponent, q, substantially improve and generalise functional-response models.

Feeding rate experiments

We integrated data of prior feeding and functional-response studies (Brose *et al.* 2008; Vucic-Pestic *et al.* 2010b; Rall *et al.* 2011) with additional feeding experiments. These experiments used different treatment designs, but where all employing exactly the same microcosm set-up and environmental conditions (see Table S2 in Supplementary Material for a list of predator–prey pairs and reference to previous publications). In total, this yielded *per capita* feeding rates of 25 species of generalist arthropod predators (Coleoptera: Carabidae, Staphylinidae; Araneae: Lycosidae, Pisauridae, Salticidae; Chilopoda: Lithobiidae) on eight differently sized prey species [Collembola; Diptera (larvae and adults); Coleoptera (larvae); Isopoda; Orthoptera) varying between one and 1000 prey individuals per arena (0.04 m², see Table S1 for species names and density levels for each predator–prey pair]. All experimental units comprised a single predator individual and prey density was varied systematically (e.g. 1, 3, 5, 10, 30, 50 individuals per arena). Here, the definition of a predator includes its taxonomy and size class (narrow size ranges). Predators were sampled in the field, and only a small fraction of juvenile centipedes and lycosid spiders were reared in the laboratory until they reached the designated size. Prey populations were reared in the laboratory. Body masses of predators were determined individually. Prey body masses were estimated as averages across prey populations (see Table S2 for predator and prey species with ranges of body masses). Prey density levels were replicated two to eight times resulting in a total number of 2564 experimental units (see Table S2).

The predator individuals were kept separate in plastic jars dispersed with water and were deprived of food for at least 48 h before the start of the experiments. The experiments were performed in acrylic glass arenas (0.2 × 0.2 × 0.1 m) covered with lids permeable to air. The arena was floored with moist plaster of Paris (200 g dry weight) to provide constant humidity during the experiments. Habitat structure in the arenas was provided by moss (*Polytrichum formosum*, 2.35 g dry weight) that was first dried for 3 days at 40 °C to exclude animals and then re-moisturised prior to the experiments. Prey individuals were placed in the arenas half an hour in advance of the predators to allow them to disperse in the arenas. The experiments were run for 24 h with 12 h dark and 12 h light at a constant temperature of 15 °C in temperature cabinets. Initial and final prey densities were used to calculate the number of prey eaten. Predators were weighted before and after the experiments to calculate mean body mass. Control experiments without predators showed that prey mortality or escape was negligible.

Functional-response models

Different candidate functional-response models were fitted to the feeding-rate data that were evaluated according to their ΔAIC (difference in Akaike Information Criterion). As null models, we estimated constant parameters for non-allometric models of type-II (b and a in eqn 1) and type-III (b, b and q in eqn 2) functional responses. The first allometric model was a type-II functional response (eqn 1) with fixed allometric-scaling exponents according to Yodzis & Innes (1992), where the handling time,

$$b = b_0 m_r m_c^{-0.75}, \tag{3a}$$

as well as the capture rate,

$$a = a_0 m_r^{-1} m_c^{0.75}, \tag{3b}$$

are described with b_0 and a_0 as constants and the body masses [g], m_c and m_r, of the predator c, and the prey r, respectively. These null models of allometric relations are based on the simplifying assumption that interaction parameters should scale with body masses in the same way as metabolic rates with a ¾ power law (Peters 1983; Brown *et al.* 2004; Brose 2010; see Supplementary Information for a detailed description of the derivation of functional-response

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parameters from the models in Yodzis & Innes 1992). Subsequently, we will refer to this first model (inserting eqns 3a,b into eqn 1) as the allometric type-II functional response.

In the second model, allometric relationships were included according to a prior study (Rall *et al.* 2011) where handling time, h, follows power-law relationships with predator and prey body mass:

$$h = h_0 m_r^{\alpha_r} m_c^{\alpha_c}, \tag{4a}$$

where and α_c and α_r are allometric exponents (Rall *et al.* 2011). As capture rates follow hump-shaped relationships with predator–prey body-mass ratios (Wahlström *et al.* 2000; Aljetlawi *et al.* 2004; Vonesh & Bolker 2005; Vucic-Pestic *et al.* 2010b; McCoy *et al.* 2011) we estimated the allometry of the capture rate, a, using a combined equation comprising a power-law relationship with prey body mass and an exponential Ricker function that describes a humped curve with increasing body-mass ratios of the predator to the prey:

$$a = a_0 m_r^{\beta_r} \frac{m_c}{m_r} e^{\varepsilon \frac{m_c}{m_r}}, \tag{4b}$$

where a_0 is a constant, β_r is the exponent for the scaling of m_r, and ε is a constant which determines the width of the hump (Rall *et al.* 2011). This pattern of decreases and increases in capture rates at low and high prey body mass yields a hump-shaped attack model (Wahlström *et al.* 2000; Aljetlawi *et al.* 2004; Vucic-Pestic *et al.* 2010b; McCoy *et al.* 2011). We will refer to this second model as the hump-shaped allometric functional response.

