

Effects of predator richness on prey suppression: a meta-analysis

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Abstract. It is well established that species richness of primary producers and primary consumers can enhance efficiency of resource uptake and biomass production of respective trophic levels. At the level of secondary consumers (predators), however, conclusions about the functional role of biodiversity have been mixed. We take advantage of a recent surge of published experiments (totaling 46 since 2005) to both evaluate general effects of predator richness on aggregate prey suppression (top-down control) and explore sources of variability among experiments. Our results show that, across experiments, predator richness enhances prey suppression relative to the average single predator species (mean richness effect), but not the best-performing species. Mean richness effects in predator experiments were stronger than those for primary producers and detritivores, suggesting that relationships between richness and function may increase with trophic height in food webs. The strength of mean predator richness effects increased with the spatial and temporal scale of experiments, and the taxonomic distinctness (TD, used as a proxy of phylogenetic diversity) of species present. This latter result suggests that TD captures important aspects of functional differentiation among predators and that measures of biodiversity that go beyond species richness may help to better predict the effects of predator species loss.

Key words: biodiversity; carnivores; complementarity; ecosystem function; phylogenetic diversity, PD; taxonomic distinctness, TD.

INTRODUCTION

Human-driven species invasions and extinctions are changing levels of biodiversity across nearly all of Earth's ecosystems (Naeem et al. 2012). Predators are known to be disproportionately prone to anthropogenic extinction compared to other trophic groups (Terborgh et al. 2001), and the ecosystem-level consequences of losing entire predator guilds or trophic levels have been widely documented (Schmitz et al. 2000, Estes et al. 2011). However, biodiversity loss may also occur through the deletion of species within guilds of predators, reducing species richness (or other aspects of diversity) while leaving the guild in place. Theory and experiments suggest that these more insidious, within-predator level, biodiversity losses may also influence top-down control of prey populations and have cascading impacts on ecosystem-level processes (Duffy 2002, Ives et al. 2005, Duffy et al. 2007).

Since the mid-1990s, a large number (>400) of experiments have tested effects of within-trophic-level biodiversity on ecosystem functioning (Cardinale et al. 2012). The overwhelming majority of these studies (>85%) have focused on lower trophic levels (producers and primary consumers) and recent syntheses of this work have revealed generally positive, though deceler-

ating, effects of species richness on both biomass and resource uptake of these levels (Cardinale et al. 2006, 2011). In contrast, explicit tests of the effects of predator (secondary consumer) richness on ecosystem functioning have lagged behind, and the relatively sparse data has been ambiguous. A number of studies suggest predator richness may operate analogously to richness within lower trophic levels, enhancing ecosystem functions through so-called sampling effects and niche complementarity (Ives et al. 2005, Casula et al. 2006). Other studies, however, suggest that the added behavioral and trophic complexities of predators (e.g., intra-guild predation, IGP) may preclude a general richness–functioning relationship and even generate negative relationships (e.g., Finke and Denno 2004). It therefore remains unclear whether general effects of predator richness exist and, if so, whether they are comparable to those observed within lower trophic levels (Duffy 2002, Bruno and Cardinale 2008).

Average, or general, effects of predator richness may belie considerable variability in effect size/sign among studies. Identifying sources of variability in effects of predator richness will improve our explanatory power and ultimately predictive ability (Tylianakis and Romo 2010). In this study, we focus on two potential sources of variability that have not been previously explored within or across predator richness experiments: (1) the average taxonomic distance between predator species included in a diverse mixture (i.e., taxonomic distinctness, TD); and

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(2) the spatiotemporal scale of experiments. As with measures of evolutionary divergence based on molecular phylogenies (e.g., phylogenetic diversity, PD), TD potentially provides a useful surrogate of functional diversity that circumvents selection and measurement of specific traits (Clarke and Warwick 1998, Srivastava et al. 2012). If TD is able to effectively capture the functional diversity of predator assemblages, it may help explain the strength of predator richness effects mediated through mechanisms that depend on functional differentiation, such as niche complementarity (Petchey and Gaston 2002). Meanwhile, the greater environmental heterogeneity afforded by increases in spatial and temporal scales should increase opportunities for niche complementarity between species, potentially strengthening the effect of species richness on ecosystem functioning (Cardinale et al. 2007, Tylianakis et al. 2008, Reich et al. 2012).

We take advantage here of a recent surge in the number of experiments that have manipulated predator richness (three or more species) and measured impacts on prey suppression (top-down control) to take a fresh look at how the diversity of secondary consumers impacts ecosystem functioning. We used quantitative meta-analysis of published studies to (1) assess whether any general effects of predator richness on the functioning of predator groups (measured as aggregate prey suppression) are detectable, (2) compare the magnitude of predator richness effects to those documented for other trophic groups, and (3) explore sources of variability in the strength of predator richness effects (effect size) among studies.

