

Effect of consumer loss on resource removal depends on species-specific traits

DOROTHEE HODAPP† AND HELMUT HILLEBRAND

*Institute for Chemistry and Biology of the Marine Environment (ICBM), University of Oldenburg,
Schleusenstr. 1, 26382 Wilhelmshaven, Germany*

Citation: Hodapp, D., and H. Hillebrand. 2017. Effect of consumer loss on resource removal depends on species-specific traits. *Ecosphere* 8(3):e01742. 10.1002/ecs2.1742

Abstract. Negative effects of species loss on ecosystem functioning within and across trophic levels have been demonstrated across systems and organism groups. Recent meta-analyses showed that lower levels of consumer diversity lead to a reduction in resource removal. The strength of these effects seems to strongly depend on species identity, that is, species-specific traits, resulting in a variety of consumer interactions ranging from facilitating to strongly antagonistic effects. For a general test of trait-based effects of species loss, we conducted a meta-analysis on resource experiments including two consumer species. We calculated effect sizes of losing one of the two species, and related these to variables describing species' traits and experimental design. Our results show that loss of one species on average reduces resource removal supporting the hypothesis that loss of certain species-specific traits cannot fully be compensated for by biomass increases of the remaining consumer. However, the investigation of various consumer traits including body size did not allow for generalizations on the effect of loss of a certain consumer trait on resource removal.

Key words: biomass replacement; consumer interaction; diversity loss; meta-analysis; multi-consumer; resource removal; trait.

Received 27 January 2017; accepted 2 February 2017. Corresponding Editor: Debra P. C. Peters.

Copyright: © 2017 Hodapp and Hillebrand. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† **E-mail:** dorothee.hodapp@uni-oldenburg.de

INTRODUCTION

Despite some uncertainty on the trends in local species richness (Dornelas et al. 2014, Elahi et al. 2015), the functional consequences of species richness decline on ecosystem processes have become a cornerstone of recent ecology (Cardinale et al. 2012). Biodiversity–ecosystem functioning (BEF) experiments typically mimic random loss of species from an assemblage, establishing a series of usually nested diversity levels. A series of meta-analyses suggests a predominantly negative impact of species richness loss within a trophic level on the resource-use efficiency and biomass production (Balvanera et al. 2006, Cardinale et al. 2006, 2012). Because there is increasing evidence

that higher trophic level species face a greater risk of extinction (Cardillo et al. 2005), BEF experiments have also been conducted across trophic levels, suggesting that less-diverse consumer assemblages show lower efficiency in terms of prey biomass reduction (Griffin et al. 2013) with at times far-reaching consequences for food web structure (Petchey et al. 2004, Heithaus et al. 2008) and overall system functioning (Jonsson et al. 2002, Duffy et al. 2003, Solan et al. 2004).

Griffin et al. (2013) conducted a meta-analysis comprising 46 predator BEF experiments, looking into predator richness effects on aggregate prey suppression relative to predation effects of each predator species in monoculture. They show that predator richness enhanced prey suppression

relative to the average single predator, but resulted in less removal of prey compared to the best-performing single predator species, stressing the importance of species-specific traits.

In agreement with this expectation, a large body of literature shows that the magnitude and direction of effects of consumer loss seem to be determined by a variety of antagonistic (Finke and Denno 2005), synergistic (Cardinale et al. 2003), or neutralizing effects (Casula et al. 2006) as well as environmental context and natural history (Bruno and Cardinale 2008). For instance, species-specific behavioral mechanisms (Losey and Denno 1998, Schmitz 2007) or physiological characteristics (Basset and Angelis 2007) facilitating complementary resource use can increase overall prey consumption, whereas antagonistic interactions between consumer species like intra-guild predation negatively affect rates of prey removal (Crumrine and Crowley 2003). Apart from biomass reduction due to consumption, the density and performance of prey populations is also regulated by non-consumptive effects, for example, reduced energy intake, low mating success, and higher vulnerability to other predator species (Preisser et al. 2005, Davenport and Chalfcraft 2013). Additionally, density and diversity of prey populations themselves and the proportion of inedible prey species can influence rates of prey removal (Hillebrand and Cardinale 2004, Kratina et al. 2007, Tylianakis and Romo 2010).

