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Published in:
Oikos

DOI:
10.1111/oik.02430

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Document Version
Publisher's PDF, also known as Version of record

Publication date:
2015

Link to publication in University of Groningen/UMCG research database

Citation for published version (APA):
Katano, I., Doi, H., Eriksson, B. K., & Hillebrand, H. (2015). A cross-system meta-analysis reveals coupled predation effects on prey biomass and diversity. *Oikos*, *124*(11), 1427-1435. https://doi.org/10.1111/oik.02430

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Oikos 124: 1427–1435, 2015
doi: 10.1111/oik.02430
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Subject Editor: James D. Roth. Editor-in-Chief: Christopher Lortie. Accepted 3 July 2015

A cross-system meta-analysis reveals coupled predation effects on prey biomass and diversity

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Predator diversity and abundance are under strong human pressure in all types of ecosystems. Whereas predator potentially control standing biomass and species interactions in food webs, their effects on prey biomass and especially prey biodiversity have not yet been systematically quantified. Here, we test the effects of predation in a cross-system meta-analysis of prey diversity and biomass responses to local manipulation of predator presence. We found 291 predator removal experiments from 87 studies assessing both diversity and biomass responses. Across ecosystem types, predator presence significantly decreased both biomass and diversity of prey across ecosystems. Predation effects were highly similar between ecosystem types, whereas previous studies had shown that herbivory or decomposition effects differed fundamentally between terrestrial and aquatic systems based on different stoichiometry of plant material. Such stoichiometric differences between systems are unlikely for carnivorous predators, where effect sizes on species richness strongly correlated to effect sizes on biomass. However, the negative predation effect on prey biomass was ameliorated significantly with increasing prey richness and increasing species richness of the manipulated predator assemblage. Moreover, with increasing richness of the predator assemblage present, the overall negative effects of predation on prey richness switched to positive effects. Our meta-analysis revealed strong general relationships between predator diversity, prey diversity and the interaction strength between trophic levels in terms of biomass. This study indicates that anthropogenic changes in predator abundance and diversity will potentially have strong effects on trophic interactions across ecosystems.

Synthesis

The past centuries we have experienced a dramatic loss of top-predator abundance and diversity in most types of ecosystems. To understand the direct consequences of predator loss on a global scale, we quantitatively summarized experiments testing predation effects on prey communities in a cross-system meta-analysis. Across ecosystem types, predator presence significantly decreased both biomass and diversity of prey, and predation effects were highly similar. However, with increasing predator richness, the overall negative effects of predation on prey richness switched to positive ones. Anthropogenic changes in predator communities will potentially have strong effects on prey diversity, biomass, and trophic interactions across ecosystems.

Large predators have suffered disproportionally high rates of human-driven population reductions; many have been driven to extinction (Pauly et al. 1998, Duffy 2003, Myers and Worm 2003, Cardillo et al. 2004, Ripple et al. 2014). At the same time, exotic predators have been deliberately introduced to new areas, with dramatic consequences for the native fauna and flora through direct and indirect (e.g. trophic cascades) interactions, especially on previously predator-free islands (Blackburn et al. 2004, Croll et al. 2005). Predators play important roles in ecosystems by propagating effects on the standing biomass (Terborgh et al. 2001, Shurin et al. 2002, Borer et al. 2005), competitive interactions (Chase et al. 2002), and temporal biomass dynamics (Halpern et al. 2005) of other trophic levels. In many systems, predators are keystone species, i.e. their impact on the ecosystem and its biota is much larger than their direct contribution to energy flow and biomass production (Paine 1966, Ripple et al. 2014). Consequently, theoretical and empirical evidence suggest that changes in predator abundance and biodiversity strongly affect ecosystem processes such as energy flow and matter cycling (Stachowicz et al. 2007, Bruno and Cardinale 2008). Thus, the removal of native and the introduction of exotic predators number among the most drastic anthropogenic alterations of ecological communities worldwide (Jackson et al. 2001).

In order to understand the potential effects of this massive global change, general knowledge of potential consequences

of predator presence or absence on food web properties is needed (Ripple et al. 2014). However, this requires filling a scientific gap reflecting the historic separation of ecological research on predator–prey interactions from research dealing with causes and consequences of altered biodiversity (Ives et al. 2005). Some major progress have been made with respect to bridging this separation, but important gaps still remain.

Several studies have explicitly tested the consequences of reduced biodiversity of predators in an experimental context (Byrnes and Stachowicz 2009, Letourneau et al. 2009). A recent meta-analysis analyzed how changes in predator richness affect prey biomass suppression (Griffin et al. 2013). Predator communities with several species (polycultures) were more effective at prey removal than the predator communities with only single species (monocultures), but were no more effective at prey removal than the best-performing predator monocultures. The overall effect sizes for loss of predator richness were larger than those found for reductions in autotroph or detritivore richness, indicating a strong diversity effect at higher trophic levels (Letourneau et al. 2009, Griffin et al. 2013). The effect sizes were especially strong for experiments with larger spatiotemporal scales and predator assemblages with higher phylogenetic distance.

