

# Convergence of trophic interaction strengths in grassland food webs through metabolic scaling of herbivore biomass

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## Summary

1. Food web theory hypothesizes that trophic interaction strengths of consumers should vary with consumer metabolic body mass ( $\text{mass}^{0.75}$ ) rather than simply with consumer body mass ( $\text{mass}^{1.0}$ ) owing to constraints on consumption imposed by metabolic demand for and metabolic capacity to process nutrients and energy. Accordingly, species with similar metabolic body masses should have similar trophic interaction strengths.

2. We experimentally tested this hypothesis by assembling food webs comprised of species of arthropod predators, small sap-feeding and large leaf-chewing insect herbivores and herbaceous plants in a New England, USA meadow grassland. The experiment comprised of a density-matching treatment where herbivore species were stocked into field mesocosms at equal densities to quantify baseline species identity and metabolic body mass effects. The experiment also comprised of a metabolic biomass-matching treatment where smaller sap-feeding herbivore (SH) species were stocked into mesocosms such that the product of their density and metabolic body mass (metabolic biomass) was equal to the large herbivore (LH) species. We compared the magnitude of the direct effects of herbivore species on plants in the different treatments. We also compared the magnitude of indirect effects between predators and plants mediated by herbivores in the different treatments.

3. Consistent with the hypothesis, we found that increasing metabolic biomass translated into a 9–14-fold increase in magnitude of herbivore direct effects and up to a fivefold increase in indirect effects on plants. Moreover, metabolic biomass matching caused interaction strengths among herbivore species to converge. This result came about through increases in the herbivore mean effects as well as decreases in variation in effects among treatment replicates as herbivore metabolic biomass increased.

4. We found, however, that herbivore feeding mode rather than herbivore metabolic biomass explained differences in the sign of indirect effects in the different food webs.

5. We conclude that increasing herbivore metabolic biomass not only strengthened the direct and indirect effects on plants but also made those effects more consistent across space. Nevertheless, metabolic biomass alone could not completely explain variation in the nature of indirect effects in the food web, suggesting that additional consideration of consumer traits like feeding mode will provide a more nuanced understanding of trophic interaction strengths in food webs.

**Key-words:** direct and indirect effects, food webs, interaction strength, metabolic biomass, metabolic scaling, predators and herbivores, trophic cascade

## Introduction

There is a concerted effort in food web ecology to identify and quantify patterns in interaction strengths between consumer and resources species. The impetus for this effort is the call-to-arms to improve the quality of food web data (Cohen *et al.* 1993; Berlow *et al.* 2004) with the hope that such infor-

mation will enhance the reliability of predicting the nature and stability of food web dynamics as well as predicting the fate of attendant biodiversity (Emmerson & Raffaelli 2004; Wootton & Emmerson 2005; Berlow *et al.* 2009).

Empirically measuring interaction strengths presents a daunting logistical challenge even for food webs with modest species complexity owing to the need to conduct factorial experiments that explore all possible pairwise combinations of consumer and resource species comprising the system

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(Emmerson & Raffaelli 2004). Ecologists are consequently searching for more easily measurable surrogates to address questions of food web structure and dynamics. Ecological theory (Yodzis & Innes 1992; Berlow *et al.* 2004; Shurin & Seabloom 2005; Wootton & Emmerson 2005) proposes that the body mass of consumer species is one such promising and easily measurable surrogate. Accordingly, resolving body mass–interaction strength relationships has become a central focus for understanding patterns in the strength and nature of direct and indirect effects in food webs (Emmerson & Raffaelli 2004; Shurin & Seabloom 2005; Woodward *et al.* 2005; Berlow *et al.* 2009). Much current empirical work builds insights from efforts to quantify interaction strengths for different-sized species within and across ecosystems to provide synthetic understanding of patterns (Wootton & Emmerson 2005; Brose *et al.* 2006; Berlow *et al.* 2009; Hillebrand *et al.* 2009; Wood *et al.* 2010). Such synthesis has led to the hypothesis that the strength of direct species interactions in food webs scales to metabolism through allometric relationships with the body mass of consumer species (Berlow *et al.* 2009; Hillebrand *et al.* 2009; Brose 2010; Wood *et al.* 2010).