METHODS

Selection of experiments.—Our review focused on studies published through 2010 that have experimentally manipulated the richness of predators and/or other natural enemies and measured effects on the density of prey (resources). We used standard literature search techniques (detailed in Appendix A) to identify experiments that met the following criteria: predator richness was under direct experimental control; the highest diversity level included three or more species; all species in the qualifying diversity level (i.e., more than three species) were represented in parallel as single-species treatments (monocultures); and the monoculture treatments had the same mean density of predators as the species rich treatment (i.e., a substitutive experimental design was used). When orthogonal experimental factors (e.g., predator density) were employed, each level of this second factor was considered an independent predator richness experiment. Experiments were categorized based on the broad ecosystem type in which they were conducted: coastal (marine), agricultural (see Plate 1), or freshwater. We found a total of 46 individual experiments from 19 published papers that met the above criteria (Cochran-Stafira and von Ende 1998, Aquilino et al. 2005, Bruno and O'Connor 2005, Wilby et al. 2005,

Byrnes et al. 2006, Snyder et al. 2006, 2008; Straub and Snyder 2006, 2008; Jonsson et al. 2007, Douglass et al. 2008, Finke and Snyder 2008, Griffen et al. 2008, Griffiths et al. 2008, Nilsson et al. 2008, O'Connor et al. 2008, Byrnes and Stachwicz 2009, O'Connor and Bruno 2009, Northfield et al. 2010). All studies had a maximum species richness of between three and five (mean of 3.63). Further details of the studies can be found in Appendix B.

In order to compare effects of predator richness to the effects of richness at other trophic levels, we used an existing database (Cardinale et al. 2006, 2011, 2012) that has summarized studies published through 2009 that have measured effects of species richness on suppression of resource densities (e.g., total soil N for plant studies; plant biomass for herbivore studies). This yielded 34 herbivore-level studies, 15 producer-level studies, and 32 detritivore-level studies to compare to the 46 predator-level studies. To control for the generally higher levels of species richness in plant studies and to reflect predator studies, we performed an additional analysis that considered a sub-set of treatments used in experiments to isolate effects of species richness at comparable (i.e., three or four species) maximal levels.

Quantification of effect sizes.—For each experiment considered, we used the densities of prey (abundance per area or volume) reported in single-species treatments (monocultures) and the highest predator richness treatment (polyculture) at the final time point of experiments (to maximize the potential for treatments of varying diversity levels to diverge) to calculate two metrics (log-response ratios; see Hedges et al. [1999]) of the predator richness effect on prey suppression. The first of these log-response ratios quantifies the mean richness effect (LR_{mean}) and measures whether the most species rich predator mixture suppresses prey to a lesser or greater degree than the average of its component species in monoculture. The second log ratio, LR_{max} , gauges the performance of the polyculture relative to the predator species that is most effective at suppressing prey (i.e., highest efficiency). These metrics were both reflected (multiplied by minus 1) to convert from measures of effects on final prey density (the common response reported in studies) to effects on the level of prey suppression achieved by a predator group. This meant that positive effects can be interpreted more intuitively as a positive effect of diversity on the magnitude of the aggregate process of interest, i.e., prey suppression. LR_{mean} was therefore calculated as $-1 \times \ln(Y\bar{p}/Y_{im})$ and LR_{max} as $-1 \times \ln(Y\bar{p}/Y_{im})$, where Y is the mean final prey density, \bar{p} is the polyculture (diverse species mixture), and im and \hat{im} are the average and best-performing single-species treatments (monocultures), respectively (e.g., Cardinale et al. 2006, 2011).

Candidate explanatory variables.—Temporal and spatial scales were calculated with respect to the species included in the diverse species mixture. Because all species in diverse mixtures also occurred in parallel