Finally, we extended the second model by including a sigmoid scaling of the capture exponent, q, with the predator–prey body-mass ratio R:

$$q = \frac{q_{max} R^2}{q_0^2 + R^2}, \tag{5a}$$

where q_{max} and q_0 are scaling parameters defining the sigmoid relationship. The capture coefficient, b, follows the same allometric scaling relationships as the capture rate, a, in the previous model (eqn 4b), with the constant b_0 instead of a_0:

$$b = b_0 m_r^{\beta_r} \frac{m_c}{m_r} e^{\varepsilon \frac{m_c}{m_r}}. \tag{5b}$$

Inserting eqns 4a, 5a,b into eqn 2 yielded our third model, the generalised allometric functional response, accounting for hyperbolic as well as sigmoid forms of the response in dependence on predator and prey body masses.

Fitting the models to the data set of experimental observations by nonlinear least squares methods requires integrating the functional response to predict N_e, the number of prey individuals eaten during the experimental time as a function of the initial prey density ('nls' in R; Bolker 2008; R Development Core Team 2010). The application of Rogers' random predator equation accounts for decreasing prey densities during the experiment (Rogers 1972; Vonesh & Bolker 2005; McCoy & Bolker 2008) and can be solved using the Lambert W function (implemented in the package 'emdbook' for the statistical software R; Bolker 2008; R Development Core Team 2010 see Supplementary Information for details on equations and fitting procedure).

Model analyses

To illustrate the different consequences of these functional-response models for population dynamics, we performed bioenergetic simulations of simple predator–prey pairs (Yodzis & Innes 1992; Otto *et al.* 2007; Heckmann *et al.* 2012; Schneider *et al.* 2012) for each of the three different functional response models: the allometric type-II, the hump-shaped allometric and the generalised allometric functional response (see Supplementary Information for methodological details of the model simulations). We compared the resulting persistence domains of the model simulations (i.e. the combinations of prey and predator body masses at which the predator is predicted to persist) to a new data base on predator and prey body masses of terrestrial soil food webs from a large biodiversity research project in Germany (see Supplementary Information for details on food-web assembly). On basis of the predicted persistence domains, the three models were compared using a dimensionless score value, S. We defined this value to be a product of two ratios calculated within to the total area of the comparison, A_{total} (see Supplementary Information, Fig. S1 for the definition of this comparison envelope):

$$S = \frac{L_{pers}}{L_{emp}} \times \frac{A_{total} - A_{pers}}{A_{total}}. \tag{6}$$

The first fraction is the percentage of predator–prey pairs for which persistence is predicted by the model, L_{pers}, among all empirically observed links, L_{emp}. It is multiplied with the fraction of the area where no persistence of the predator is possible (total area, A_{total}, minus the persistence domain, A_{pers}). Thus, S penalises large persistence domains, which *per se* include larger proportions of the empirical links. For the same set of empirical predator–prey pairs, the score is maximised for a model that includes a maximal number of predator–prey pairs while predicting a minimal persistence domain.

RESULTS

The comparison via AIC revealed that the generalised functional-response model with allometric scaling of all parameters including q was the best-fitting model (AIC = 34087.74; ΔAIC = 0.0; d.f. = 9) compared to the hump-shaped allometric functional response (ΔAIC = 566.54; d.f. = 7) and the allometric type-II functional response (ΔAIC = 1586.69; d.f. = 3). The application of non-allometric type-II and type-III functional-response models to the data set scored worst (ΔAIC = 1688.54, d.f. = 3 and ΔAIC = 2134.58, d.f. = 3 respectively; see Table 1 for an overview of all parameter estimates). Together, these results imply that the generalised allometric functional-response model provides a substantially better fit to the feeding data over a wide variety of species, and the subsequent results will be based on this best-fitting model.

For handling time h, we found a significant negative power-law scaling with predator body mass (b_0 = 43 280; standard error = 8.364; $P < 0.001$; $\alpha_c = -0.283$; SE = 0.0218; $P < 0.001$; Fig. 1a), and a positive power-law scaling with prey body mass (α_r = 0.568; SE = 0.022; $P < 0.001$; Fig. 1a). Hence, handling times are highest at very low predator–prey body-mass ratios (i.e. the prey is larger than the predator, Fig. 1a). Furthermore, we found a hump-shaped relationship for the capture coefficient b with the predator–prey body-mass ratio ($b_0 = 1.680 \times 10^{-8}$; SE = 4.469×10^{-9}; $P < 0.001$; β_r = 0.0033; SE = 0.0371; P = 0.378; $\varepsilon = -0.0182$; SE = 0.0008; $P < 0.001$; Fig. 1b). Finally, the capture exponent q scaled positively with the predator–prey body-mass ratio R following a sigmoid relationship (q_0 = 1.009; SE = 21.84; $P < 0.001$; q_{max} = 3.306; SE = 0.148; $P < 0.001$; Fig. 1c) implying that the higher the body-mass ratio the more sigmoid the functional