Theoretically, an allometric relationship should come about because individual metabolic demand for nutrients and energy and accordingly consumption rate of nutrients and energy scale with consumer mass<sup>0.75</sup> (hereafter metabolic body mass) rather than with body mass directly, i.e. mass<sup>1.0</sup> (Peters 1983). Such metabolic scaling theoretically is a powerful way to link consumer size and food web interaction strengths because it offers a way to unify consumer metabolic demand and constraints on resource intake to meet demand, based on allometric relationships with consumer body mass (Yodzis & Innes 1992; Brose *et al.* 2008; Hillebrand *et al.* 2009; Brose 2010). This theory predicts that consumers with equal metabolic body mass should have equal interaction strengths in food webs. Whether or not one sees such convergence in food web interaction strengths following experimental manipulation of metabolic body mass remains untested. The goal of our study was to experimentally test this hypothesis using a field experiment that assembled food webs comprised of different arthropod herbivore species that are known to differ in body mass and interaction strength (Schmitz 2008, 2010).

We used two kinds of experimental treatments. The baseline treatment equalized the density of the different-sized herbivore species and measured their interaction strength on plants. We expected that smaller herbivores would have weaker interaction strengths than larger herbivores. The other treatment adjusted densities of the smaller herbivore species so that their collective 'metabolic body mass' – hereafter called metabolic biomass – matched that of the larger species. We expected interaction strengths to converge among herbivore species in this treatment.

Herbivore species also occupy intermediate positions in food webs. Thus, in addition to exerting control over food web interactions and dynamics through direct consumptive effects on their plant resources, they also exert control by

mediating the indirect effects of their own consumers (predators) on plant resources. We, therefore, also tested whether equalizing herbivore metabolic biomass caused the magnitude and the sign of predator indirect effects on plants, mediated by the herbivore species, also to converge.

## Materials and methods

### BACKGROUND

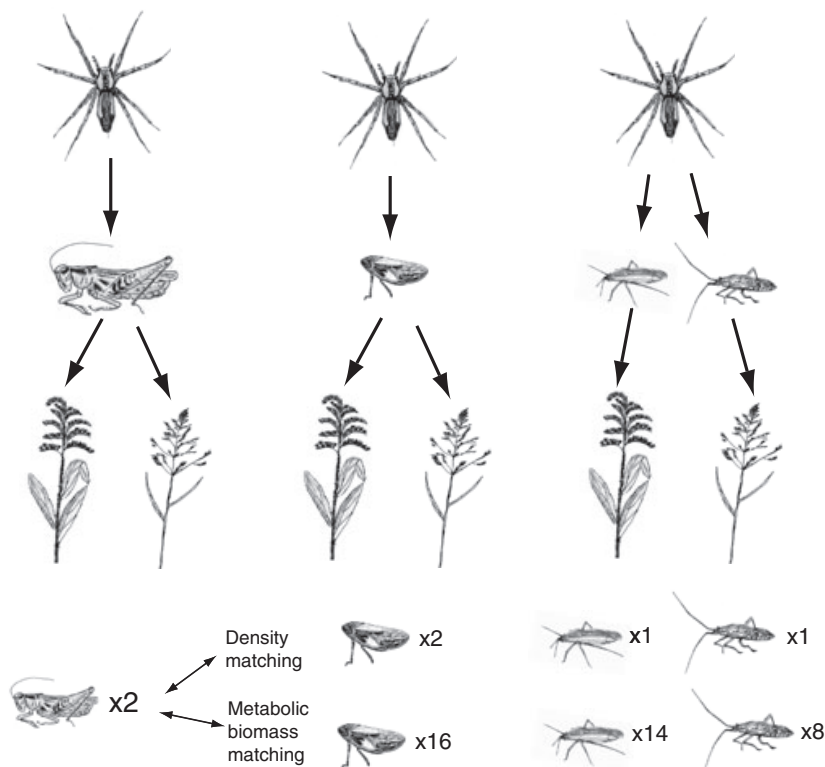
The study was conducted in a 1.5 ha meadow at the Yale-Myers Research Forest in north-eastern Connecticut USA. The most abundant plant species are the competitively dominant perennial herb *Solidago rugosa* and grass *Poa pratensis*. Other herb species include the following: *Chrysanthemum leucanthemum*, *Daucus carota*, *Fragaria canadensis*, *Hieracium aurantiacum*, *Potentilla simplex*, *Rudbeckia hirta*, *Solidago altissima*, *Solidago graminifolia* and *Trifolium repens* (Schmitz 2004). The field site mainly contains two insect herbivore feeding guilds: sap feeders and leaf chewers (Schmitz 2004). The insect herbivores face several species of hunting spider predators that exist in the vegetation layer of the field during the entire summer period (Schmitz 2004).