The mechanisms driving such predator biodiversity effects have been explored in a series of models on the effects of predator richness on prey biomass and diversity (Ives et al. 2005). These models detected different scenarios: higher removal of prey biomass and lower prey richness with increasing predator richness was predicted when predators were generalists, intra-guild predation was absent (or low) and synergistic interactions (facilitation) between predator species were prevalent. By contrast, antagonistic interactions such as interference between predator species and high degree of omnivory prevented any strong effects of predator richness. None of their models provided the evidence for a positive effect of predators on prey diversity. However, if predators engage in interference competition, their combined effects on prey biomass may be lower than their species-specific effects (Amarasekare 2002), which potentially also increases prey diversity.

Prey biomass removal, however, does not only depend on predator diversity (top–down), but also on prey diversity (bottom–up). Different mechanisms were proposed to explain effects of prey diversity on consumption (Hillebrand and Shurin 2005). Higher prey diversity might have positive effects on predators by increasing total prey biomass (Thebault and Loreau 2003), quality of prey biomass (DeMott 1998) or predator abundance through apparent competition (Holt et al. 1994). By contrast, empirical evidence suggests that higher prey diversity relates to a reduced prey removal via a higher probability of including inedible species and via mutualistic interactions between prey species leading to associational resistance (Hillebrand and Cardinale 2004, Edwards et al. 2010).

In order to promote a more general understanding of potential consequences of altered predator guilds, a cross-system approach is necessary, as the structure of trophic interactions differs substantially between terrestrial and aquatic systems (Shurin et al. 2006). Quantitative syntheses have revealed systematic differences between land and sea for the strength of trophic cascades (Shurin et al. 2002), the relative importance of decomposer and herbivore pathways in the fate of primary production (Cebrian and Lartigue 2004), or the effects of herbivores on plant biomass (Gruner et al. 2008) and plant diversity (Hillebrand et al. 2007). However, mechanisms discussed for these differences such as size and stoichiometry all address the plant–herbivore link (Shurin et al. 2006). Whereas the body size ratio between autotrophs and herbivores potentially differs dramatically between terrestrial and aquatic systems, this is not true for carnivorous predators and their prey (Brose et al. 2006). The difference in autotroph and consumer C:nutrient ratios between terrestrial and aquatic systems (Elser et al. 2000) drives much of the difference in herbivory and decomposition (Cebrian and Lartigue 2004), but such a stoichiometric difference is unlikely for carnivorous predators. Thus, predation may be much more similar between ecosystem types than herbivory or decomposition.

Here, we complement previous approaches by assessing a different set of literature, predator removal experiments, to provide an independent synthesis of consequences of altered predator guilds. This data set complements the approach by Griffin et al. (2013), which focused on potential consequences of reduced predator diversity, thus experiments comparing the effects of multispecies predator assemblages to effects of single predators. By contrast, the experiment we examined manipulated the presence and absence of predators, testing for the more severe consequences if a predator guild collapses completely. The literature on this topic is vast, but here we focus on the subset of experiments measuring simultaneously the predation effect on both prey diversity and prey biomass.

This cross-system analysis of consequences of predator loss was performed to achieve three objectives: 1) testing whether effects of predator presence on prey biomass show similar system-specific differences as those observed for herbivore effects on plant biomass (Gruner et al. 2008) and plant diversity (Hillebrand et al. 2007); 2) comparing the effects of predators on prey biomass and on prey diversity, and especially testing for significant relations between the two responses, which remains underexplored (Hillebrand and Shurin 2005); 3) evaluating how much predator presence and predator diversity affect the prey assemblages and how removal of prey biomass is constrained by prey diversity. For each of these objectives, concise hypotheses are tested.

Objective 1

If system-specific differences in trophic structure prevail only because of differences in the plant–herbivore link, we expect consistent predator effect sizes across systems (hypothesis H1A). However, we expect to see differences in predation effects driven by differences between assemblages. A previous meta-analysis of trophic cascades suggests some candidate variables impacting predation effects relating to predators' metabolism or mobility such as predators being either vertebrates or invertebrates or prey being either sessile or mobile (Borer et al. 2005). Thus, we test for significant impact of these organismic traits across system boundaries (H1B).

Objective 2

The association between responses of prey biomass and prey diversity responses seems to be straightforward at first glance. The presence of a predator trophic level results in prey removal, which leads to lower diversity simply by reduced sampling abundance (Gotelli and Colwell 2001).

In this case, we expect a strong positive correlation between effect sizes on biomass and diversity, which both consistently show negative signs (H2A). However, the net effect of predator presence on prey diversity might not only reflect reduced prey abundance, but also involves the interaction between predation and prey competition (Chase et al. 2002). Classically, predation has been thought to weaken the exclusion of species by competition, but theory has shown that the mere presence of predation does not necessarily reduce the competition without changing in the ratio of inter- to intraspecific density-dependence (Chase et al. 2002). Predation then only increases prey diversity if it creates new types or distributions of resources or if it affects the competitive dominant more strongly, i.e. limits the dominant's growth (Holt et al. 1994, Chase et al. 2002). Chesson and Kuang (2008) generalized this finding by showing that it is the relative strength of competition and predation that affects prey coexistence. If prey species respond differently to predation (i.e. show little niche overlap with regard to their predators) but do not partition resources, predation will enhance the chance for coexistence. If prey species respond equally to predation but show strong niche differentiation in their resource use, then increasing predation will enhance competitive exclusion. In this case, the positive correlation between effects on prey abundance and effects on prey diversity potentially remains significant, but we expect to see positive predation effects on prey diversity in studies with weak predation effects on biomass (H2B).

