

# Beyond diversity: how nested predator effects control ecosystem functions

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## Summary

**1.** The global decline in biodiversity is especially evident in higher trophic levels as predators display higher sensitivity to environmental change than organisms from lower trophic levels. This is even more alarming given the paucity of knowledge about the role of individual predator species in sustaining ecosystem functioning.

**2.** The effect of predator diversity on lower trophic level prey is often driven by the increasing chance of including the most influential species. Furthermore, intraguild predation can cause trophic cascades with net positive effects on basal prey. As a consequence, the effects of losing a predator species appear to be idiosyncratic and it becomes unpredictable how the community's net effect on lower trophic levels changes when species number is declining.

**3.** We performed a full factorial microcosm experiment with litter layer arthropods to measure the effects of predator diversity and context-dependent identity effects on a detritivore population and microbial biomass.

**4.** We show that major parts of the observed diversity effect can be assigned to the increasing likelihood of including the most influential predator. Further, the presence of a second predator feeding on the first predator dampens this dominant effect. Including this intraguild predator on top of the first predator is more likely with increasing predator diversity as well. Thus, the overall pattern can be explained by a second identity effect, which is nested into the first.

**5.** When losing a predator from the community, the response of the lower trophic level is highly dependent on the remaining predator species. We mechanistically explain the net effects of the predator community on lower trophic levels by nested effects of predator identities. These identity effects become predictable when taking the species' body masses into account. This provides a new mechanistic perspective describing ecosystem functioning as a consequence of species composition and yields an understanding beyond simple effects of biodiversity.

**Key-words:** biodiversity–ecosystem functioning, body size, multi-trophic, sampling effect, species identity, species richness, trophic cascade

## Introduction

The relationship between biodiversity and ecosystem functioning (B–EF) has become a major topic of ecological research (Hooper *et al.* 2005; Balvanera *et al.* 2006), and its economic consequences have gained attention at a global-political scale (Huston 1997). Research addressed this topic early in plant diversity–productivity experiments (Tilman & Downing 1994) and subsequently included the effects of predator communities on lower trophic levels (Finke & Denno 2004; Schmitz 2007). The

latter, however, is still underrepresented in experimental and theoretical studies (Balvanera *et al.* 2006; Letourneau *et al.* 2009). Some previous studies have been aimed at partitioning B–EF into three types of effects: the fixed effect of a particular species ('identity effect'), the effect of a particular species in the context of a particular community ('composition effect') and the effect of altering the continuous parameter species richness *per se* ('diversity effect') (Sih, Englund & Wooster 1998; Loreau & Hector 2001; Fox 2005, 2006; Bell *et al.* 2009). This descriptive approach can help to quantify the partitioned effects well for competitive plant communities, but is limited in explanatory power when including multi-trophic

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interactions, where indirect effects among species render direct contributions of single species intangible (Sih, Englund & Wooster 1998; Reiss *et al.* 2009, 2011). To standardise the three types of effects in multi-predator communities, recent approaches apply elaborate experimental designs accounting for individual and biomass density (Bell *et al.* 2009; Byrnes & Stachowicz 2009; Reiss *et al.* 2009, 2011) and develop theory to connect underlying trophic mechanisms and ecosystem patterns (Thébault & Loreau 2003; Ives, Cardinale & Snyder 2005). In a recent study, however, Reiss *et al.* (2011) could show that fundamentally different linear modelling approaches are required to separate the effects of consumers in diversity experiments.