Given the number of possible interactions within and across trophic levels, the reliable prediction of changes in rates of prey removal based on general concepts such as ratio dependence (Arditi and Ginzburg 1989) or multiplicative risk model (Soluk and Collins 1988) has proven to be challenging (McCoey et al. 2012, Abrams 2014). Furthermore, Byrnes and Stachowicz (2009) show that different research fields analyzing multiple-predator systems and consumer diversity effects usually employ varying experimental designs (additive vs. replacement). As a consequence, comparisons of outcomes across studies are bound to result in divergent patterns as the two designs reveal different types of interaction.

One approach to assess the generality of BEF experimental results is to explore different sets of experimental approaches. A recent meta-analysis on 291 predator removal experiments evaluated predation effects across ecosystem types and

different levels of consumer and resource diversity (Katano et al. 2015). Complementary to the study by Griffin et al. (2013), Katano et al. (2015) analyzed the effects of removing entire predator guilds of varying diversity. They revealed highly similar and negative effects of predator presence on prey biomass across systems, but significantly weakened effects with increasing predator diversity. They attributed these weaker effects of more diverse predator assemblages on their prey to more enhanced antagonistic effects between consumer species.

In consequence, predicting the effects of consumer loss in different ecosystems requires knowledge about the characteristics of the species involved, that is, their traits. One trait often considered in this context is body mass as it relates to a number of important ecological characteristics such as metabolic rates (Brown et al. 2004) or prey size range (Brose et al. 2006) and thus affects competitive ability of predator species and species-specific effect sizes (Aljetlawi and Leonardsson 2003). Size ratios of predator species have also been shown to influence non-consumptive effects in multi-predator systems (Krenek and Rudolf 2014). Based on these assumptions, Schneider et al. (2012), for example, applied a reductionist approach deriving predator abundance, diet breadth, and feeding rate from empirically supported body mass constraints and were able to explain varying effects of predators of differing size on decomposer biomass in a microcosm experiment. However, a more general test of trait-based effects of consumer loss on prey removal is missing.

Here, we use information from a set of experiments outside a BEF context, which allows analyses of specific combinations of consumer species in reductionist settings of only two species: Many experiments have analyzed the combined predation effects of two species (A+B) in comparison with each of the single species (A or B), with a predator-free control (0) as a baseline allowing us to directly connect the loss of one consumer species from a two-species system to their respective traits. We performed a meta-analysis using this rather large body of consumer-resource literature on experiments following such a 0/A/B/AB design (additive or replacement). Since additive designs confound the loss of certain species traits with the loss of consumer biomass, we used

biomass replacement studies only in a first test on whether loss of one consumer species and its respective traits affects rates of resource removal. In a second analysis, we used additive and biomass replacement studies to investigate associations between effect size of consumer species loss and physiological as well as life history traits of the lost, respectively remaining, species.

METHODS

For study selection, we searched the Web of Science (Thompson Reuters, Toronto, Ontario, Canada) with the terms (diversity OR biodiversity OR rich*) AND (predat* OR consum* OR graz* OR herbivor*) AND (manipul* OR experiment* OR mesocosm*) AND (biomass OR abundance OR density OR produc*) AND (replace* OR substitut* OR identit* OR combin*). Using these keywords, we obtained a disproportionately high number of aquatic compared to terrestrial studies so we complemented the list of publications by a second search including the following terms (biological control OR biocontrol) AND (multiple predator OR multi enem* OR multi-predat*). We evaluated all resulting studies and citations therein on whether they met our selection criteria. For inclusion in the meta-analysis, each experiment had to follow a 0/A/B/AB design including a consumer-free control, monocultures of both consumer species, and a combined treatment with both consumers present.