Long-term research with the arthropod-herbaceous plant food web within the study field revealed that hunting spiders exert indirect control over the plant community by altering herbivore direct effects on the dominant grass *P. pratensis* and a competitively dominant herb *S. rugosa* that suppresses the abundance of other herb species (Schmitz 2010). The strength of that top-down control varies with herbivore species (Schmitz 2008, 2010). Most herbivore species directly affect plants and mediate the top predator effects on plants only weakly (i.e. are weak interactors). The weak interactors are small-bodied (4–10 mg body mass, 4–9 mm body length) herbivores (SHs), with the dominant species being the generalist sap-feeding spittlebug *Philaenus spumarius*, the sap-feeding grass specialist plant bug *Leptopterna dolabrata* and the sap-feeding *Solidago* specialist *Lopidea media*. The strong interactor in this system is the large-bodied herbivore (LH) (200 mg body mass, 17–27 mm body length) the generalist grasshopper *Melanoplus femurrubrum*. We chose to work with these four herbivore species because they were collectively the most abundant herbivores at the field site (Schmitz 2010). Moreover, we could configure them into experimental food webs in such a way as to ensure that a dominant spider predator in our system *Pisaurina mira* could be linked to both functional groups of plants used in our experiments through feeding links between the herbivore species and plants (Fig. 1).

### EXPERIMENT

We compared the direct effects of herbivore species on the two broad functional groups of plants in the study system (Schmitz 2010): grasses and herbs (dominated by *S. rugosa*). We also compared the degree to which herbivore species mediated the strength of top-down cascading effects of the spider predator *P. mira* on those plant functional groups. To those ends, we assembled three kinds of food webs (Fig. 1): one involving the large generalist leaf-chewing grasshopper *M. femurrubrum*; a second involving the small generalist sap-feeding spittlebug *P. spumarius*; and a third involving the small grass specialist plant bug *L. dolabrata* and the small *Solidago* specialist *Lopidea media*.

We compared trophic interaction strengths by equalizing the number of individual herbivores among treatments – which we call density-matching treatments (Fig. 1). We choose a density of two



**Fig. 1.** The configuration of experimental food webs used to examine the strength of direct and indirect effects in a New England meadow system. The experiments involved the same hunting spider predator *Pisaurina mira* and the same herbs (primarily *Solidago rugosa*) and *Poa pratensis* grass. The species were chosen because of their natural dominance in the field and configured in the experimental food webs so that the top predator would be linked to both grasses and herbs among all herbivore treatments. Interaction strengths were compared by altering the mediating herbivore species (from left to right): the large generalist leaf-chewing grasshopper *Melanoplus femurrubrum*; the small generalist sap-feeding spittle bug *Philaenus spumarius*; and the small specialist plant bugs *Lopidea media* and *Leptopterna dolabrata*. The herbivore species were stocked such that there was a matching of total density (density matching) or metabolic biomass (metabolic biomass matching).