Here, we apply a mechanistic perspective and assume that the B–EF pattern emerges only from the trophic interactions of the predator species. From this mechanistic viewpoint, identity effects manifest as systematic sampling-probability effects, as the chance of including a particular species identity increases systematically with species diversity (Duffy 2002; Ives, Cardinale & Snyder 2005). In this way, a single species with strong influence on ecosystem functioning might shape the observed overall B–EF relationship (a ‘sampling effect’; Huston 1997; Tilman, Lehman & Thomson 1997). However, this concept fails to predict ecosystem functioning by species diversity if multiple predator species interact antagonistically or synergistically to yield a community effect which is smaller or larger than the sum of their individual effects (Ives, Cardinale & Snyder 2005). This phenomenon occurs commonly in communities of generalist predators, where indirect effects among species are caused by intraguild predation (Sih, Englund & Wooster 1998; Finke & Denno 2004; Bell *et al.* 2009; Worsfold, Warren & Petchey 2009). Predators may control the biomass and abundance of their direct prey species, but they can also consume each other, which dampens the net effect on the basal prey species (Finke & Denno 2004). Depending on the relative feeding rates within this three-species motif, this yields indirect cascading effects of variable intensity (Halaj & Wise 2001; Borer *et al.* 2005). The net effect of a predator on a basal prey is the sum of its direct feeding and the positive indirect effects mediated by intraguild predation. Therefore, the sign of a predator’s net effect should depend on the food-web context. For generalist consumer communities, the number of intraguild-predation motifs should increase with diversity rendering predictions of effects on ecosystem functions highly uncertain. As a consequence, positive and negative net effects of increasing predator diversity on the lower trophic level were observed empirically, with a skew towards positive effects (Schmitz 2007; Letourneau *et al.* 2009). How these trophic mechanisms interact in concert to shape the net effect of the whole predator community remains a fundamental gap in our knowledge.

Interestingly, in previous studies, the mechanisms determining feeding rates (Brose *et al.* 2008; Vucic-Pestic *et al.* 2010; Rall *et al.* 2011), intraguild predation (also

‘omnivory’; Digel, Riede & Brose 2011; Riede *et al.* 2011) and food web structure (Petchey *et al.* 2008) were all related to the species’ body masses. In a prior study, we integrated these concepts to show that the feeding rates and the resulting net effects of losing single predators on lower trophic levels can be explained by simple allometric constraints (Schneider, Scheu & Brose 2012). These constraints predict the identity effect of each predator within a species community only based on body mass by differentiating diet breadth and feeding rates. Thus, depending on the species body mass and the food web context, the identity effect of a particular species may be negative (if feeding directly on the basal prey), positive (if triggering a trophic cascade via intraguild predation) or neutral (if direct and indirect effects cancel each other out; Schneider, Scheu & Brose 2012).

In this study, we now adopt this mechanistic perspective to decompose the effects of multiple predators on the lower trophic levels while systematically varying consumer diversity. We carried out a full factorial microcosm experiment with three generalist predators of the litter layer of deciduous forests and hypothesised that predator diversity effects can be explained by nested identity effects of the predator species. Thus, we assume that the net effect of consumer diversity is emerging only from the identities of the interacting species instead of from species richness *per se*. With this approach, we go beyond a simple description of the relationship between species diversity and ecosystem functioning by unravelling nested levels of predator composition and providing a mechanistic understanding of multiple trophic effects in a predator community.

## Materials and methods

### EXPERIMENT

Our experiment focused on the predator community of the litter layer of terrestrial ecosystems which comprises generalist arthropods. We set up an experimental microcosm system with three predator species of different body masses: the large centipede *Lithobius forficatus* Linnaeus, 1758, the intermediately sized spider *Pardosa lugubris* (Walckenaer, 1802) and the small mite *Hypoaspis miles* (Berlese, 1892). The population of the detritivore springtail *Heteromurus nitidus* (Templeton, 1835) and the microbial biomass on the litter served as a proxy for the ecosystem function of decomposition.

The acrylic-glass microcosms were sized 30 × 30 × 15 cm. A layer of dental cast containing activated charcoal was added to buffer the moisture. The filling of soil (1000 g) and dry grassland litter (12 g) was defaunated and inoculated twice with a population of 50 springtails at four and two weeks before initiation of the predators. The experiment took place in a controlled greenhouse climate chamber, with temperature varying between 15 °C at night and up to 22 °C during the day (total average 16.2 °C). Humidity was automatically regulated to approximately 70%.