We included studies applying additive or replacement designs. In order to prevent strong interactive effects between consumer species, we excluded all studies where intra-guild predation was likely to be an issue (according to the respective authors). If several samples were recorded, we used the data from the last sampling occasion. Both consumer species had to be able to feed on the majority of resource organisms to prevent unequal resource limitation between consumers. Studies had to report some measure of resource removal, for example, remaining biomass, biovolume, abundance, percent cover, or proportion of removed resource. The reported data were extracted from each publication using the graph and chart digitizer Grab It! (MS Excel). Values on log-scales were back-transformed. We only included studies where all prey types had

been measured in the same unit to allow for exact comparison between treatments.

For each experiment, we compiled information on ecosystem type, temporal and spatial extent, temperature, and experimental setup. We also recorded body weight, generation time, relative initial biomass in monoculture and mixture and feeding type of both consumer species, as well as the number of species, trophic level, and degree of mobility of resource organisms. This set of variables was included to reflect stoichiometric as well as allometric constraints or differences between consumer organisms to test for general patterns in consumer trait-related effects on resource removal. Where possible, we extracted trait information on the relevant species from the original paper, otherwise from publications or online databases (Appendix S2). Most of the trait values varied considerably (several orders of magnitude) across consumer species and were strongly positively skewed. We therefore log-transformed these variables for the statistical analysis.

To compare effect sizes (ES) of loss of each consumer species on resource removal, we calculated log response ratios (Hedges et al. 1999). To account for effects other than consumer species, we first subtracted the values of remaining resource in the treatments containing consumers from the remaining resource in the control. The effect size of losing one consumer from the assemblage was then obtained by calculating log response ratios of the resource consumption in each monoculture treatment over the resource consumption in the mixture treatment.

$$ES_A (\text{loss of species A}) = \log \left(\frac{(\text{Ctrl} - \text{treat B})}{(\text{Ctrl} - \text{treat A} + \text{B})} \right)$$

$$ES_B (\text{loss of species B}) = \log \left(\frac{(\text{Ctrl} - \text{treat A})}{(\text{Ctrl} - \text{treat A} + \text{B})} \right)$$

Negative ESs indicate that the loss of a single species reduced the amount of prey consumed. The log response ratio of the remaining resource biomass in the control over remaining resource biomass in the mixture treatment served as a measure of effect size of loss of both consumers.

$$ES_{AB} (\text{loss of both species}) = \log (\text{ctrl}/\text{treat A} + \text{B})$$

To test for differences between the average effect size in treatments consisting of both consumers in comparison with effect sizes in the treatments representing loss of one species, we applied a

weighted T test (“Hmisc” package) on the data from replacement biomass experiments. Weights were assigned to each study according to the number of experiments they contributed to the analysis.

Based on Spearman’s correlation analyses, we chose a set of non-correlated explanatory variables for the linear mixed-effect model testing for trait- and study design-related effects on the consequences of consumer species removal. In order to account for within-study correlations, we included study identification number (ID) as random effect. In addition, the following independent variables were used: consumer body weight, resource trophic level (autotroph/heterotroph), number of prey species (single/multiple), consumer body weight ratio, type of ecosystem, temperature, and experimental design (additive or replacement). In order to account for confounding effects between experimental design and biomass of removed consumer species, we also tested for interactions between body weight and study design, but assumed independence of explanatory variables otherwise. All statistical analyses were performed in R 3.3.1 (R Core Team 2016). We used robust estimation methods provided in the “lme4” package to estimate the linear mixed-effect model coefficients and bootstrapping procedures (“boot” package) for the calculation of confidence intervals. To assess model fit, we calculate marginal and conditional r -squared values (“MuMIn” package) as described in Nakagawa and Schielzeth (2013).

RESULTS

Overall, we found 66 studies comprising 204 experiments that satisfied our selection criteria. Experiments were roughly evenly distributed across ecosystem types: marine (52), lotic (66), lentic (30) terrestrial (56). Despite including the second set of search terms to target terrestrial studies, the majority of experiments we found were conducted in aquatic environments. Additive (93) and replacement (111) designs were similarly common across experiments. The size range of consumer organisms across experiments spanned eight orders of magnitude from protozoans weighing less than a microgram to medium-sized fish of a few hundred grams. The weight ratios of the two consumer species also varied considerably between one (same body

weight) and differences of three orders of magnitude or more.