individuals of each species because this reflected natural field densities of the grasshopper (field densities of the sap feeding species range between 2 and 3× higher than grasshoppers, O.J. Schmitz, unpublished data). Equalizing herbivore density allowed us to obtain a baseline measure of herbivore species effect, independently of density effects. Moreover, differences in body mass between these species enabled us to compare effects of herbivores with different metabolic biomasses. We also equalized herbivore metabolic biomass through metabolic scaling of individual body mass ( $M$ ) and density – which we call metabolic biomass-matching treatments (Fig. 1). Individual herbivore metabolism (and hence resource demand) and herbivore consumption rate all scale as  $\sim M^{0.75}$  (Peters 1983; Yodzis & Innes 1992; Brose *et al.* 2008; Hillebrand *et al.* 2009; Brose 2010). We equalized herbivore metabolic biomass by stocking densities ( $N$ ) of the SH species within designated treatments such that the product of their metabolic body mass and density (i.e. metabolic biomass) matched that of the LH species, i.e. stocked  $N_{SH}$  such that  $N_{SH}M_{SH}^{0.75} = N_{LH}M_{LH}^{0.75}$  (Fig. 1). In this formula,  $N_{LH} = 2$  when matching the generalist sap feeder, and  $N_{LH} = 1$  to match each of the specialist sap feeders.

The experiment deployed 55, 1.25 m high  $\times$  0.25 m<sup>2</sup> cylindrical mesocosms. The frame of a mesocosm was constructed of 16-gauge vinyl-coated welded wire fencing with a 5.1  $\times$  7.6 cm mesh. Aluminium insect screen was then stapled to the frame. The mesocosms were placed over naturally growing vegetation in the field in which initial proportions of grass and herbs were similar among mesocosm locations. The mesocosms were sunk into the ground by opening a 3 cm wide  $\times$  15 cm deep trench around the circumference of each mesocosm. Each mesocosm was covered by with a 0.6 m<sup>2</sup> piece of fibreglass insect screen stapled to the frame. This design does not introduce significant biases in biophysical conditions (Schmitz 2004).

The mesocosms were arrayed in five replicate blocks with 11 treatments randomly assigned to mesocosms within each block. Quantifying the strength of trophic control in food webs requires assembling

three basic sets of trophic levels (Schmitz 2008, 2010): a plant-only control (1-level); a plant–herbivore treatment (2-level); and a plant–herbivore predator treatment (3-level). We assigned one 1-level control to each block. We assembled five, 2-level treatments (Fig. 1). One 2-level treatment comprised of the large grasshopper herbivore as a reference. Two other treatments matched small herbivore densities to the large herbivore density, and the remaining two matched small herbivore metabolic biomasses to the large herbivore metabolic biomass (Fig. 1). We assembled 5, 3-level treatments that included the spider with herbivore species in the same configurations assembled in the 2-level treatments. The 1-level and 2-level treatments allowed us to quantify direct interaction strengths of herbivores on plants. The 2-level and 3-level treatments allowed us to quantify the degree to which herbivores mediated the strength of indirect effects of the predator on plants (Schmitz 2008).

The 100-day experiment began at the beginning of the growing season in late May by catching arthropods from the study field with a sweep net and stocking them to the mesocosms according to treatment designation. The experiment was terminated at the end of the growing season in early September at which time all aboveground plant biomass was harvested, sorted into functional groups, dried at 70 °C for 48 h and weighed.