The centipedes and spiders were caught by hand in the field and weighed individually (average body mass:  $m_{\text{centipedes}} = 0.125 \text{ g} \pm 0.041 \text{ SD}$ ,  $n = 84$ ;  $m_{\text{spiders}} = 0.026 \text{ g} \pm 0.006$

SD,  $n = 42$ ). The mites were purchased at Katz Biotech AG (Baruth, Germany). The springtails were reared in laboratory cultures. Average body masses of mites and springtails were obtained by pooled weighing ( $m_{\text{mites}} = 0.00016$  g,  $n = 366$ ;  $m_{\text{springtails}} = 0.00010$  g,  $n = 553$ ; obtained from dry weight, multiplied by water fraction factor 4 after Peters 1983).

The three predators were combined in a full factorial treatment design, that is, each possible combination of predators was realised, yielding a gradient from 0 to 3 predator species. An additive allometric design was applied (Schneider, Scheu & Brose 2012). Therefore, for each predator  $i$ , the initial population density,  $N_i$ , was defined from a negative  $\frac{3}{4}$  power law with average body mass,  $m_i$  ( $N_i = 0.5 m_i^{-0.75}$ ). This yields two individuals of centipedes, eight spiders (reduced to four to prevent cannibalism) and 350 mites per microcosm. These densities were combined additively in the different diversity treatment levels. The negative  $\frac{3}{4}$  exponent is an *a priori* definition which affects the biomasses and consequently the energetic balance between the predator species during the experiment, and thus affects the measured identity effect (Griffiths *et al.* 2008; Schneider, Scheu & Brose 2012). It is a conservative estimate from naturally observed mass–abundance relationships (Peters 1983) which may be much shallower on local scales (around  $1/4$ ; White *et al.* 2007). Nonetheless, classical fixed-density or fixed-biomass designs would imply exponents of 0 or  $-1$ , respectively, which most certainly would bias the measured identity effects. Therefore, the allometric design produces identity effects much closer to those measured in removal experiments or in experiments using field densities (e.g. Finke & Denno 2004).

The centipedes and spiders were weighed individually before and after the experiment. At the end of the experiment, the mites and springtails were extracted by heat (Macfadyen 1961) from one quarter of the microcosm content into saline solution to count their abundances. The biomass was estimated by multiplying abundances with their average body mass. Microbial biomass on the litter layer was estimated from a fresh sample (2.8 g) taken at the end of the experiment by measuring substrate-induced  $O_2$  consumption in an electrolytic microrespirometer (Scheu 1992; Beck *et al.* 1997).

## LINEAR MODELLING

Data analyses were performed with R 2.14.0 (R Development Core Team 2011). To account for heteroscedasticity, the abundance of springtails (ind. microcosm $^{-1}$ ) was  $\log_{10}$ -transformed before analyses. An explorative linear modelling approach was chosen to test whether a significant effect of the continuous parameter predator diversity on  $\log_{10}$  springtail abundance per microcosm (subsequently springtail density) can be detected within different subsets of predator composition. First, we assumed a linear null model which explains springtail density,  $N$ , just by predator species diversity  $S$  (subsequently ‘null model’). The model equation

$$N = a + bS + \varepsilon, \quad \text{eqn 1}$$

is defined by the intercept  $a$ , the slope  $b$  and the normally distributed residual error  $\varepsilon$ . This equation was fitted to the observed data using least squares regression. The slope  $b$  was tested for significance by applying a two-tailed Student’s  $t$ -test. Insignificance would indicate a lack of any diversity effect. Alternatively, the

linear effect of predator diversity was nested into different levels of a factorial parameter predator composition,  $C$ , yielding

$$N = a_C + b_C S + \varepsilon, \quad \text{eqn 2}$$

a model predicting  $N$  within composition by one intercept  $a$  and one slope  $b$  for each level of  $C$ . This procedure is equivalent to the fit of an ANCOVA but instead of testing the overall significance of the parameters is testing the significance of the obtained coefficients (slopes and intercepts) by  $t$ -tests (Crawley 2007). Significant slopes would indicate unexplained diversity effects within the subsets; for example, if a diversity effect in the null model emerged only from an identity effect of species  $i$ , the slopes in the compositional subsets with species  $i$ ,  $b_{+i}$  and without  $i$ ,  $b_{-i}$  would be insignificant.