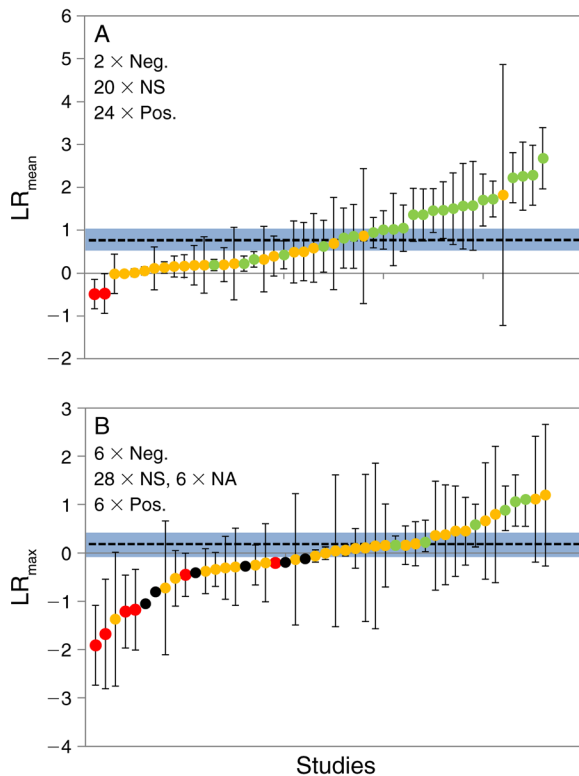


FIG. 1. Effects of predator richness on prey suppression (A) in terms of the mean richness effect (log-response ratio, LR_{mean}) and (B) relative to the best-performing individual species (log-response ratio, LR_{max}). Studies are arranged in order of effect size. Effects from each experiment are color coded: negative effect (Neg., red), no effect (NS, yellow), and positive effect (Pos., green). Black points indicate that confidence interval (and therefore statistical significance) could not be established. The horizontal dashed black lines show the grand means of each biodiversity effect, while the shaded blue areas show the 95% confidence intervals of these means.

monocultures in all studies, our scale measures provide representative experiment-wide estimates. Temporal scale was calculated for each experiment (i) as $\ln(\text{duration}_i / \text{mean generation time}_i)$, where both duration of the experiment and the mean generation times of all of the predator species used in experiment i are expressed in days. Spatial scale was calculated as $\ln(\text{area}_i / \text{mean body size}_i)$ for terrestrial systems and $\ln(\text{volume}_i / \text{body size}_i)$ for aquatic systems, where area is expressed in square meters, volume in liters, and the mean body sizes of all of the predator species used in experiment i expressed in grams. Spatial and temporal scale of experiments exhibited a strong positive correlation, indicating that larger experiments were also run longer (Pearson's $r = 0.764$, $P < 0.001$). We therefore used principal-components analysis (PCA) to reduce these to a single variable (the first principal component, henceforth referred to as scale), explaining 88% of the joint variance in these two dimensions of scale. We also calculated a proxy of predator phylogenetic diversity included in the

highest species richness treatment in each experiment in our meta data set. Because molecular phylogenies are not currently available for all of the taxa included in our meta data set, we based our estimation of phylogenetic diversity on the topology of the Linnaean taxonomic classification (i.e., phylum, class, order, family, genus) dendrogram of all species used in focal experiments. This measure, taxonomic distinctness (TD), quantifies the mean taxonomic distance between species in a community and is calculated as $TD = [\sum \sum_{i < j} \omega_{ij}] / [s(s-1)/2]$, where ω is the branch length between all possible species pairs (i and j) and s is the total number of species in the diverse predator treatment (see Clarke and Warwick 1998). We assumed equal branch lengths for all taxa across each level of hierarchical classification.

Analysis.—Analyses were performed in the R package nlme (available online).⁵ In all statistical models, we accounted for the fact that several independent experiments were included within some studies (resulting from, e.g., inclusion of factors orthogonal to species richness) by fitting a mixed model with experiment included as a random effect using Restricted Maximum Likelihood (REML). We also evaluated all results using a variance-weighted approach, but we found no differences that would alter our main conclusions. We thus present the unweighted results because these do not penalize more realistic, but more variable, field studies (Cardinale et al. 2006). To assess variability in biodiversity effects across individual experiments, we began by tallying positive and negative effects with respect to both LR_{mean} and LR_{max} , based on means \pm 95% confidence intervals. We then used a mixed model to evaluate general mean effect sizes of LR_{mean} and LR_{max} . To test whether effects of predator richness on prey suppression (LR_{mean} and LR_{max}) differ from other well-studied trophic groups (i.e., herbivores, plants, and detritivores) we fitted mixed-effects models that allowed variances to differ among trophic groups (after initial inspection of residuals). Because the number of species included in the most diverse polyculture varied across trophic levels (mean \pm SD; predators, 3.63 ± 1 species; herbivores, 4 ± 1 species; plants, 14 ± 6.6 species; detritivores, 5 ± 3 species), we also performed this test with diversity effects resulting from equivalent numbers of species (i.e., 3–4). We further explored sources of variability in effect sizes among predator studies by fitting a general linear mixed-effects model (GLMM) with study system, scale and taxonomic diversity (TD) as fixed effects. We did not attempt to include interactions between study system and scale or TD because one of the three systems (agricultural) showed insufficient variation in these factors. TD was mean centered and scaled (to SD units) prior to analysis.