Spearman’s correlation analyses revealed significant correlations between several of the recorded trait and experimental design variables. As to be expected, body weight was positively correlated with generation time (0.71, $P < 0.001$) and size of experimental unit (0.62, $P < 0.001$). However, study duration showed slightly negative correlations with body size (-0.28 , $P < 0.001$) and generation time (-0.16 , $P < 0.001$). Body size and the range of size ratios between consumer species also differed between study designs. Both were considerably lower in replacement than in additive designs.

Similar to results in previous multi-consumer studies, effect sizes varied markedly between (var: 0.931) and within (var: 0.595) studies. As expected, log response ratios of consumer influence on resource removal confirmed that the presence of both consumer species in the mixture treatments considerably reduced resource amount (-0.840 ; CI -1.043 , -0.637) compared to the consumer-free control.

The exclusion of one consumer species from the system while accounting for loss in overall consumer biomass by increasing the biomass of the remaining consumer species resulted in a significant reduction of resource removal compared to the two consumer treatments (mean ES: -0.192 ; CI -0.296 , -0.089). This implies that losing one species from a two-consumer system has an overall negative effect on prey consumption, mediated by the particular traits or trait combination which illustrates the importance of differences in consumer traits as opposed to overall consumer abundance or biomass. These effects were consistent across ecosystem types (Fig. 1).

Stepwise model selection produced a model including a significant interaction between body size and experimental design for the fixed effect part of the model (Appendix S1: Table S1). A mixed-effect model with study ID as a random effect confirmed the significant interaction effect of body weight and study design on effect size of species loss (Table 1). However, these two variables only explained small amounts of the variability in the data (marginal explained variance: 9.27%, conditional explained variance: 11.02%). In studies applying an additive design, the negative effect on resource removal increased with

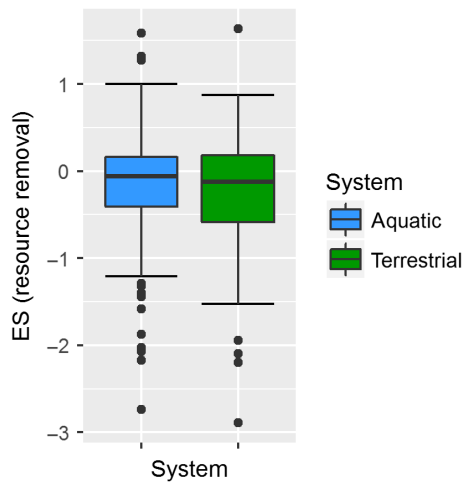


Fig. 1. Effect size (LRR) of the loss of one predator species on resource removal for aquatic and terrestrial biomass replacement design experiments.

increasing body weight of the lost consumer, whereas body weight did not show any effects in studies where missing biomass was replaced (Fig. 2). This effect seems to be independent of the size ratio between the two consumer species as body weight and size ratio were neither correlated nor did size ratio influence the effect size of species loss in general. None of the remaining explanatory variables yielded significant model coefficients.

DISCUSSION

Our meta-analysis used experimental data across disciplines and ecosystems from studies following a 0/A/B/AB design to test for general patterns of species-specific traits and experimental conditions on the effect size of species loss on resource removal. We found that single species loss on average resulted in reduced resource removal. The loss of the entire predator guild

Table 1. Mixed-effect model parameter estimates and bootstrapped 95% confidence intervals.