In a first step, three identity models were fitted to the data to test if any predator identity exerts a dominant effect on springtail density. Therefore, for each predator  $i$ ,  $C$  either takes the value ‘+ $i$ ’ for a replicate containing  $i$  or the value ‘- $i$ ’ for a replicate lacking  $i$ . The three identity models and the null model were compared via Akaike Information Criterion (AIC). Among these models, the best explanatory identity model (with lowest AIC) was chosen for further analyses. If any  $b_C$  was significant, this level of composition was further extended by including a second predator identity  $j$ ; for example, if  $b_{-i}$  is insignificant and  $b_{+i}$  is significant,  $C$  was extended to take one of the three levels ‘- $i$ ’, ‘+ $i$  - $j$ ’ or ‘+ $i$  + $j$ ’. In case of the two latter subsets, the slope describes the difference in means of the two treatments included in this particular composition level.

This analysis targeted the question of which composition model of the three predators could remove (and thus explain) the overall diversity effect from the null model. A model that lacks significance in all  $b_C$  allowed discarding the parameter diversity from the model. Thus,

$$N = a_C + \varepsilon \quad \text{eqn 3}$$

would be assumed as the most parsimonious model explaining variance in the springtail population only by the different levels of predator composition. Subsequently, differences in springtail density and litter microbial biomass across these levels of predator composition were tested by Tukey’s HSD *post hoc* comparison of means.

## Results

A full factorial experimental design of all possible predator combinations allowed identification of the composition effects by nesting linear models within different subsets of predator composition. First, a null model that did not include predator identity as an explanatory parameter indicated a significant negative effect of predator diversity on springtail density, explaining 12.7% of the variation (probability of  $b$  being different from 0:  $P = 0.024$ , Std. Error = 0.087, two-tailed  $t$ -test, AIC = 55.20, Table 1; Fig. 1a). The AIC-based model comparison of the null model with the three identity models indicated whether the use of the particular predator identity as an explanatory for the prediction of springtail density was justified (Tables 1 and 2). The identity model

with spiders explained more variation than the null model, but the higher AIC renders the use of this predator composition variable unwarranted ( $R^2 = 18.2\%$ , AIC = 56.60). Furthermore, the effect of diversity within the treatments without spiders remained significantly negative ( $P = 0.040$ , SE = 0.361, Table 2; Fig. 1b). Including the centipedes in the model improved the prediction ( $R^2 = 38.1\%$ , AIC = 45.45), although the diversity effects remained significantly negative (Table 2; Fig. 1c). Finally, the identity model including the presence and absence of mites scored better than all previous models ( $R^2 = 69.5\%$ ; AIC = 17.09). In addition, there was no significant diversity effect in treatments without mites ( $P = 0.694$ , SE = 0.088, Table 2; Fig. 1d, open symbols).

**Table 1.** The null model describes  $\log_{10}$  springtail density,  $N$ , as a linear function of species number,  $S$  ( $N = a + bS$ )

	Estimate	SE	<i>t</i> -Value	<i>P</i> -value
Intercept <i>a</i>	3.728	0.145	25.62	<0.001***
Slope <i>b</i>	-0.204	0.087	-2.35	0.024*
d.f./ $R^2$ /AIC	3/12.7%/55.20			