Objective 3

We compared the effects of predator absence to the predator diversity effects in the meta-analysis by Griffin et al. (2013). In addition to overall averages of predator absence effects, we specifically tested whether the effects of predator absence are larger than the effects of reducing predator diversity (H3A). Moreover, we grouped effect sizes of predator absence for predator assemblages of different diversity and thereby tested whether predator diversity explains the effects of predator presence and whether this relationship scales to the effects observed by Griffin et al. (2013) for experiments reducing diversity directly (H3B, Fig.1). This analysis enables us to see whether diversity effects within a community (according to Griffin et al. 2013) can be compared in sign and magnitude to diversity effects between communities (by our analysis of experiments differing in predator diversity). Finally, we explicitly include prey diversity into this consideration. On one hand, we ask whether prey diversity responses scale to the richness of the predator guild manipulated (H3C). On the other hand, we test whether prey diversity affects the removal of prey biomass by predators across these experiments (H3D), as has been suggested for benthic microalgae and benthic marine assemblages (Hillebrand and Cardinale, 2004, Edwards et al. 2010).

In the following, we synthesize the effects of predation in a cross-system meta-analysis of prey diversity and biomass responses to local manipulation of predator presence, using 291 experiments from freshwater, marine and terrestrial ecosystems. The overall number of predator removal studies obviously is much larger, but only this subset measured the response of prey biomass and prey diversity simultaneously. We used this database to test the eight hypotheses outlined above. These experiments derived from 87 studies, and we carefully analyzed for potential artifacts in our results by addressing study identity effects and tested for significant differences in the predation effects using additional explanatory variables describing the experimental approach, the organisms and the ecosystem.

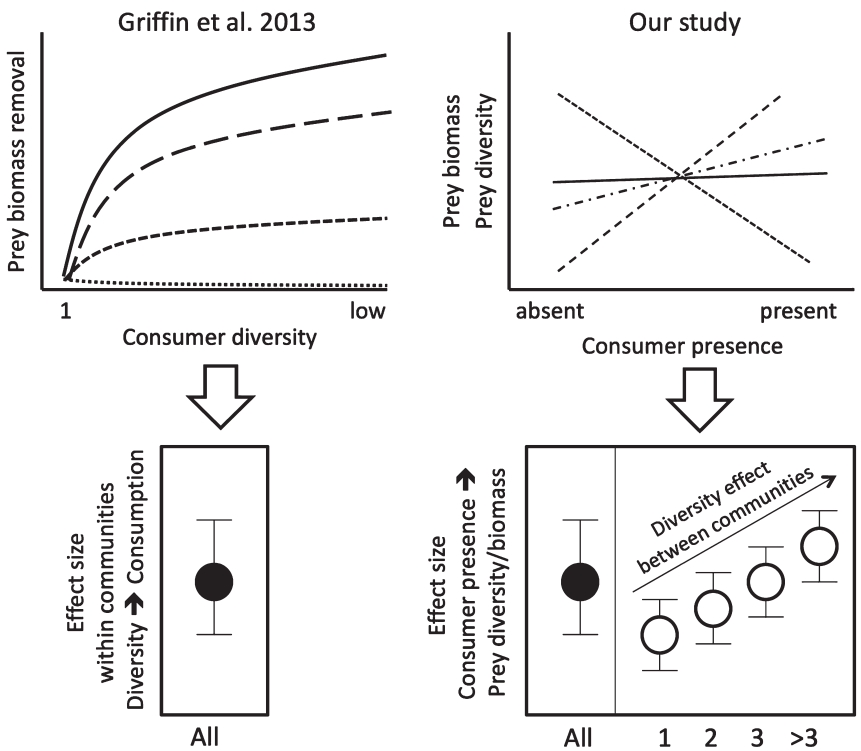

Figure 1. Comparison of analysis designs between our study and Griffin et al. (2013).

Material and methods

We searched data from published sources using ISI Web of Science. The search term was '(divers* OR richness OR biodiversity) AND (experiment* OR manipulat*) AND (prey OR consumer OR predator*)'. The search was conducted on 22 Aug 2012. From these studies, we selected studies contrasting the presence and absence of carnivorous predators by exclosures or enclosures, which ranged from lab experiments to large field experiments. We only used experiments directly manipulating the presence of carnivorous predators feeding on living animal prey biomass (i.e. no detritivory or herbivory was included). The direct manipulation had to consist of a predator-free treatment and a control with an intact predator community, thus experiments manipulating only the structure (diversity, size) or abundance of the communities were not considered, reflecting our focus on the effects of predator absence/presence. Experiments further had to be replicated to be included and give information on prey biomass (or abundance) and prey diversity, either as species richness or evenness.

With these unequivocal selection criteria, we finally retrieved 291 experiments from 87 studies, from which we collected the average prey diversity and abundance or biomass data for the predation treatment and the predator-free control (Supplementary material Appendix 1). We followed the rationale of a previous herbivore–plant meta-analysis (Hillebrand et al. 2007) for selecting multiple experiments from single studies as long as they had a separate control (e.g. experiments conducted at different sites or in different seasons). If studies had multiple levels of predator assemblages (diversity, density), we always compared the predator-free treatment with the most complete predator community (highest richness or abundance level). This is complementary to the approach taken in biodiversity studies, where highest richness levels are compared to single species monocultures (Griffin et al. 2013).