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Table 1 Summary of the fitted parameters for the competing functional-response models

Parameter	Estimate	SE	t	P
Type-II functional response (ΔAIC = 1688.54, d.f. = 3)				
a	$8.478 \cdot 10^{-8}$	$2.703 \cdot 10^{-9}$	31.37	<0.0001***
h	$1.475 \cdot 10^{2}$	$2.321 \cdot 10^{1}$	6.35	<0.0001***
Type-III functional response, $q = 1$ (ΔAIC = 2134.58, d.f. = 3)				
b	$1.609 \cdot 10^{-11}$	$7.812 \cdot 10^{-13}$	20.60	<0.0001***
h	$5.999 \cdot 10^{2}$	$1.632 \cdot 10^{1}$	36.76	<0.0001***
Traditional allometric type-II functional response (ΔAIC = 1586.69, d.f. = 3)				
a_0	$1.673 \cdot 10^{-10}$	$7.305 \cdot 10^{12}$	22.90	<0.0001***
b_0	$4.084 \cdot 10^{5}$	$1.853 \cdot 10^{4}$	22.04	<0.0001***
Hump-shaped allometric functional response (ΔAIC = 566.54, d.f. = 7)				
a_0	$1.074 \cdot 10^{-7}$	$3.305 \cdot 10^{-8}$	3.25	0.0012**
b_0	$8.263 \cdot 10^{4}$	$2.101 \cdot 10^{4}$	3.93	<0.0001***
ε	$-1.892 \cdot 10^{-3}$	$1.116 \cdot 10^{-4}$	−16.96	<0.0001***
β_r	$5.218 \cdot 10^{-1}$	$4.069 \cdot 10^{-2}$	12.82	<0.0001***
α_r	$6.936 \cdot 10^{-1}$	$3.056 \cdot 10^{-2}$	22.70	<0.0001***
α_c	$-3.116 \cdot 10^{-1}$	$5.363 \cdot 10^{-2}$	−5.81	<0.0001***
Generalised allometric functional response (ΔAIC = 0, d.f. = 9)				
b_0	$1.680 \cdot 10^{-8}$	$4.469 \cdot 10^{-9}$	3.76	0.0002***
β_r	$3.276 \cdot 10^{-2}$	$3.711 \cdot 10^{-2}$	0.883	0.3775
ε	$-1.821 \cdot 10^{-2}$	$8.122 \cdot 10^{-4}$	−22.43	<0.0001***
q_{max}	3.306	$1.482 \cdot 10^{-1}$	22.30	<0.0001***
q_0	$1.009 \cdot 10^{3}$	$2.184 \cdot 10^{1}$	46.20	<0.0001***
h_0	$4.328 \cdot 10^{4}$	$8.364 \cdot 10^{3}$	5.18	<0.0001***
α_r	$5.681 \cdot 10^{-1}$	$2.183 \cdot 10^{-2}$	26.02	<0.0001***
α_c	$-2.825 \cdot 10^{-1}$	$2.177 \cdot 10^{-2}$	−12.98	<0.0001***

ΔAIC: difference in Akaike Information Criterion, AIC, to the generalised allometric functional response (AIC = 34 087.74); d.f.: degrees of freedom used by the model, SE: standard error; t: students t; P: two-sided P-value.
*$P < 0.05$.
**$P < 0.01$.
***$P < 0.001$.

response. This translates into type-II-like responses for small predators consuming relatively large prey, while large predators should be feeding on small prey following type-III-like responses according to the traditional categorisation of functional responses.

These general allometric scaling relationships of handling time, capture coefficient and capture exponent with predator and prey body masses allow predicting feeding rates for any combination of predator and prey body mass, and thus for any predator–prey pair (shown as solid lines in Fig. 2a-c for three exemplary taxonomic predator–prey pairs, see Fig. S1 for more examples). Embedding the parameters of these generalised allometric functional responses in population models yield predictions of predator–prey biomass dynamics (shown exemplarily in Fig. 2d-f for the taxonomic pairs of a-c). Subsequently, we have used one aspect of these biomass dynamics, predator survival, to compare the predictions of the three allometric functional-response models. We found that the simulations of the dynamic population model with the three functional responses predict very different persistence domains of predator and prey body masses enabling predator survival (non-red areas in Fig. 3). While the predator in the allometric type-II functional-response model only persists at very low prey body masses (Fig. 3a), the other two models produce a more band-shaped persistence domain across the range of predator–prey masses (Fig. 3b-c). However, these two domains exhibit pronounced differences including that under the hump-shaped allometric functional responses large predators can persist across a wide range of prey body masses (Fig. 3b), whereas the generalised allometric functional responses produces a cone-shaped persistence domain where the largest predators can only persist on a very small range of prey body masses (Fig. 3c).