We calculated the herbivore species direct effect magnitude (DEM) on end of season plant functional group biomass ( $P_i$ ) within each block ( $B$ ) using the formula (Schmitz, Hambäck & Beckerman 2000)  $DEM = \ln(P_{i2 - levelB}/P_{i1 - levelB})$ . We calculated predator indirect effect magnitude (IEM) on plants mediated by herbivore species using the formula (Schmitz, Hambäck & Beckerman 2000)  $IEM = \ln(P_{i3 - levelB}/P_{i2 - levelB})$ . The magnitudes of direct and indirect effects were calculated for each treatment pair within each block. We then estimated the mean and standard error of effect magnitudes across all blocks. The formulae for DEM and IEM also provide a sign of effect, where + implies the consumer species directly or indirectly enhanced the abundance of the resource species

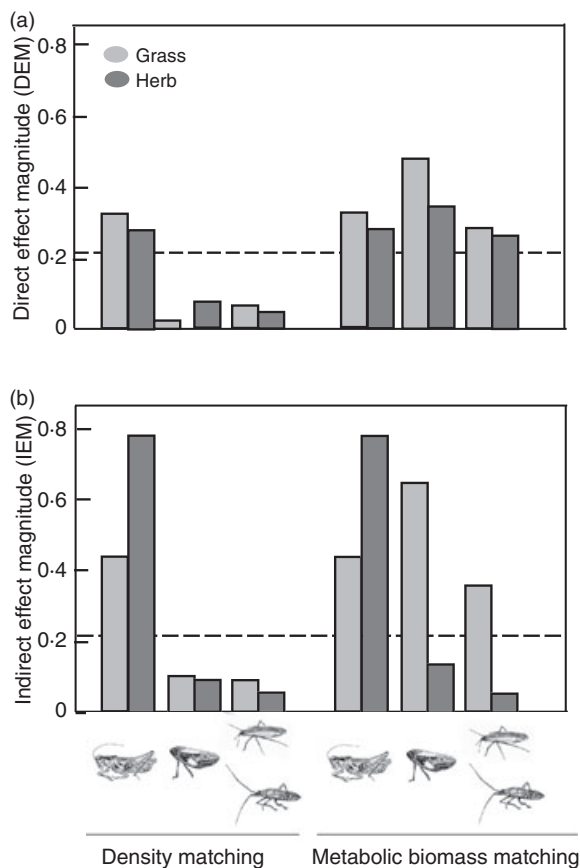
and – implies that the consumer species reduced the resource species' abundance.

We tested whether the DEM and IEM for each species on each plant was significant by testing for a deviation from zero (no net effect). We used one-sample *t*-tests (Bonferroni corrected  $t_{\alpha} = 0.05$ ) to compare the observed mean against the expected mean of 0. For those treatments for which a significant deviation from zero was detected, we tested whether the DEM and IEM differed among herbivore species using a randomized block ANOVA. We tested for differences by plant functional group for DEM and IEM, respectively.

Estimates of DEMs are typically standardized to a per capita basis to estimate species interaction strength for food web analysis (Berlow *et al.* 2004; Wootton & Emmerson 2005; Wood *et al.* 2010). We estimated the per capita interaction strengths of herbivore species *i* on grass and herb plants in two ways. We divided the mean DEM<sub>*i*</sub> by treatment density ( $N_i$ ). We also divided the mean DEM<sub>*i*</sub> by mean herbivore metabolic biomass ( $N_i M_i^{0.75}$ ).

## Results

In the density-matching treatment, the leaf-chewing grasshopper herbivore had significant (non-zero) DEM on grasses and herbs, respectively, whereas the SHs did not (Fig. 2a).



**Fig. 2.** Effect of herbivore species on two functional groups of plants (grasses and herbs) when herbivore species are matched by density and by metabolic biomass. The data are separated into (a) the magnitude of herbivore direct effects (DEM) on plants and (b) the magnitude of herbivore-mediated indirect effects of predators on plants (IEM). Bars falling below the horizontal dashed line are not significantly different from zero.