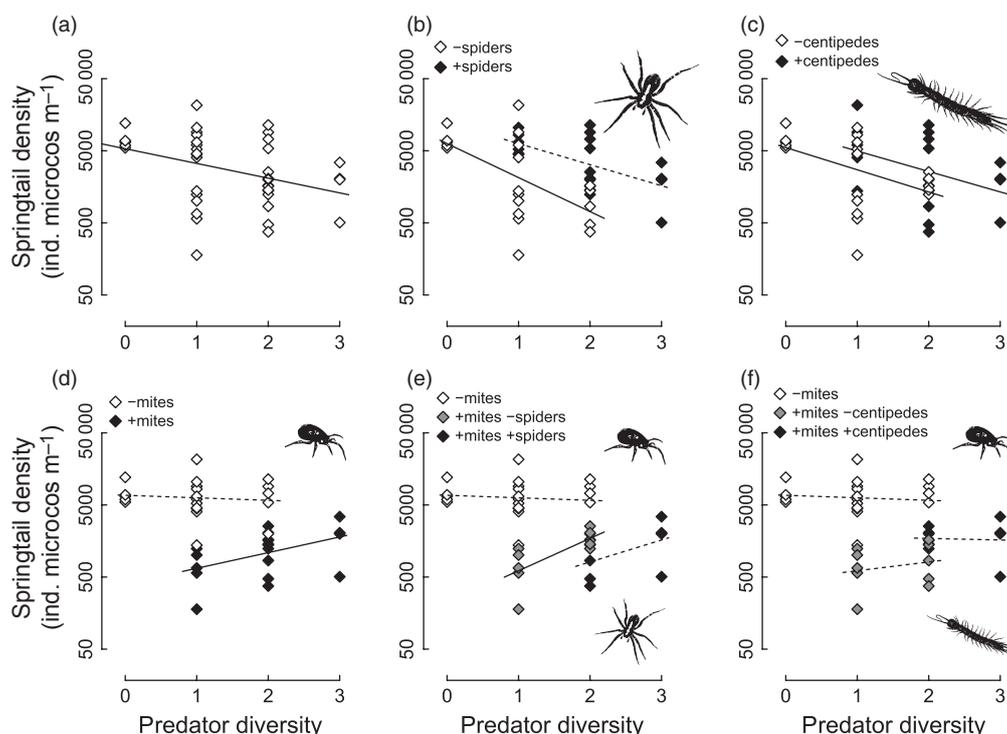
The *t*-statistic gives the probability of the estimates equalling zero (two-tailed *t*-tests). Asterisks denote the level of significance: \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ .

d.f., number of parameters used by the model;  $R^2$ , coefficient of determination; AIC, Akaike Information Criterion.

However, there was a positive diversity effect within the subset of experimental units containing mites ( $P = 0.025$ , SE = 0.093, Table 2; Fig. 1d, filled symbols). This implies that predator diversity increased the detritivore abundance in treatments with mites present.

To further explore the positive diversity effect in the subset including mites, we nested a second predator *j* (either spiders or centipedes) into the identity model and tested for diversity effects within three levels of predator composition *C*: '-mites', '+mites -*j*' and '+mites +*j*'. If including the spider as a second predator *j*, there remained a significant unexplained diversity effect within the composition subset '+mites -spiders' ( $P = 0.013$ , SE = 0.172, Table 3; Fig. 1e). Subdividing the set of replicates containing mites by the presence and absence of centipedes yielded a composition model lacking significant diversity effects ( $b_{+mites +centipedes}$ :  $P = 0.904$ ;  $b_{+mites -centipedes}$ :  $P = 0.483$ , Table 3; Fig. 1f). Note that both models ended up with the same coefficient of determination ( $R^2 = 72.7\%$ , AIC = 16.69) because the slopes within the subsets equal the difference in means of the two included treatments within each composition subset.

What validates the model with mites and centipedes over the model with mites and spiders is the lack of any significant diversity slope  $b_C$  in the first. This means, all effects of increasing diversity can finally be attributed to the difference in the three levels of species composition. Hence, the most parsimonious model explained 72.2% of



**Fig. 1.** Linear models describe springtail density in dependence of predator diversity and predator composition: (a) null model; diversity effect within subsets (b) with and without spiders, (c) with and without centipedes, (d) with and without mites. The mites explain most of the variance in springtail density. The subset with mites is further divided into subsets (e) with and without spiders and (f) with and without centipedes. The latter explains all observed diversity effects. Broken lines have insignificant slopes ( $P > 0.05$ ; two-tailed *t*-test).