To quantify the effects of predators, we calculated ln-transformed response ratios between the mean value at predator presence and the mean value at predator absence [$RR_X = \ln(X_{presence} / X_{absence})$] (Hedges et al. 1999). We did so for the predation effects on prey richness (RR_S), prey assemblage evenness (RR_E) and prey biomass (or abundance, if biomass data were not available) (RR_B). We made sure that RR_B based on biomass did not systematically differ from RR_B based on abundance and used both in a single analysis (Supplementary material Appendix 2).

Response ratios for species richness have recently been criticized for being sensitive to the grain and extent of sampling as well as the size of the species pool (Chase and Knight 2013), even when sampling is standardized by area or effort. Chase and Knight (2013) suggest using a derivate of Hurlbert's (Hurlbert 1971) probability of interspecific encounter (PIE) as a much less sensitive diversity metric. However, the information on the Simpson index underlying PIE (Jost 2006) was not reported in many studies and the information on species proportions necessary to calculate it was not reported either. As the discussion on the severity of the sampling effects on log response ratios is ongoing, we constructed a sensitivity analysis testing RR on laboratory experiments only. The most severe potential bias according to Chase and Knight (pers. comm.) is if experiments differ largely in their species pools and in how complete they analyzed the species assemblages for presence/absence. Lab experiments often have a small, completely known species pool and show an almost complete coverage of sampling the diversity of predator and prey assemblages. Thus, we hypothesized that if this well-comparable subset of studies show the same overall trends as the entire data set including field experiments, we can be confident that our conclusions are not strongly affected by different sampling efforts between studies. In fact we found no significant differences between the RR_S from laboratory experiments and the RR_S from all experiments (Supplementary material Appendix 3). Therefore, we remain confident that any bias in the log response ratios for specie richness – if present – were not large enough to alter the central tendencies and thus our main conclusions.

We also extracted relevant spatial, temporal and abiotic factors for as many studies as possible to include as explanatory variables in a selection of the best general linear model (GLM) for each RR_X. Thus, we characterized each experiment according to ecosystem type (freshwater, marine or terrestrial), study type (field or lab experiment), the richness of the predator assemblage manipulated in the experiment, the duration of the experiment (ln-transformed number of days), the generation times of the predators and the prey, the latitude (°N or S) and the prey richness in the predator-absent treatments. Moreover, we assigned the predators as either vertebrates or invertebrates and the prey as either sessile or mobile, because both have been found to impact predation effects before (Borer et al. 2005). We characterized predator richness from the information in the primary study as the number of species manipulated, which we categorized as 1, 2 3 or >3 species. Generation times of prey and predator species were estimated from published sources and – if necessary – averaged across multiple taxa.

We performed an unweighted meta-analysis (Hillebrand et al. 2007). First, we obtained grand mean effect sizes for RR_S, RR_E and RR_B across all studies as well as average effect sizes within the major ecosystem types freshwater, marine and terrestrial. Both laboratory and field experiments were combined to calculate mean effect sizes, because RR_S, RR_E and RR_B did not significantly differ between both experimental types. The 95% confidence intervals were used to test whether these were significantly different from zero. Second, we used a general linear model (GLM) to explain variation in RR_S, RR_E and RR_B, respectively, using the variables described above. For RR_S and RR_E we additionally used RR_B as explanatory variable, and for RR_B we additionally used prey richness. It should be noted that the GLM were run on a subset of experiments for which information on all the above mentioned variables was provided, whereas all other analyses as well as the figures in the main text and the online supplement contain all experiments. We selected the best GLM by downward stepwise selection based on Akaike information criterion (AIC) (Burnham and Anderson 2002, Johnson and Omland 2004).

We checked the publication bias effect on our analysis. One of the most common forms of publication bias is the failure to publish small effects (close to zero), which can lead to a overestimation of the mean effect size (Borenstein et al. 2009). A simple test or this publication bias is a correlation analysis between the number of replicates and the absolute magnitude of the effect size, testing for an under-representation of studies with both low sample size (*N*) and low effect size. We did not find such a correlation between