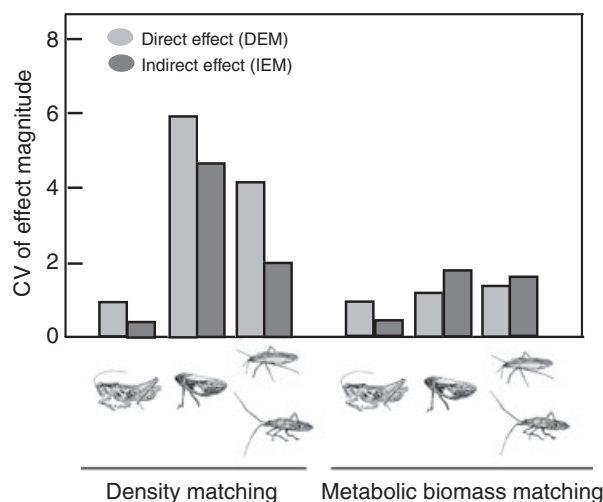
Metabolic biomass matching caused all herbivore species to have significant DEMs on grasses and herbs, respectively. This came about because of a 9–14-fold rise in effect magnitude of SH species (Fig. 2a). Consequently, the DEMs of the SHs on grass and herb did not differ significantly from those of the leaf-chewing grasshopper in the metabolic biomass-matching treatments (both ANOVA's  $P > 0.05$ , d.f. = 2,8).

In the density-matching treatment, the mediated IEM on grasses and herbs was only significant for the leaf-chewing grasshopper (Fig. 2b). Metabolic biomass matching caused a 3–5-fold rise in SH-mediated IEMs on grasses (Fig. 2b). There was no net effect on herbs between the density-matching and metabolic biomass-matching treatments. The strength of mediated indirect effects on grass was not significantly different between sap-feeding and leaf-chewing herbivores in the metabolic biomass-matching treatment (ANOVA  $P > 0.05$ , d.f. = 2,8). However, the mediated IEM of leaf-chewing herbivore on herbs was significantly higher than that of the SH species (ANOVA  $P < 0.05$ , d.f. = 2,8).

The difference in significance of effect magnitudes between density-matching and metabolic biomass-matching treatments did not come about just by a rise in effect magnitude. Metabolic biomass matching also caused the coefficient of variation in effect magnitude to decline by 11% to 75% in comparison with the density-matching treatments (Fig. 3).

Despite the convergence in effect magnitude with convergence in metabolic biomass of herbivore species, the signs of direct and indirect effects remained idiosyncratic to herbivore species (Table 1).

Herbivore per capita interaction strength remained weak between the density-matching and metabolic biomass-matching treatments when per capita effects were calculated on the basis of herbivore density (Table 2). Moreover, the per capita



**Fig. 3.** Effect of experimental treatment (density matching vs. metabolic biomass matching) on the coefficient of variation (CV) of herbivore effect magnitude on plants. The data are divided into CV of the magnitude of herbivore direct effects on plants (direct effect) and CV of the magnitude of herbivore-mediated indirect effects of predators on plants (indirect effect). Values are means for effects on grasses and herbs combined.

**Table 1.** Signs of herbivore direct effect on plant functional groups and signs of the indirect effect of predators on plant functional group biomass mediated by herbivores. The direct effect sign is a reflection of a pairwise consumer–resource interaction. The indirect effect sign is a reflection of emergent food web effects

	Generalist leaf chewer		Generalist sap feeder		Specialist sap feeders	
	Direct	Indirect	Direct	Indirect	Direct	Indirect
Density Matching						
Grass	–	+	0	0	0	0
Herb	–	–	0	0	0	0
Mass Matching						
Grass	–	+	–	+	–	–
Herb	–	–	0	0	+	0

**Table 2.** Estimates of per capita interaction strengths of herbivore species on plants in the density-matching and metabolic biomass-matching treatments. Per capita effects for each species were estimated by dividing the ln ratio direct effect magnitudes (Fig. 2a) either by the treatment densities (Fig. 1) or by treatment metabolic biomass (treatment density  $\times$  body mass<sup>0.75</sup>)