We compared the persistence domains predicted by the dynamic population models to empirical body-mass data of forest soil invertebrates. These data were selected for model evaluation, because they include many of the predator and prey taxa that were used in the functional-response experiments and thus in the models' parameterisation. We evaluated the three models according to the percentage of natural predator–prey links (grey-shaded squares in Fig. 3a-c) that fall within the persistence domains. This comparison revealed that the allometric type-II functional-response model yielded a persistence domain that included only 21.9% of the natural body-mass combinations (Fig. 3a), which is considerably less than the persistence domain of the hump-shaped allometric functional-response model including 95.8% of the interaction pairs (Fig. 3b). The generalised allometric functional-response model performed best by yielding a persistence domain matching 97.7% of the links in the food-web data base (Fig. 3c). However, as the sizes of the predicted persistence domains differ (19.9, 66.0 and 50.8% of the total area for the allometric type-II, the hump-shaped and the generalised functional-response model respectively), the chances of correctly including a predator–prey pair in the domain are not equal. To account for these differences between the models, we penalise for the size of the predicted persistence domain in the score S (see Methods). This yielded score values of $S = 0.17$ for the allometric type-II model, $S = 0.32$ for the hump-shaped allometric model and $S = 0.48$ for the generalised allometric functional-response model. Hence, the generalised model predicts the persistence domains substantially better than the other models, even after accounting for the different sizes of persistence domains.

DISCUSSION

We examined how the body masses of predators and prey constrain their interaction strengths. Corroborating prior functional-response studies (Wahlström *et al.* 2000; Aljetlawi *et al.* 2004; Vonesh & Bolker 2005; Vucic-Pestic *et al.* 2010b; McCoy *et al.* 2011; Rall *et al.* 2011), we found power-law relationships between handling time and predator as well as prey mass and hump-shaped relationships between capture rates and predator–prey body-mass ratios. In addition, our study demonstrates for the first time a systematic body-mass dependency of the capture exponent, converting hyperbolic (type-II) into sigmoid (type-III) functional responses with increasing predator body mass and decreasing prey body mass. This suggests that these functional-response types are not strict categories but rather gradually shift from type-II predation of small predators on equally sized prey to type-III functional responses of large predators on small prey. Thus, we were able to support prior findings that sigmoid type-III responses can come about in simple one predator – one prey systems (Sarnelle & Wilson 2008; Vucic-Pestic *et al.* 2010a,b) and are not necessarily related to the multi-prey environments as most previous studies on type-III responses and switching behaviour suggested (Murdoch *et al.* 1975; Kalinkat *et al.* 2011). Hence, our study represents an incremental advancement of prior studies on allometric constraints on functional responses

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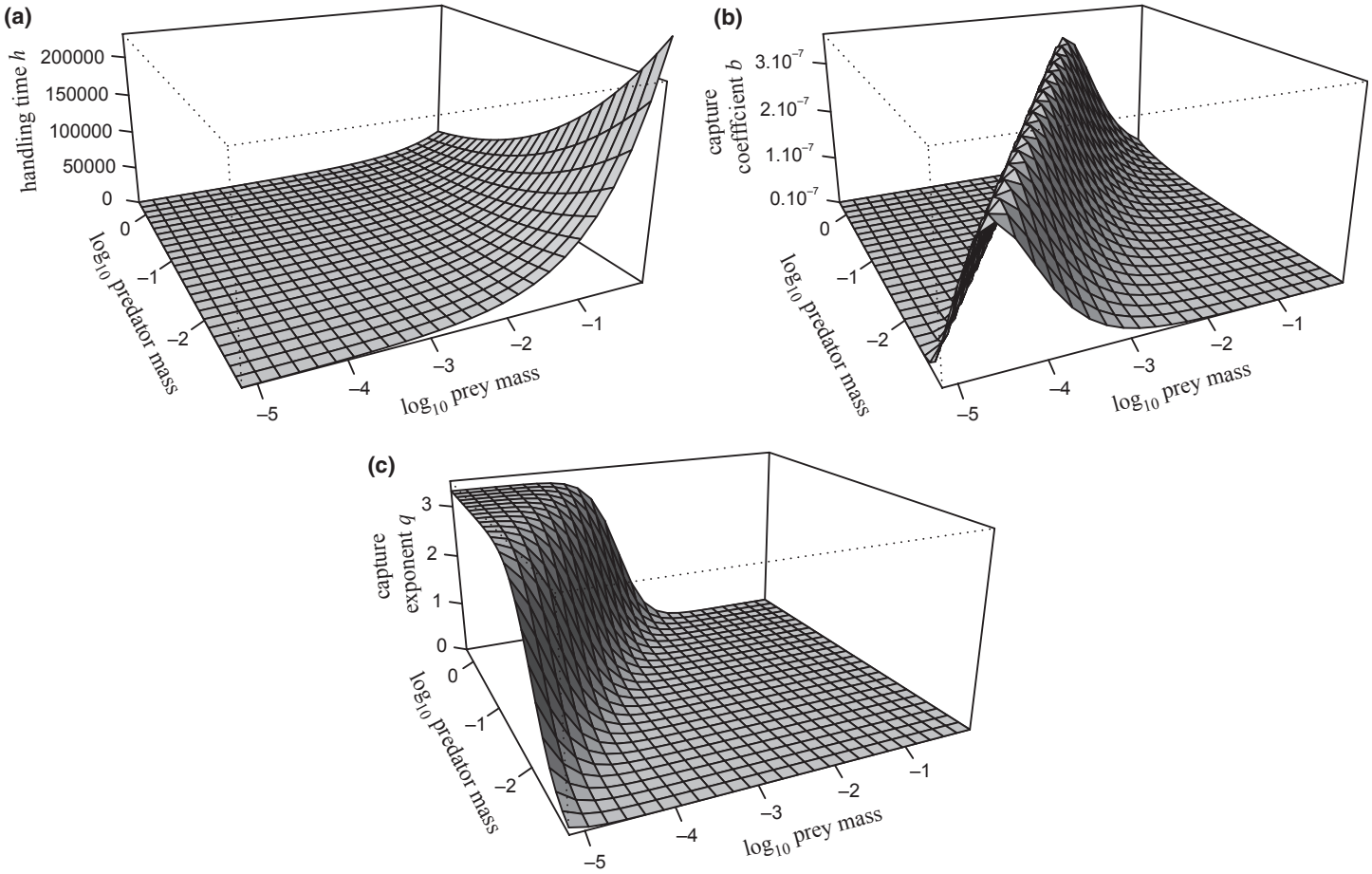