**Table 2.** Springtail density,  $N$ , as linear effect of predator species number,  $S$ , within the subsets of predator composition,  $C$  ( $N = a_C + b_C S$ )

	$i = \text{Centipedes}$				$i = \text{Spiders}$				$i = \text{Mites}$			
	Estimate	SE	$t$ -Value	$P$ -value	Estimate	SE	$t$ -Value	$P$ -value	Estimate	SE	$t$ -Value	$P$ -value
$a_{-i}$	3.798	0.154	24.69	< 0.001***	3.743	0.176	21.34	< 0.001***	3.833	0.107	35.80	< 0.001***
$a_{+i}$	0.293	0.300	0.98	0.335	0.236	0.361	0.65	0.517	-1.231	0.220	-5.59	< 0.001***
Effect of $S$ within $C$												
$b_{-i}$	-0.471	0.126	-3.75	0.001***	-0.308	0.144	-2.13	0.040*	-0.035	0.088	-0.40	0.694
$b_{+i}$	-0.292	0.127	-2.30	0.027*	-0.284	0.153	-1.86	0.071	0.217	0.093	2.33	0.025*
d.f./ $R^2$ /AIC	5/38.1%/45.45				5/18.2%/56.60				5/69.5%/17.09			

Here,  $C$  can take the value '+ $i$ ' for replicates containing species  $i$  and '- $i$ ' for replicates lacking species  $i$ . The tables were generated with the R-function `summary.lm()`, showing the probability of  $a_{-i}$  to be zero, of  $a_{+i}$  to be  $a_{-i}$  and of  $b_{-i}$  and  $b_{+i}$  to be zero (two-tailed  $t$ -tests). Asterisks denote the level of significance: \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ .

d.f., number of parameters used by the model;  $R^2$ , coefficient of determination; AIC, Akaike Information Criterion.

**Table 3.** Extended linear models for springtail density using three levels of predator composition,  $C$  ( $N = a_C + b_C S$ )

	$j = \text{Centipedes}$				$j = \text{Spiders}$			
	Estimate	SE	$t$ -Value	$P$ -value	Estimate	SE	$t$ -Value	$P$ -value
$a_{-mites}$	3.833	0.104	36.76	< 0.001***	3.833	0.104	36.76	< 0.001***
$a_{+mites -j}$	-1.169	0.291	-4.02	< 0.001***	-1.495	0.291	-5.14	< 0.001***
$a_{+mites +j}$	-0.554	0.466	-1.19	0.243	-1.534	0.466	-3.29	0.002**
Effect of $S$ within $C$								
$b_{-mites}$	-0.035	0.086	-0.41	0.686	-0.035	0.086	-0.41	0.686
$b_{+mites -j}$	0.122	0.172	0.71	0.483	0.449	0.172	2.61	0.013*
$b_{+mites +j}$	-0.022	0.182	-0.12	0.904	0.305	0.182	1.67	0.103
d.f./ $R^2$ /AIC	7/72.7%/16.69				7/72.7%/16.69			

Here,  $C$  can take the value '-mites', '+mites - $j$ ' for replicates containing species  $j$  besides mites and '+mites - $j$ ' for replicates lacking species  $j$  while containing mites. The probabilities corresponds to Table 2, but with three levels for  $C$ . Asterisks denote the level of significance: \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ .

d.f., number of parameters used by the model;  $R^2$ , coefficient of determination; AIC, Akaike Information Criterion.

**Table 4.** Final model describing springtail density,  $S$ , by three levels of predator composition,  $C$ , omitting predator species number ( $N = b_C S$ )

	Estimate	SE	$t$ -Value	$P$ -value
$a_{-mites}$	3.798	0.057	66.23	< 0.001***
$a_{+mites -centipedes}$	-0.951	0.101	-9.42	< 0.001***
$a_{+mites +centipedes}$	-0.573	0.105	-5.47	< 0.001***
d.f./ $R^2$ /AIC	5/72.2%/11.48			

d.f., number of parameters used by the model;  $R^2$ , coefficient of determination; AIC, Akaike Information Criterion.