Coefficient	Estimate	Confidence interval
Intercept	-0.501	-0.663, -0.345
Replacement design	0.173	-0.062, 0.411
Body weight	-0.046	-0.065, -0.029
Replacement design: body weight	0.032	0.008, 0.057

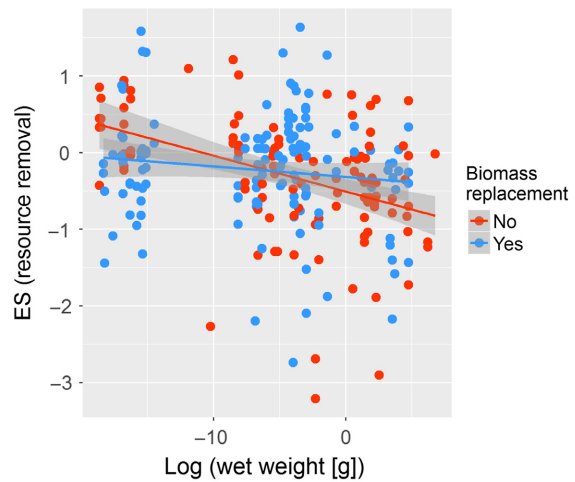


Fig. 2. Linear relationship between the log wet weight of the lost consumer species and the size of the effect of species loss on resource removal for additive (red) and replacement (blue) design experiments. The slope of the regression on replacement design studies is not significant, but was added for comparison.

always had higher impacts than the loss of a single species. From the range of organism traits and study design variables included in our analysis, only the interaction between body size and experimental design significantly influenced the ES of single species.

Most multi-consumer experiments focus on the effects of positive or negative consumer species interactions on resource removal. Our study analyzes multi-species experiments from a different angle in that we were interested in the effect size of species loss in relation to specific traits of each consumer species. Publication bias in terms of effect sizes as a result of species loss is therefore unlikely to be an issue in this analysis since the studies we compiled aim at investigating various kinds of consumer species interactions. Although we explicitly excluded studies which assumed intra-guild predation, other unobserved positive interactions such as enhanced catchability of prey caused by behavioral changes due to the presence of the other predator species (Losey and Denno 1998) and strong negative interactions due to, for example, competitive displacement of one predator species (Atwood et al. 2014) are likely part of the reason for the high range of effect sizes. Nevertheless, we are confident that the general pattern is attributable

to complementarity in species traits instead of direct consumer interactions.

Our study differs from recent meta-analyses (Griffin et al. 2013, Katano et al. 2015) in that we do not quantify effect sizes of species loss across a diversity gradient, but intend to link the loss of species-specific trait values to consequences on resource removal by explicitly looking at single species loss from two-consumer systems. Griffin et al. (2013) found prey removal of multiple consumers to be higher than the average species, but not higher than the most effective consumer species in monoculture. While this result is plausible given the huge number of possible interactions between consumer species, our analysis implies that on average the loss of one species and its according set of traits from a two-consumer system significantly will still reduce resource removal, highlighting the importance of complementarity in consumer traits as opposed to consumer density. Griffin et al. (2013) also point out that the better performance of some monocultures could vanish with increasing length of study duration as only rarely temporal extent of experiments exceeds the generation time of investigated organisms. The experiments in our analysis also showed relatively short study durations compared to consumer generation times (on average). As a consequence, study duration mostly limited reproduction of the remaining species and prevented the replacement of missing biomass in the one consumer treatments. However, in additive design experiments where we found increasingly negative effect sizes with increasing body size of the lost consumer species, study duration might have played a role, because consumer size within the same experiment was highly positively correlated (Appendix S1: Fig. S2). As a consequence, experiments with very small organisms more likely exceeded the generation times of the consumer species and therefore possibly allowed for partial replacement of consumer biomass mitigating consumer loss effects. Other explanations for greater negative impacts on resource removal in case of loss of large consumer species (Basset and Angelis 2007) are differences in prey size range across consumer species due to varying body size (Brose et al. 2006, Boudreau et al. 2013) or simply loss of greater amounts of consumer biomass.

However, this explanation unlikely applies to our analysis as size ratios between consumers did not show any effect on resource removal.

CONCLUSIONS

Overall, our analysis of over 200 consumer loss experiments supports the hypothesis that the reduction in resource removal due to loss of a consumer species can on average not be fully compensated for by biomass increases in the remaining species. However, we did not find significant associations between single traits and the magnitude of effect size.