Figure 1 The generalised allometric functional-response model includes dependencies of the three fundamental functional-response parameters (a) handling time *h*, (b) capture coefficient *b* and (c) the capture exponent *q* on predator mass and prey mass. These relationships were estimated by fitting functional-response models to feeding data of terrestrial arthropods (n = 2,564).

(Wahlström *et al.* 2000; Aljetlawi *et al.* 2004; Vonesh & Bolker 2005; Brose 2010; Vucic-Pestic *et al.* 2010b; McCoy *et al.* 2011; Rall *et al.* 2011) but additionally entails far-reaching and important consequences for population and community ecology.

The allometric scaling of handling time is consistent with prior studies (Aljetlawi *et al.* 2004; Vucic-Pestic *et al.* 2010b; Rall *et al.* 2011, 2012). Compared to established null models based on the metabolic theory of ecology (Yodzis & Innes 1992; Brown *et al.* 2004), our results suggest that the power-law exponent of the relationship between handling time and predator mass (−0.28) is much shallower than the expected negative ¾ exponent. Moreover, the power-law increase in handling time with prey mass is also shallower (0.56) than the expected isometric scaling. These shallow scaling relationships of handling time with predator and prey masses are consistent with the findings from a recent and comprehensive meta-study on the allometry of feeding rates (Rall *et al.* 2012). Together, these results suggest that handling time is constrained by more complex processes and not solely by metabolism. For instance, the scaling relationship for predator mass might be biased by different feeding modes such as sucking or chewing that shift with increasing body masses. In our data set, liquid-feeding spiders (mean body mass: 0.036 g; n = 618) and centipedes (0.082 g; n = 903) are generally smaller than chewing beetles (0.126 g; n = 1044). Therefore, small liquid feeders that ingest less unpalatable parts of their prey such as sclerotised cuticles have relatively quicker handling times than larger chewers ingesting whole prey items, which could explain the shallower relationships. On the basis of a large data base, our results suggest that the assumption of negative ¾ power-laws should be replaced by shallower scaling relationships for handling time.

The intentional exclusion of the taxonomic information in our generalised modelling approach is supported by previous work that has shown how allometric functional-response models can explain a large part of the variation in empirically observed feeding rates of taxonomically different predator–prey pairs with a minimal number of parameters (Rall *et al.* 2011). Nonetheless, generalised allometric models can be easily integrated with taxonomic approaches by making one or several parameters (e.g. the optimal prey body mass) dependent on predator taxonomy (Rall *et al.* 2011). In contrast, traditional taxonomy-based approaches describe each particular predator–prey pair with a set of parameters (e.g. Vucic-Pestic *et al.* 2010b). This traditional approach might produce more precise predictions (see examples in Fig. 2a-c and Fig. S1 in the Supplementary Information), but it comes at the cost of using more parameters: While the generalised model is very efficient in the use of parameters (eight parameters, d.f. = 9), a taxonomic model would have