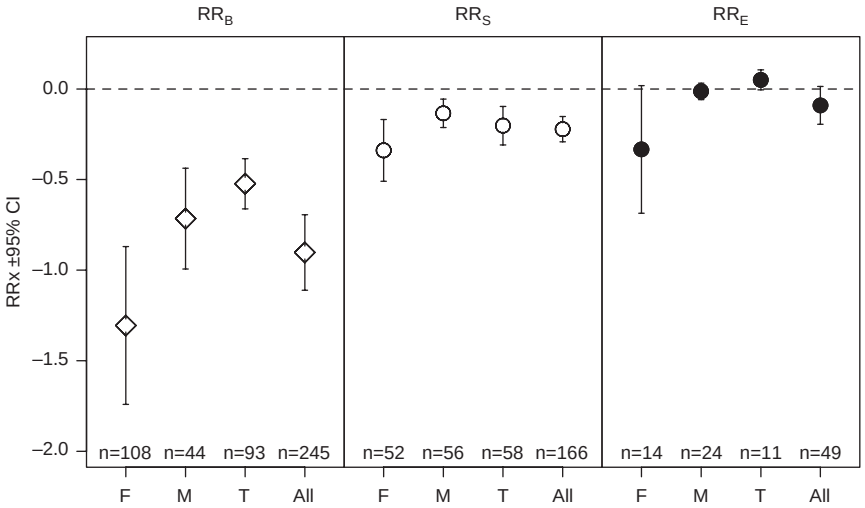

Figure 2. Average log response ratio (RR_x) to predator presence of total prey biomass/abundance (RR_B), prey richness (RR_S), and prey evenness (RR_E, all ± 95% confidence intervals) for all studies and separately for freshwater (F), marine (M), and terrestrial (T) ecosystems, respectively. Confidence intervals not including zero indicate a significant negative or positive effect across studies, whereas non overlapping confidence intervals between groups indicate significant differences between groups.

RRx and N for any of the response variables ($r < 0.2$, $p > 0.3$ for two-sided tests for RR_S, RR_E and RR_B) and thus no evidence for such a publication bias.

As multiple experiments were derived from single papers, we carefully tested whether single study identity was affecting results by including study as a random factor into a general linear mixed model (GLMM). The GLMM did not alter our results (for details see Supplementary material Appendix 4) and we present the GLM results in the manuscript. All statistics were performed using R ver. 3.1.0 (<www.r-project.org>).

Results

The predator effect on prey biomass or abundance (RR_B) was strongly negative, corresponding to an average removal of 57% of prey individuals or biomass (Fig. 2, for histograms see Supplementary material Appendix 5 Fig. A3). The difference between ecosystem types was not significant, but RR_B was significantly affected by both prey and predator richness (Table 1). Strongest prey biomass removal was clearly limited to prey assemblages comprising > 10 species (Fig. 3A). Additionally, experiments with predator assemblages of >3 species exerted weaker control on prey biomass than less diverse assemblages, but RR_B remained on average negative at all richness levels (Fig. 3B). Biomass removal effects were significantly different from zero only with single predator species, whereas highly variable estimates for three species were based on small sample size. Moreover, RR_B was stronger at higher latitudes and – albeit non-significantly – for prey communities with shorter generation time (Supplementary material Appendix 5 Fig. A4). The final GLM explained 54% of the variance in RR_B, 25% were explained by predator richness alone (Table 1).

Table 1. General linear models explaining predation effects (RR) on prey biomass, richness and evenness, selected by a downward stepwise procedure using Akaike information criteria. The categorical factors are; Ecosystem type: marine, freshwater or terrestrial ecosystems, Study type: laboratory, exclosure or enclosure experiments. Predator type: invertebrate or vertebrate, and Prey mobility: sessile or mobile. For each factor retained in the best model, we report the parameter estimate and its significance (***, ** and *, indicate p < 0.001, 0.01, and 0.05, respectively, ns = not significant). We also give the full model coefficient of determination R^2 and the partial R^2 for each significant factor. n.i. = not included, – = not retained. Please note that the statistical results are on a subset of experiments providing information on all requested variables.

	RR_B		RR_S		RR_E	
Factor	Est (sign)	R^2 part	Est (sign)	R^2 part	Est (sign)	R^2 part
Ecosystem type	Mar > FW^{ns}	0.02	–		–	
Study type	–		–		–	
RR_B	n.i.		0.136***	0.330	–	
Predator richness	2.39***	0.25	0.029*	0.020	–	
Prey richness	0.050***	0.041	n.i.		n.i.	
Latitude (°N or S)	–0.051***	0.121	0.011**	0.133	–	
Duration (ln days)	–		–0.048*	0.032	–	
Predator type	–		–		–	
Prey mobility	–		Ses > mob^{ns}	0.005	–	
Prey gen. time	0.2^{ns}		0.012***	0.014	0.186*	0.09
Full model R^2	0.478***		0.461***		0.072*	