Herbivore species	Density matching		Metabolic biomass matching	
	Grass	Herb	Grass	Herb
Per capita effects based on density				
Generalist leaf chewer	0.16	0.12	0.16	0.12
Generalist sap feeder	0.001	0.04	0.03	0.02
Specialist sap feeders	0.001	0.01	0.01	0.01
Per capita effects based on metabolic biomass				
Generalist leaf chewer	0.60	0.47	0.60	0.47
Generalist sap feeder	0.04	0.15	0.94	0.07
Specialist sap feeders	0.02	0.24	0.54	0.43

interaction strengths of SHs were consistently weaker than the per capita interaction strength of the generalist leaf-chewing herbivore. However, a different picture emerged when per capita effects were scaled by metabolic biomass (Table 2). Now, per capita effects of sap feeders remained weaker than the LH in the density-matching treatment but became equal in the metabolic biomass-matching treatment.

## Discussion

Research evaluating the effect of consumer mass on interaction strength has capitalized on natural size variation among different consumers and resource species sizes to assess patterns of interaction strengths within and across environmental contexts (Emmerson & Raffaelli 2004; Wootton & Emmerson 2005; Brose *et al.* 2006; Berlow *et al.* 2009; Hillebrand *et al.* 2009; Wood *et al.* 2010). These studies have found significant relationships between interspecific consumer size – and more specifically metabolic body mass – and interspecific interaction strengths. We provide complementary experimental insight through a test of the hypothesis that the strength of

direct species interactions in food webs is positively related to metabolism through the body mass of consumer species. We directly manipulated densities of the same herbivore species within the same system to equalize metabolic biomass and measured their corresponding strengths and nature of direct and indirect effects on that system.

We found that equalizing herbivore metabolic biomasses caused a rise in and convergence of effect magnitudes among herbivore species, relative to the density-matching treatment (Fig. 2). One interpretation for this outcome is that metabolic scaling of mass also altered the per capita interaction strength of consumers on resources. The alternative interpretation is that the rise in effect magnitude resulted merely from an increase in the density of individual consumers with fixed per capita effects. If this were the case, however, then the per capita interaction strengths based on density for the SH species should be identical between the density-matching and metabolic biomass-matching treatments. Instead, they are quite different (Table 2), which indicates that the increased herbivore species effects on plants arose from more than simply a change in herbivore density. Indeed, the densities in our experiments were precisely adjusted based on allometric scaling of body mass and metabolism to ensure that in the metabolic biomass-matching treatment all herbivore species were equally constrained in their resource consumption. Such scaling should lead to mass-dependent differences in per capita interaction strength between the density-matching and metabolic biomass-matching treatments, which is observed in our study (Table 2). This underscores that interpretation of consumer effects in food webs will depend on the biological properties (e.g. species density vs. biomass) on which one bases calculations of per capita interaction strengths (Berlow *et al.* 2004; Wootton & Emmerson 2005; see also Table 2). Our results support earlier ideas that metabolic body mass is the appropriate basis on which to estimate per capita interaction strength because it reflects constraints on the capacity for consumer species to impact resources because of allometric relationships among body mass, metabolic demand and consumption (Yodzis & Innes 1992; Brose 2010).

Our observation of a rise in interaction strength with increasing herbivore biomass does not conform to the general theoretical prediction that the relationship between interaction strength and consumer biomass (and by extension scaled metabolic biomass) is hump shaped and hence not generally positive (Aljetlawi, Sparrevik & Leonardsson 2004; Brose *et al.* 2008; Vucic-Pestic *et al.* 2010). This difference between observation and theory may have arisen either because there is no hump-shaped relationship in our system or that the species chosen for our study have body masses that would cause them only to fall along the increasing part of a hump-shaped relationship.