ACKNOWLEDGMENTS

This study was funded by the Ministry of Science and Culture of Lower Saxony as part of the project “Biodiversity-Ecosystem Functioning across marine and terrestrial Ecosystems (BEFmate)”.

LITERATURE CITED

- Abrams, P. A. 2014. Why ratio dependence is (still) a bad model of predation. *Biological Reviews of the Cambridge Philosophical Society* 90: 794–814.
- Aljetlawi, A. A., and K. Leonardsson. 2003. Survival during adverse seasons reveals size-dependent competitive ability in a deposit-feeding amphipod, *Monoporeia affinis*. *Oikos* 101:164–170.
- Arditi, R., and L. R. Ginzburg. 1989. Coupling in predator-prey dynamics: ratio-dependence. *Journal of Theoretical Biology* 139:311–326.
- Atwood, T. B., E. Hammill, D. S. Srivastava, and J. S. Richardson. 2014. Competitive displacement alters top-down effects on carbon dioxide concentrations in a freshwater ecosystem. *Oecologia* 175: 353–361.
- Balvanera, P., A. B. Pfisterer, N. Buchmann, J.-S. He, T. Nakashizuka, D. Raffaelli, and B. Schmid. 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters* 9:1146–1156.
- Basset, A., and L. D. Angelis. 2007. Body size mediated coexistence of consumers competing for resources in space. *Oikos* 116:1363–1377.
- Boudreau, M. L., M. R. Boudreau, and D. J. Hamilton. 2013. The influence of body size on foraging facilitation and kleptoparasitic behavior in the green crab (*Carcinus maenas*). *Journal of Experimental Marine Biology and Ecology* 449:330–334.