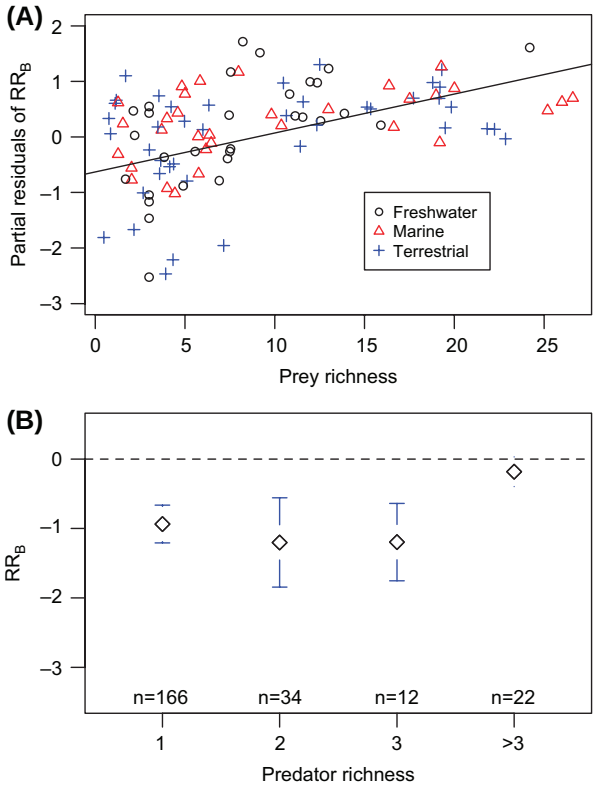

Figure 3. (A) Relationship between partial residual of prey species richness and the log response ratio of prey biomass (RR_B) to predator presence. The partial residual of RR_B is to account for the variation explained by other predictors using the best GLM model. The line indicates a significant regression ($p < 0.05$, GLM). For clarity, two extreme values are omitted from the plot. Colours code for freshwater (black), marine (red) and terrestrial (blue) studies. (B) Average $RR_B \pm 95\%$ confidence intervals for studies involving different predator richness (1, 2, 3 species and > 3 species). Scale breaks were introduced to three of the panels to maximize clarity of presentation. Horizontal dashed line at 0 indicates no response to predation.

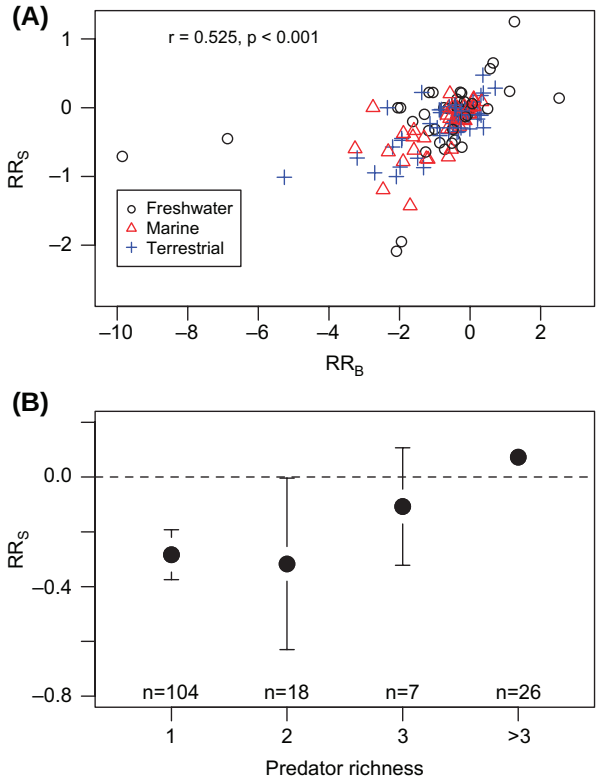

Figure 4. (A) Relationship between the log response ratios to predation presence on prey biomass (RR_B) and prey richness (RR_S). Colours code for freshwater (black), marine (red) and terrestrial (blue) studies. (B) Average $RR_S \pm 95\%$ confidence intervals for studies involving different predator richness (1, 2, 3 species and > 3 species). Scale breaks were introduced to maximize clarity of presentation. Horizontal dashed line at 0 indicates no response to predation.

Predator presence reduced prey richness on average as RR_S was significantly negative across all studies (Fig. 2). Although effect sizes were slightly weaker in marine than in terrestrial or freshwater environments, ecosystem type was not retained in the best general linear model explaining variation in RR_S (Table 1). The final GLM explained 49% of the variation in RR_S with five predictor variables (Table 1). The most important variable was biomass removal as RR_S strongly and significantly increased with RR_B (Fig. 4A). Thus, a more complete removal of prey individuals (or biomass) by the predator also excluded more prey species. However, whereas almost no study showed a positive effect of predation on prey biomass (3%), a substantial proportion (24.1 %) showed a positive response of prey richness to predation (Supplementary material Appendix 5 Fig. A3). These studies were characterized by rather low to intermediate biomass removal through predation (Fig. 4A). Moreover, the negative predation impact on prey richness was restricted to studies with species poor predator assemblages, whereas in experiments manipulating a more diverse predator assemblage, predator presence tended to maintain or even increase prey diversity (Fig. 4B, Table 1). Thus, experiments with single to few predator species contributed most strongly to the overall negative predator effect on RR_S, whereas increasing predator richness weakened – and at > 3 species even reversed – the predation impact on prey richness (Fig. 4B). In addition, predation caused greater reduction in prey richness in experiments of longer duration, and if prey had shorter generation times (Table 1). The tendency to reduce prey richness especially in mobile prey communities remained non-significant.

Across ecosystems, RR_E was marginally not significantly different from zero. On average predator presence reduced evenness by 9% (Fig. 2). RR_E tended to be positive in terrestrial ecosystems, and was negative in both marine and freshwater systems, but ecosystem type was not retained in the best GLM (Table 1). The GLM contained only prey generation time, with more negative effects on prey evenness if prey had shorter generation times.

Discussion

Objective 1. Testing whether effects of predator presence show similar system-specific differences as those observed for herbivore effects on plant biomass and plant diversity

Predators on average removed 57% of prey individuals or biomass (mean $RR_B = -0.85$), which corresponds well to the

average removal of producer biomass by herbivores (mean $RR_B = -0.82 \sim 55\%$ removal) analyzed in a synthesis of 191 experiments (Gruner et al. 2008). This estimate of predation effect size is made on a subset of predation experiments published (those also measuring prey diversity), but is potentially a good unbiased estimate of average predation effects, as an independent dataset on trophic cascades revealed an average prey removal of 60% (Shurin et al. 2002). Prey richness was reduced by predator presence by 19% on average. Both negative general effects on biomass as well as diversity were consistent across ecosystem types (supporting hypothesis H1A).