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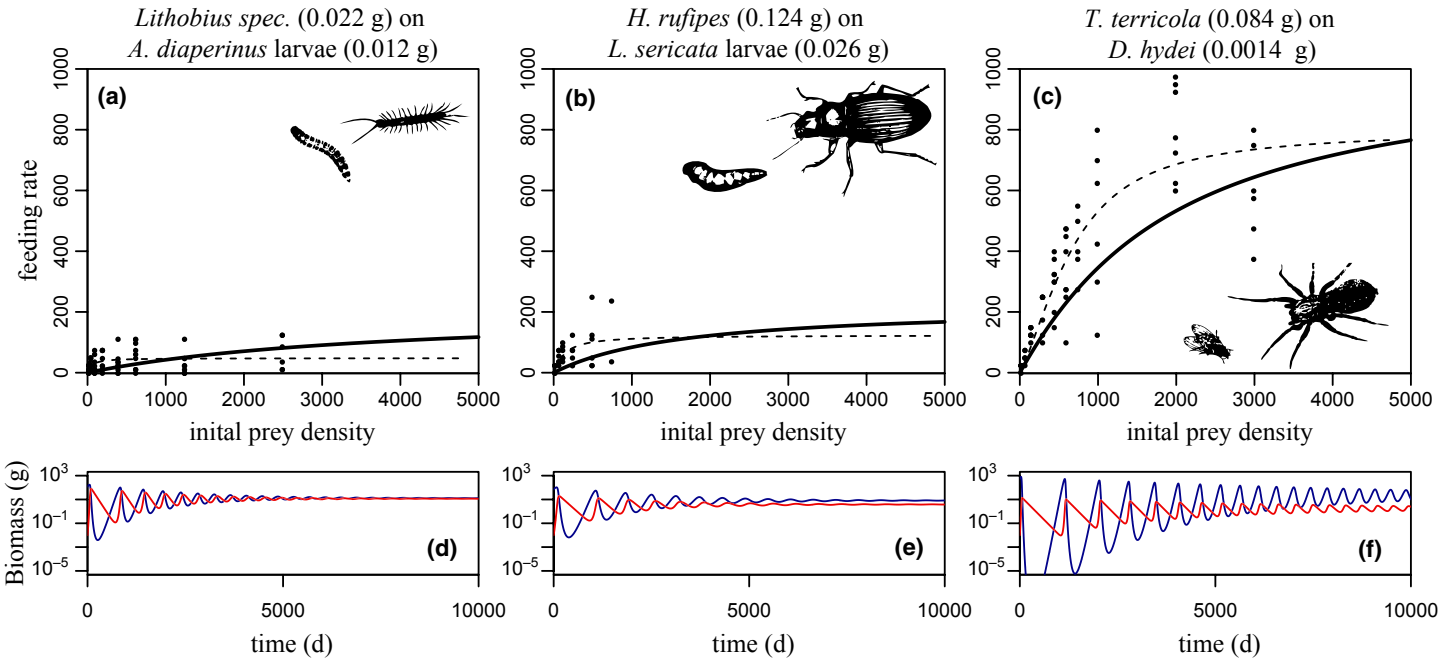

Figure 2 (a-c) The generalised allometric functional-response model (solid line) describes experimentally observed feeding rates (black dots) as a function of initial prey density and predator and prey body mass. The generalised model predicts similar feeding rates as independent models for the particular predator–prey pairs (dashed lines) without the necessity of taking taxonomic differences into account. (d-f) Simulated dynamics of predator (red line) and prey (blue line) population biomasses as predicted by a generalised model for the predator–prey pairs of panels a-c.

required 216 parameters for 72 taxonomic predator–prey pairs (72 times the three parameters h, b and q, d.f. = 217). In a prior study, we have shown that focussing on these taxonomic differences while lumping individuals of the same species but different body size yield less accurate predictions of feeding rates than allometric models that lump species of different taxonomies (Rall *et al.* 2011). Furthermore, generalised models are applicable to predict the feeding rates of predator–prey pairs depending on their body size, whereas classical taxonomic models are restricted to predict feeding of those predator–prey pairs that were used for parameterisation. This last feature is of high relevance when it comes to estimating feeding rates for the innumerable trophic interactions in natural communities, where an experimental measurement of all pairwise interactions is impossible. Accordingly, increased application of such 'purely allometric approaches' in community ecology has recently been demanded (e.g. Blanchard 2011), but until now such taxonomy-neglecting allometric approaches have exclusively been used in the description of pelagic communities ('size spectra', e.g. Sheldon *et al.* 1972; Jennings & Mackinson 2003; but see Reuman *et al.* 2008 for an application to soil food webs). The allometric functional-response approach of our study thus gives up accuracy in predicting feeding strengths of specific interactions while allowing generalising across the myriads of interactions in natural ecosystems.