If we metaphorically consider herbivore metabolic biomass to collectively represent the functional consumptive unit of herbivores, then our experiment may also provide a test of theory (Shurin & Seabloom 2005) that the strength of predator indirect effect on plants mediated by herbivores (so-called trophic cascade strength) should become stronger

when the size ratio of herbivores to plants increases. In our experiment, increasing herbivore biomass through metabolic scaling effectively increased the size ratio between sap feeders and their plants. Consistent with the theoretical expectations (Shurin & Seabloom 2005), this mass increase, in turn, leads to an increase in the strength of predator indirect effects, at least on grasses (Fig. 2b).

While the altered magnitudes of direct and indirect effects resulted from alteration of herbivore biomass, there was a contributing factor to the overall statistical significance of effect magnitudes. In many instances, variation among replicates within experimental treatments is large owing to spatial variation in plot or site condition (i.e. context dependency of local sites [Schmitz 2010; Wood *et al.* 2010; ]). This variation, coupled with the potential for small consumers to have weak effects, often results in measured effect magnitudes that do not differ statistically from zero. We found that increasing herbivore metabolic biomass tended to decrease the magnitude of variation in DEMs and IEMs (Fig. 3). Thus, increasing herbivore biomass not only strengthened the direct and indirect effects on plants but also made those effects more consistent among plot sites (i.e. diminished effects of context dependency). This may have come about because under natural field densities, the leaf-chewing grasshopper roams widely through the vegetation and thus has a broad and even impact on the vegetation, whereas SH species tend to be sedentary and create patchy impacts. However, the high densities of SHs needed to accomplish metabolic biomass matching of herbivore treatments may have caused the SHs to spread broadly throughout the vegetation and thus have a more even (less variable) impact.

In our experiment, the signs of herbivore species direct effects differed within and between the density-matching and metabolic biomass-matching treatments (Table 1). This difference also translated into different indirect effects among herbivore species within and between treatments (Table 1). Thus, herbivore metabolic biomass cannot explain the sign of the direct effects on plants nor how herbivores mediated predator indirect effects on plants. This result differs from outcomes observed in simulation studies presented by Berlow *et al.* (2009). We suggest that herbivore feeding mode (e.g. sap feeding vs. leaf chewing; generalist vs. specialists) may explain the difference between our results and those of Berlow *et al.* (2009) who did not consider feeding mode. Feeding mode is a trait that may determine how herbivores interact with their predators, and hence, the way herbivores mediate top-down effects in food webs because herbivores maintain nutrient balance in different ways that are related to their feeding mode (Schmitz 2008, 2010). Leaf-chewing herbivores consume structural tissues that tend to be high in carbon (comparatively poor quality). They regulate their intake of different plant species and parts to achieve balanced nutritional intake. This requires being selective in resource choice and thereby moving widely to encounter suitable, high-quality (e.g. N-rich grass) plant tissue. This roaming behaviour also means that they are able to avoid predation risk by switching to refuge habitats like leafy herbs (Schmitz 2008,

2010) and hence the positive indirect effect of predators on grass and negative indirect effect on herbs (Table 1). Sap-feeding insects do not ingest structural tissue but instead have high daily feeding rates by moving large amounts of fluids through their bodies. Sap-feeding species remain comparatively stationary once they have found a resource-rich host plant, and so we hypothesize that they may be unlikely to switch to alternative resources when facing predators. This is consistent with the observation that the addition of predators did not cause SHs to lessen impact on one plant functional group and increase impact on another (Table 1).

Our findings help to reinforce an emerging empirical consensus that consumer metabolic body mass is likely a key determinant of the strength of consumer direct interactions on resources and hence a reasonable surrogate measure (Emmerson & Raffaelli 2004) to obtain quantitative understanding of trophic interactions in food webs. Nevertheless, we also show that metabolic body mass alone cannot completely explain variation in the nature and strength of indirect effects in food webs. Such understanding will require additional consideration of consumer traits like foraging mode that determines the nature of herbivore resource selection and hence movement behaviour (Schmitz 2010). This argues further for developing empirical approaches to food web analysis that nuance size-based measures of interaction strength with consumer behavioural ecology (Ings *et al.* 2009; Beckerman, Petchey & Morin 2010).

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