The generally negative effects of carnivorous predators on prey richness marks a major contrast to the analogous effects of herbivores on producer richness, which has been analyzed across ecosystems before (Hillebrand et al. 2007). Herbivore effects on producer richness did not differ from zero across all studies, which reflected a major discrepancy between freshwater (negative effects) and terrestrial (positive effects) ecosystems. Thus, only aquatic herbivores showed negative effects on producer richness, whereas carnivorous predators reduce prey richness in both terrestrial and aquatic systems. We propose that the ecosystem difference in herbivory effects holds the explanation for the stronger and more uniform predation effects. Aquatic herbivores are highly efficient consumers and often larger than their food, i.e. they ingest entire individuals. Terrestrial herbivores mostly consume only parts of the plants they feed upon – often they are also smaller than the plants – which causes less effective and non-lethal consumption (Shurin et al. 2006). Predation, by contrast, is characterized by similar and large predator–prey body size ratios across ecosystems (Brose et al. 2006). Consequently, predation is equally lethal in all ecosystems leading to a consistent reduction in prey richness.

In the absence of differences between ecosystems, we found that both RR_B and RR_S were significantly explained by predictor variables related to organism traits (supporting hypothesis H1B). The removal of prey biomass was linked mainly to diversity at both the prey and predator level (see below on objective 3) and also had a significant negative latitudinal gradient. Thus, at higher latitudes, more negative effect sizes and higher prey removal was observed, probably because lower prey richness at high latitudes reducing the trophic interactions due to changing in the compositions of edible to inedible species. Our meta-analysis contributes to the mounting evidence that both strength and sign of biotic interactions varies across latitudinal gradients (Schemske et al. 2009). As latitude and manipulated predator richness were not correlated in our database, the mechanism to this latitudinal gradient remains unclear (Supplementary material Appendix 4). Neither the differentiation between vertebrate and invertebrate predator type nor between sessile ,and mobile prey significantly affected biomass removal as had been previously observed to trophic cascades (Borer et al. 2005).

The main predictor for RR_S was biomass removal by the predator (see below on objective 2). Additionally, we found more negative effects of predation on prey richness with increasing duration of the experiment and decreasing prey generation time. Thus, if more prey generations can occur, because experiments run longer or prey reproduce faster, there is obviously a higher risk of extinction through consumer-induced mortality, a result also seen in a meta-analysis on herbivore – producer experiments (Hillebrand et al. 2007). RR_S increased (i.e. became less negative) with increasing latitude, an interesting contrast to the latitudinal gradient of RR_B. However, the basis for this observation is not clear.

Our analysis did not generate conclusive evidence for predation effects on evenness across ecosystems, although the results indicate that predator presence on average may increase the dominance of few prey species, which is in strong contrast to the positive effects herbivores have on producer evenness (Hillebrand et al. 2007). These negative effects on evenness were especially seen in freshwater systems and predominant for prey with short generation times.

Objective 2. Comparing the effects of predators on prey biomass and on prey diversity

More negative impacts of predation on prey richness were strongly related to higher biomass removal across ecosystems (supporting hypothesis H2A). Variation in RR_B alone explained almost 30% in the variation of RR_S, indicating that higher removal of biomass increased mortality to levels exceeding the tolerance of some prey species. These results suggest that lower prey richness under predation reflects lower abundance and thus probability of detection (Gotelli and Colwell 2001). Our sensitivity analysis suggests that these effects were not strongly affected by differences in species pool and sampling effort (Supplementary material Appendix 4).

The fact that predator presence on average reduced prey richness may appear surprising given the attention for consumer-mediated coexistence, especially in the keystone predation literature (Paine 1966, Menge 1995). Keystone predators are supposed to maintain prey species richness by controlling an otherwise dominating prey species. Notably, much of the keystone predation literature focuses on sessile prey and in fact the predation effect size on prey richness tended to be more negative for mobile prey in our analysis. Additionally, the majority of empirical studies on keystone predation addresses only a subgroup of strongly interacting species, whereas the studies synthesized in our meta-analysis often quantify the entire prey assemblage or at least all species within one type of prey. Even if predators act as a keystone species modifying the interactions between the dominant species, they can simultaneously eliminate rare species in a community by increasing mortality towards a level no longer compensated for.

However, if biomass removal would have been the only cause for reduction in prey richness, we would have expected only negative effect sizes for both response variables. By contrast, we found that 24.1% of the studies showed a positive RR_S, especially those small effects on biomass. Thus, consumer-mediated coexistence is possible also in these predation experiments, but is overridden by the loss of species through removal of prey biomass and increased mortality at large magnitudes of RR_B.

Objective 3. Evaluating how much predator presence and predator diversity affects the prey assemblages and how removal of prey biomass is constrained by prey diversity

Comparing the results of our analysis of predator removal experiments with the results from predator diversity

experiments (Griffin et al. 2013) reveals important insights. Their estimate for RR_B based on losing all species except one (mean = 53% reduction when comparing mixtures to average monoculture) was in the same range than our estimate based on losing the entire assemblage (57% reduction). However, the effect of diversity in their study became much smaller when comparing mixtures to the best performing monoculture (mean = 33% reduction). Thus, losing the entire predator assemblage produces on average larger effect sizes than losing the majority of components (supporting H3A) – however, a reduction in biodiversity of the predator guild affects biomass control in the same order of magnitude than losing all predators.