This generality of allometric models also allows investigating how body masses constrain population dynamics of a wide range of predator and prey pairs. Indeed, allometric scaling of metabolism, growth and maximum feeding (i.e. the inverse of handling time) with average individual body masses are the core assumptions of a bioenergetic model that predicts population dynamics of simple predator–prey modules (Yodzis & Innes 1992; McCann *et al.* 1998; Otto *et al.* 2007) and complex food webs (Brose *et al.* 2006; Stouffer & Bascompte 2010; Heckmann *et al.* 2012). The early applications of this model retained some shortcomings such as an arbitrary choice of free parameters, the basal carrying capacity and the capture exponent determining the functional-response type, and an unrealistic power-law scaling of capture rates. A prior model improvement included an allometric scaling relationship of carrying capacities and more realistic scaling relationships of capture rates (Weitz & Levin 2006). In recent years, hump-shaped scaling of capture rates with predator–prey body-mass ratios became widely accepted (Wahlström *et al.* 2000; Aljetlawi *et al.* 2004; Vonesh & Bolker 2005; Vucic-Pestic *et al.* 2010b; McCoy *et al.* 2011; Rall *et al.* 2011). Altogether, these efforts helped to eliminate biologically unrealistic trait combinations (Brose 2010) and implementations of these improved allometric constraints into the bioenergetic model were successfully employed to predict population dynamics in complex multi-predator communities (Boit *et al.* 2012; Schneider *et al.* 2012). The generalised allometric functional-response models of the present study allow dropping assumptions on the functional-response type (II or III) in future studies, which will have far-reaching consequences for stability analyses (e.g. Brose *et al.* 2006; Rall *et al.* 2008).

The biological mechanisms that can lead to type-III functional responses include prey refuges and optimal foraging processes (Murdoch & Oaten 1975). Subsequently, we will discuss how they fit into the allometric framework of our study. The habitat structure of the moss in our feeding experiments provides refuges for small prey that are not accessible for large predators. Thus, at very low prey densities, small prey individuals will have a reduced risk of predation and the population will not be over-exploited, as it is characteristic for type-III responses (Crawley 1992, p. 53). Consequently, this would imply that we would not have found type-III responses

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in treatments without habitat structure which was corroborated by one prior study (Vucic-Pestic *et al.* 2010a). However, this represents an extremely artificial environment for the litter-dwelling arthropods of our experiments, which does not characterise natural ecosystems that should generally exhibit sufficient habitat structure to provide refuges for small prey. As a second possibility, sigmoid predation curves might arise due to behavioural responses of the predators to the level of prey densities (Sih 1984). Especially at high predator–prey body-mass ratios it might not be energetically profitable to pursue relatively small prey individuals at very low densities. Due to evolutionary optimisation, the predator might 'activate' its 'foraging mode' aimed at small prey species only if their overall density is reaching a certain threshold (Sih 1984). It is important to note that these active mechanisms of size-driven prey selection evolved in the context of having alternative prey species available, but nonetheless will influence the predator individuals' behaviour in the experiments with only one prey species present. Overall, both processes, the availability of prey refuges and optimal foraging, may contribute to the allometric functional-response patterns documented here.

The functional-response data used for our analyses are obtained under simplified laboratory conditions which include the restriction that only combinations of single predator and single prey species were used here. However, predators exhibit active prey selection in environments with two prey species present (Kalinkat *et al.* 2011). Moreover, these active preferences go beyond the expectations derived from single-prey experiments and are by themselves functions of predator and prey body masses (Kalinkat *et al.* 2011). In reverse, predators should tend to disregard prey whose individual body mass is too far from this optimum as exemplified by several zero-consumption replicates in our data set. This is especially important for the comparison of our model results (i.e. predator persistence domain) with the soil food-web data (Fig. 3) as the first was parameterised on base of the 'single-prey world' in our experimental setting, whereas the second represents the 'real, multi-prey world'. Specifically, our model employs simple predator–prey structures that in some cases lead to predator extinction if the prey as the only resource does not support the predator population. However, this would rarely be observed in natural ecosystems, in which predators have multiple prey. Hence, we assume that the empirically observed feeding links should represent those interactions that provide the major energy channels supporting predator biomass. We acknowledge that this is a reductionist test for the validity of allometric constraints on feeding rates since in nature predator populations rely on multiple prey species of different mean body masses that often also comprise intraspecific size-structure. Prior studies including these features such as ontogenetic niche differentiation or cannibalism (e.g. Rudolf 2008; Rudolf & Armstrong 2008) have demonstrated their importance for population dynamics. Neverthe-