Asterisks denote the level of significance: \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$

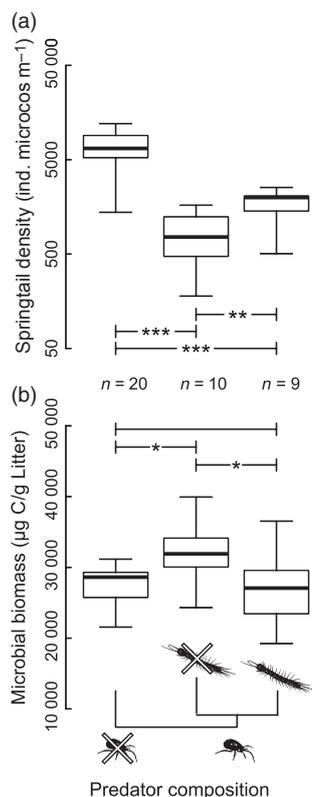
the variation in springtail density by the three levels of predator composition '-mites', '+mites -centipedes' and '+mites +centipedes' while discarding predator diversity (AIC = 11.48; Fig. 2a). Describing springtail density by model equation 3, using one mean value,  $a$ , for each level of predator composition,  $C$ , yielded highly significant parameters (Table 4,  $a_{+mites -centipedes}$ :  $P < 0.001$ , SE = 0.101;  $a_{+mites +centipedes}$ :  $P < 0.001$ , SE = 0.105). A Tukey's

HSD *post hoc* test showed that all levels of predator composition differed significantly in pair-wise comparison (Fig. 2a). This indicates two nested predator effects: First, mites reduced springtail density. Second, if mites were present, centipedes enhanced springtail density. The effect of predator diversity on springtail density (Fig. 1) emerges from these nested predator effects.

Interestingly, the predator effects on springtails cascaded to the next lower trophic level composed of microorganisms: The composition level '+mite -centipede' resulted in significantly higher microbial biomass than the treatments without mites and treatments containing both predators ( $P < 0.05$ , Tukey's HSD; Fig. 2b). The latter two did not differ significantly. This indicates that microbial biomass responded significantly to the composition of the predator community.

## Discussion

There is a need for an integrated understanding of the multiple mechanisms that drive the B-EF correlation. In this study, we investigated the interactive nature of single



**Fig. 2.** (a) The most parsimonious model describes springtail density by three levels of predator composition '–mites', '+mites –centipedes' and '+mites +centipedes'. (b) The microbial biomass responds anti-parallel to the predator composition levels. Asterisks show  $P$ -values from Tukey's HSD test: \* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ .  $n$ , Number of replicates contained in the subsets of predator composition.

species' identity effects in producing the community's net effect on lower trophic levels. The apparent effect of predator diversity on springtail density in our experiment was due to counteracting effects of differing predator identities. As a first identity effect, the probability of randomly drawing a replicate including mites increased with predator diversity, which caused the overall negative relationship. As a second effect, in replicates including mites, the likelihood of drawing a replicate containing centipedes increased with predator diversity yielding a reduction in the overall net effect. Thus, we found that changes in predator diversity affect ecosystem functioning via nested effects of predator identity.

With our explorative modelling, we unravelled the distinction in predator composition that most effectively describes the variation in ecosystem functioning. The final model explained 72.2 % of the variation in the springtail density. In contrast to other modelling approaches (Fox 2005, 2006; Bell *et al.* 2009), our linear modelling approach does not assume a diversity effect *per se*. Instead, all of the non-random variation in ecosystem function is assigned to few nested composition levels. In this approach, any unexplained diversity slope in a composition level would finally be explained by subdividing

the composition level into further sublevels. For example, in the case of the model with mites and spiders, there remains a positive slope in the subset ' $b_{+mites -spiders}$ ' (Table 3), which would finally be explained by a model which further subdivides into five explanatory levels of predator composition and omits diversity as an explanatory variable. However, this model would be less efficient (d.f. = 6;  $R^2 = 70.3$ ; AIC = 16.03) than the final model. The analyses presented here provide a mechanistic insight into the nested and interdependent effects of the predators reaching beyond diversity effects.

From an ecosystem perspective, the loss of one randomly selected predator species from the experimental three-predator food web has unpredictable consequences: If spiders become extinct, no significant changes in detritivore abundance will be expected; if centipedes become extinct, detritivores should decrease in abundance, because mites are released from a top-down pressure; if the mites become extinct, detritivores will be enhanced in abundance. In a prior study, these apparently idiosyncratic effects were assigned to the predators' body masses (Schneider, Scheu & Brose 2012). Simple allometric constraints differentiate the predators' prey range and preference for intraguild feeding in two ways. First, predators feed preferably on prey of a certain body mass, with decreasing intensity towards smaller as well as larger prey (Brose *et al.* 2008; Vucic-Pestic *et al.* 2010). Second, small predators are present in higher abundances than large predators due to individual metabolism (White *et al.* 2007; Ehnes, Rall & Brose 2011). Consequently, relatively small predators should diminish the shared resource, whereas large predators should affect the resource positively due to intraguild predation.