- Brose, U., T. Jonsson, E. L. Berlow, P. Warren, C. Banasek-Richter, L.-F. Bersier, J. L. Blanchard, T. Brey, and S. R. Carpenter. 2006. Consumer-resource body size relationships in natural food webs. *Ecology* 87:2411–2417.
- Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a metabolic theory of ecology. *Ecology* 85:1771–1789.
- Bruno, J. F., and B. J. Cardinale. 2008. Cascading effects of predator richness. *Frontiers in Ecology and the Environment* 6:539–546.
- Byrnes, J. E., and J. J. Stachowicz. 2009. The consequences of consumer diversity loss: different answers from different experimental designs. *Ecology* 90:2879–2888.
- Cardillo, M., G. M. Mace, K. E. Jones, J. Bielby, O. R. P. Bininda-emonds, and W. Sechrest. 2005. Multiple causes of high extinction risk in large mammal species. *Science* 309:1239–1241.
- Cardinale, B. J., C. T. Harvey, K. Gross, and A. R. Ives. 2003. Biodiversity and biocontrol: emergent impacts of a multi-enemy assemblage on pest suppression and crop yield in an agroecosystem. *Ecology Letters* 6:857–865.
- Cardinale, B. J., D. S. Srivastava, J. E. Duffy, J. P. Wright, A. L. Downing, M. Sankaran, and C. Jouseau. 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature* 443:989–992.
- Cardinale, B. J., et al. 2012. Biodiversity loss and its impact on humanity. *Nature* 486:59–67.
- Casula, P., A. Wilby, and M. B. Thomas. 2006. Understanding biodiversity effects on prey in multi-enemy systems. *Ecology Letters* 9:995–1004.
- Crumrine, P. W., and P. H. Crowley. 2003. Partitioning components of risk reduction in a dragonfly-fish intraguild predation system. *Ecology* 84:1588–1597.
- Davenport, J. M., and D. R. Chalcraft. 2013. Nonconsumptive effects in a multiple predator system reduce the foraging efficiency of a keystone predator. *Ecology and Evolution* 3:3063–3072.
- Dornelas, M., N. J. Gotelli, B. McGill, H. Shimadzu, F. Moyes, C. Sievers, and A. E. Magurran. 2014. Assemblage time series reveal biodiversity change but not systematic loss. *Science* 344:296–299.
- Duffy, E. J., J. Paul Richardson, and E. A. Canuel. 2003. Grazer diversity effects on ecosystem functioning in seagrass beds. *Ecology Letters* 6:637–645.
- Elahi, R., M. I. O'Connor, J. E. K. Byrnes, J. Dunic, B. K. Eriksson, M. J. S. Hensel, and P. J. Kearns. 2015. Recent trends in local-scale marine biodiversity reflect community structure and human impacts. *Current Biology* 25:1938–1943.
- Finke, D. L., and R. F. Denno. 2005. Predator diversity and the functioning of ecosystems: the role of intraguild predation in dampening trophic cascades. *Ecology Letters* 8:1299–1306.
- Griffin, J. N., J. E. K. Byrnes, and B. J. Cardinale. 2013. Effects of predator richness on prey suppression: a meta-analysis. *Ecology* 94:2180–2187.
- Hedges, L. V., J. Gurevitch, and P. S. Curtis. 1999. The meta-analysis of response ratios in experimental ecology. *Ecology* 80:1150–1156.
- Heithaus, M. R., A. Frid, A. J. Wirsing, and B. Worm. 2008. Predicting ecological consequences of marine top predator declines. *Trends in Ecology and Evolution* 23:202–210.
- Hillebrand, H., and B. J. Cardinale. 2004. Consumer effects decline with prey diversity. *Ecology Letters* 7:192–201.
- Jonsson, M., O. Dangles, B. Malmqvist, and F. Guérol. 2002. Simulating species loss following perturbation: assessing the effects on process rates. *Proceedings of the Royal Society of London B: Biological Sciences* 269:1047–1052.
- Katano, I., H. Doi, B. K. Eriksson, and H. Hillebrand. 2015. A cross-system meta-analysis reveals coupled predation effects on prey biomass and diversity. *Oikos* 124:1427–1435.
- Kratina, P., M. Vos, and B. R. Anholt. 2007. Species diversity modulates predation. *Ecology* 88:1917–1923.
- Krenek, L., and V. H. W. Rudolf. 2014. Allometric scaling of indirect effects: Body size ratios predict non-consumptive effects in multi-predator systems. *Journal of Animal Ecology* 83:1461–1468.
- Losey, J. E., and R. F. Denno. 1998. Positive predator-predator interactions: enhanced predation rates and synergistic suppression of aphid populations. *Ecology* 79:2143–2152.
- Mccooy, M. W., A. C. Stier, and C. W. Osenberg. 2012. Emergent effects of multiple predators on prey survival: the importance of depletion and the functional response. *Ecology Letters* 15:1449–1456.
- Nakagawa, S., and H. Schielzeth. 2013. A general and simple method for obtaining R² from generalized linear mixed-effects models. *Methods in Ecology and Evolution* 4:133–142.
- Petchey, O. L., et al. 2004. Species loss and the structure and functioning of multitrophic aquatic systems. *Oikos* 104:467–478.
- Preisser, E. L., D. I. Bolnick, and M. F. Bernard. 2005. Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology* 86:501–509.
- R Core Team. 2016. R: a language and environment for statistical computing. R Core Team, Vienna, Austria.
- Schmitz, O. J. 2007. Predator diversity and trophic interactions. *Ecology* 88:2415–2426.

- Schneider, F. D., S. Scheu, and U. Brose. 2012. Body mass constraints on feeding rates determine the consequences of predator loss. *Ecology Letters* 15: 436–443.
- Solan, M., B. J. Cardinale, A. L. Downing, K. A. M. Engelhardt, J. L. Ruesink, and D. S. Srivastava. 2004. Extinction and ecosystem function in the marine benthos. *Science* 306:1177–1180.
- Soluk, D. A., and N. C. Collins. 1988. Synergistic and interference between fish and stoneflies: facilitation interactions among stream predators. *Oikos* 52: 94–100.
- Tylianakis, J. M., and C. M. Romo. 2010. Natural enemy diversity and biological control: making sense of the context-dependency. *Basic and Applied Ecology* 11:657–668.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1742/full>