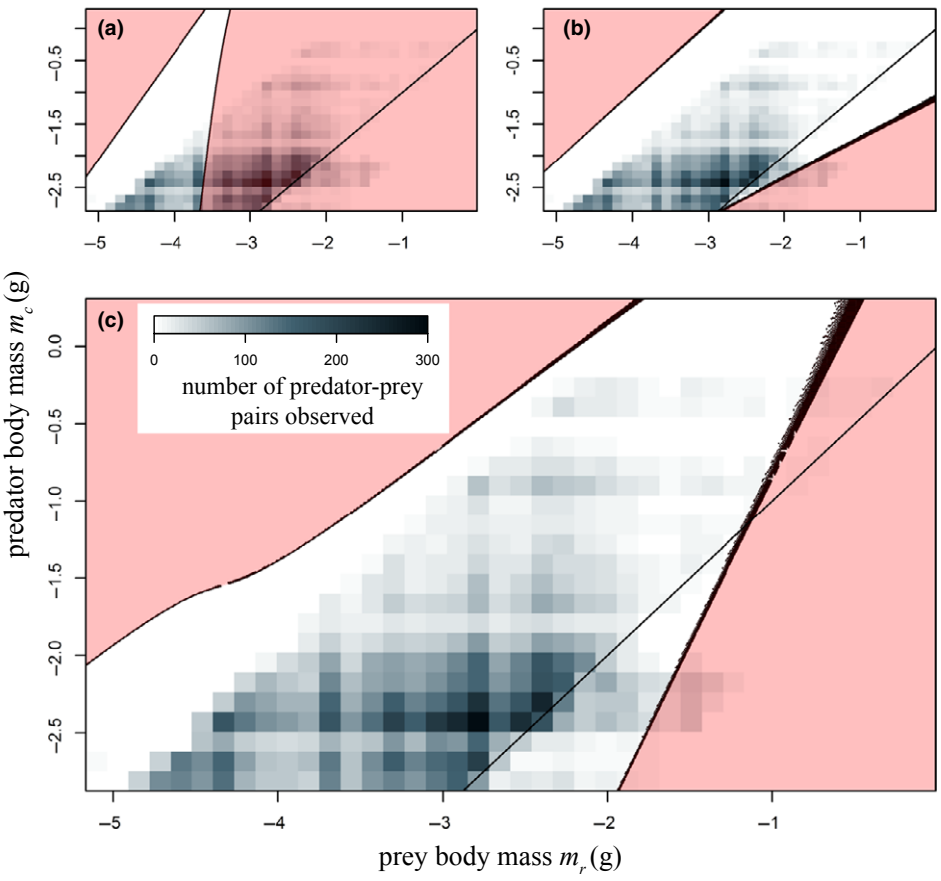

Figure 3 Densities of 18 713 empirically observed predator–prey pairs from the soil food web and predicted persistence domains for predators ($Bc > 10^{-30}$ non-red areas, black border of persistence domain appears non-continuous due to oscillating dynamics) for (a) traditional allometric type-II functional-response model (score $S = 0.17$), (b) hump-shaped allometric functional-response model ($S = 0.33$) and (c) the generalised allometric functional-response model ($S = 0.48$). S is the proportion of the predator–prey pairs that lie within the predicted persistence domain times the proportion of the area predicted as non-persistent (red areas). The thin black line represents equal body masses of predator and prey.

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less, McCoy *et al.* (2011) have demonstrated recently how size-dependent functional-response models might successfully predict prey mortality in short-term experiments with large variation in prey size although the models were developed from experiments with homogenous prey-size cohorts invigorating the reliability of our approach.

Interestingly, our intrinsic assumptions yield relatively small persistence domains for large predators (Fig. 3c). Analyses of empirical food webs have shown that larger predators tend to be more generalised than smaller predators (Digel *et al.* 2011), which could be an evolutionary response to balance their smaller persistence domains by more diverse diets. Hence, the cone-shaped persistence domain we found in our model simulations (i.e. large persistent prey size range for small predators and small persistent prey size range for large predators) complements with findings from food-web studies that generality increases with predator mass. While the allometric functional-response models may represent an important step towards a generalised understanding of natural interaction strengths, it will remain an important challenge to cope with other dimensions of natural complexity such as coexistence of multiple prey (Kalinkat *et al.* 2011) and habitat structure (Vucic-Pestic *et al.* 2010a; Kalinkat *et al.* 2013). Furthermore, the allometric scaling relationship of the capture exponent that we found for terrestrial arthropods of forest floors still has to be corroborated in studies on other organism groups and ecosystem types.

Meanwhile, we suggest employing the generalised allometric functional responses in future analyses of population dynamics (Otto *et al.* 2007), food-web persistence (Brose *et al.* 2006) or network structure (Petchey *et al.* 2008) to obtain more realistic predictions and avoid uncertainty caused by the strict distinction into type-II and -III functional-response models. Ultimately, by providing a general framework of feeding interactions that is applicable to entire communities the generalised allometric approach may bridge the gap between quantitative studies of population interactions (Holling 1959; Rall *et al.* 2011) and large-scale comparisons of community patterns (Riede *et al.* 2011).

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AUTHORSHIP

The authors have made the following declarations about their contributions: GK and FDS contributed equally to this study. Conceived and designed the experiments: GK, FDS, BCR, UB. Performed the experiments: GK, FDS, BCR, UB. Analysed the data: GK, FDS, BCR. Provided data/analytical tools: CD CG. Wrote the paper: GK, FDS, BCR, UB, with minor contributions of CG and CD.

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