Our study disentangles the interplay of differently sized predator species with increasingly complex food web structures. The experiment required a full factorial manipulation of predator composition to provide a mechanistic insight into the effect of predator species assemblages on lower trophic levels. In this vein, the community net effect emerged from the body-mass structure of the increasingly diverse food web. On the one hand, increasing diversity increased the net effect on the lower trophic level by direct feeding of small predators but on the other hand, this dampened the effect of direct feeding by enhancing intraguild predation by large predators. These effects triggered down to the basal microbial resource.

The logistic limitations of full factorial designs inhibited a wider range of species diversity, but future studies will need to scale up the mechanistic understanding obtained here to higher levels of predator diversity. Currently there are, to our knowledge, no multi-trophic diversity experiments that cover a much wider range of species richness (Cardinale *et al.* 2009), but model simulations may provide a tool for scaling up small-scale experiments to natural diversity levels (Ives, Cardinale & Snyder 2005; Cardinale *et al.* 2009; Loreau 2010). Our results suggest that it will be necessary to model the indirect effects that

are inherent to multi-trophic food webs, to achieve a realistic prediction of ecosystem functioning.

Interestingly, our results are consistent with prior field studies of the forest litter layer, where detritivores were shown to be bottom-up regulated (Scheu & Schaefer 1998; Oelbermann, Langel & Scheu 2008) despite the presence of a diverse generalist predator community. Community-level trophic cascades (sensu Polis 1999; Polis *et al.* 2000) appear to be of minor relevance in litter food webs (Mikola & Setälä 1998; Scheu & Setälä 2002). However, Ponsard, Arditì & Jost (2000) point out that bottom-up control by detritus availability indicates the presence of an effect-reducing mechanism within the predator community. Our finding of a four-level cascading effect ('species-level cascade' sensu Polis 1999; Polis *et al.* 2000) implies that intraguild predation provides a mechanism that suppresses top-down control on decomposers in the litter food web. Because predators within the litter layer are predominantly generalists, intraguild predation is widespread, which has been shown by stable isotope analyses (Ponsard & Arditì 2000; Scheu & Falca 2000). Therefore, with increasing predator diversity, the number of intraguild predation motifs – and thus the strength of four-level cascading effects – increases as well.

In general, the net effect on the lower trophic level might be reduced with increasing number of large, higher-level predators. The community-level trophic cascade should be 'trickling' (Strong 1992; Halaj & Wise 2001). Similarly, this mechanism has also been validated for above-ground systems (Finke & Denno 2004, 2005). Its maintenance is crucial, because its loss could switch the regime from bottom-up to top-down control and in consequence, may profoundly disrupt ecosystem functioning.

## Conclusion

In our experiment, the apparent effect of predator diversity emerged from the effects of two predators that were nested into each other. We anticipate that diversity effects *per se* are unlikely to be detected in predator diversity experiments. Instead, all variation of the focal ecosystem function can be assigned to nested levels of predator composition. Apparently, when losing a predator from the community, the response of the lower trophic level is highly context sensitive, but taking body masses into account may solve this puzzle. We experimentally restrict the bias by biomass or density on the measured identity effects to a minimum by defining both as a consequence of body mass. By applying allometric constraints, the body mass structure of a community explains properties that were described as important mechanisms of the B-EF relationship: niche differentiation, intraguild predation and, as highlighted in this study, sampling effects. Complementary to the paradigmatic search for a biodiversity effect *per se* (Naeem 2002; Loreau 2010), this allometric perspective provides a new understanding for the multiple mechanisms that drive ecosystem functioning.

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## Author contributions

F.D.S. and U.B. designed the experiment, analysed the data and wrote the manuscript. F.D.S. performed the experiment.

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