There is one important discrepancy between the predator absence meta-analysis we performed and the meta-analysis of predator diversity manipulations performed by Griffin et al. (2013). In their analysis, more diverse predator assemblages exerted a larger control on prey biomass (Griffin et al. 2013), whereas our results showed that experiments with more diverse predator assemblages exerted weaker control on prey biomass (refuting hypothesis H3B). Thus, the effect of predators on prey biomass scales differently within assemblages (Griffin et al. 2013) than across assemblages (this study). Reconciling our results with theory (Amarasekare 2002, Ives et al. 2005) suggests that a more diverse assemblage of predators can be less efficient in controlling prey biomass because predator species between themselves may engage in negative interspecific interactions such as interference competition and intra-guild predation when predator richness increases. Our meta-analysis does not allow an explicit test of the negative interspecific interaction hypothesis since the primary studies do not provide pairwise interaction strengths between predator species. The discrepancy between the two meta-analyses then can be explained when antagonistic interactions are less prominent in assemblages used for BEF experiments than when comparing across predator removal experiments differing in diversity. Corroborating these thoughts, less diverse predator assemblages in BEF experiments were also found to be more efficient at removing prey biomass if higher diversity levels included intra-guild predators (Finke and Denno 2005).

Alongside with a reduction in prey biomass removal, more diverse predator assemblages also reduced the loss of prey species richness – even a reversal of effect sign towards promotion of coexistence at high predator richness (supporting hypothesis H3C). The main reason for this positive effect on prey richness by multiple predators seems to be their reduced effect on biomass as discussed above.

Moreover, strongest prey removal was clearly limited to prey assemblages comprising few species (supporting hypothesis H3D). Previous findings that high algal diversity relates to reduced effects of grazers on algal biomass (Hillebrand and Cardinale 2004, Edwards et al. 2010) can apparently be generalized to other trophic interactions. Predation efficiency can be reduced if more diverse prey dilutes the encounter rate of specialist predators for their target prey, prolongs handling times, increases the probability of inedible prey being present, or promotes associational resistance among prey species (Hillebrand and Cardinale 2004, Hillebrand and Shurin 2005).

Conclusion, caveats and outlook

Our meta-analysis provides general central tendencies for predation effects on prey biomass and richness, and for the role of predator and prey richness in explaining these effects. Predation removes on average more than 50% of prey biomass in these experiments and reduces both prey richness and prey evenness. Predation control over prey biomass and richness is strongly constrained by biodiversity at both levels. Higher predator richness is associated with reduced effects on prey biomass and predation-mediated increases in prey diversity, whereas higher prey diversity relates to lower biomass removal through predation.

We base these conclusions on 291 experiments derived from 87 studies, and these conclusions are not based on disproportional influence of single studies, as including study identity as a random factor did not alter our results (Supplementary material Appendix 4). Nevertheless, meta-analyses have raised concerns for improper generalizations (Whittaker 2010) – an issue critically assessed elsewhere (Hillebrand and Cardinale 2010). Addressing these concerns, there are mainly two aspects we would like the reader to keep in mind. First, we emphasize strongly that – in contrast to a recent meta-analysis of biodiversity manipulation experiments (Griffin et al. 2013) – we analyzed diversity effects across studies. The studies differed strongly in many aspects, not only richness of predator and prey assemblages. However, we included a multitude of additional explanatory variables, and their inclusion in the model did not alter or weaken the observed patterns of predation effects with predator or prey diversity.

Second, most experiments included here were short term, on average only 1.2 generations of the prey and 0.13 generations of the predator. Thus, the experiments provided estimates for short-term changes in predation pressure, not necessarily for long-term dynamics. As many studies were field experiments quantifying predation effects at ambient abundances of the predator and the prey, these immediate effects of predator removal were measured in established dynamics, not in an artificial start-up phase of static short-term experiments.

In addition to addressing long-term effects of predator removal, the major open research question arising from this analysis is: when does higher diversity at either the prey or predator level generally weaken trophic interactions (as observed here) or when does it strengthen these interactions (as suggested by Griffin et al. 2013). There is some theoretical evidence for the plausibility of both effects (Amarasekare 2002, Ives et al. 2005) and some additional empirical evidence for reduced predation effects with increasing richness at the predator (Finke and Denno 2005, Frank et al. 2006) or prey (Hillebrand and Cardinale 2004) level. Given theoretical predictions that weak interactions stabilize food web dynamics (McCann et al. 1998), lower species richness could destabilize food webs when stronger and more negative predation effects on prey biomass and prey richness are to be expected at lower predator or prey richness. Such effects would thus have major propagating consequences for conservation.

Acknowledgements – This work was supported by the German Science Foundation (DFG grant Hi848/9 to HH) and Japanese

Society for the Promotion of Science (JSPS to HD). Jon Chase, Jon Shurin, Elizabeth Borer and Eric Seabloom provided very helpful comments on the analysis and the manuscript.

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Supplementary material (available online as Appendix oik.02430 at <www.oikosjournal.org/readers/appendix>). Appendix 1–5.

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