⁵ <http://cran.r-project.org/web/packages/nlme>

RESULTS

General effects across predator studies.—Individual experiments showed significant positive effects of predator richness on prey suppression in 24 of 46 cases, no significant effect in 20 of 46 cases, and significant negative effects in 2 of 46 cases (Fig. 1A). When averaged across all studies, the mean richness effect (LR_{mean}) was significantly greater than zero ($F_{1,45} = 50.822, P < 0.001$; Fig. 1A note black dashed line and blue band, which are the mean and 95% CI). This indicates that species rich mixtures of predators suppress prey densities to a greater degree than their component species do alone, on average. Among individual experiments there was a predominance of nonsignificant effects on LR_{max} (28 of 40 effect sizes), with positive and negative significant effects equally rare (6 of 40 for each). Relative to the best-performing single species, that is, the predator species that reduces prey populations to the lowest level, diverse mixtures of predators were equivalent to the most efficient single predator species at suppressing prey ($F_{1,45} = 0.783, P = 0.381$; Fig. 1B, note black dashed line and blue band, which are the mean and 95% CI).

Effects relative to other trophic levels.—When we estimated effects of biodiversity on resources using the highest levels of species used in an experiment, we found that LR_{mean} differed significantly among trophic levels ($F_{3,74} = 7.057, P < 0.001$; Fig. 2A). The effect of predator richness on LR_{mean} was indistinguishable from that of herbivores ($P = 0.303$). But despite much lower levels of species richness being used in experiments, predator diversity effects on prey suppression were significantly stronger than effects of plant richness on inorganic resource capture ($P = 0.005$), and for detritivore richness on consumption of dead organic matter ($P < 0.001$; Fig. 2A). When we standardized levels of richness and only compared experimental units containing three to four species (the maximum of most predator studies) the effect of trophic group on LR_{mean} (and notably the difference between predators and producers) grew slightly stronger ($F_{3,74} = 7.443, P < 0.001$; Fig. 2A). This analysis suggest that, on a per-species basis, predators have a greater impact on their resources than do lower trophic levels. LR_{max} did not differ significantly among trophic levels (at $\alpha = 0.05$) when considering the highest levels of species richness ($F_{3,73} = 2.500, P = 0.066$; Fig. 2B). However, at standardized richness, the effect of trophic level strengthened ($F_{3,73} = 3.209, P = 0.028$), with a significant difference between predator and plants emerging ($P = 0.036$, Fig. 2B). Notably, LR_{max} at the plant level was significantly negative ($P < 0.001$) but was neutral at other trophic levels, including predators ($P = 0.118$; Fig. 2B). This analysis suggest that, while diverse mixtures of predators are functionally equivalent to the best-performing individual predators, diverse mixtures of plants are functionally inferior to the best-performing individual species.

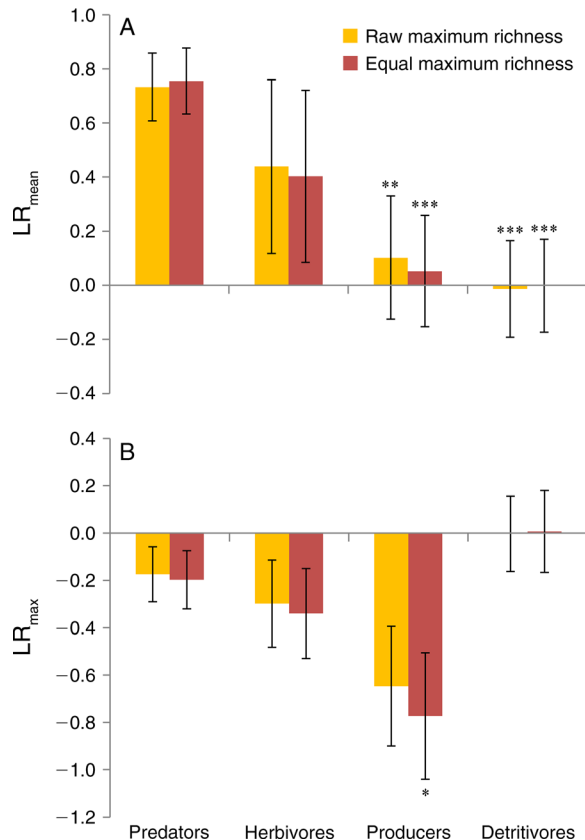


FIG. 2. Effects of species richness on resource suppression within different trophic levels. Results are shown in terms of (A) the mean richness effect (LR_{mean}) and (B) relative to the best-performing individual species (LR_{max}). Error bars are $\pm SE$. Diversity effects were calculated based on both the highest species richness level within an experiment (raw maximum richness, yellow bars), which varied across systems (see *Methods*), and at comparable levels of highest richness level (i.e., 3–4 species; equal maximum richness, red bars). Quantitative (but not qualitative) estimates of mean effects of predator richness slightly diverge from Fig. 1 due to inclusion of extra terms in the mixed model to test trophic-level effect and allow variances to differ among groups (see *Methods*). Asterisks indicate trophic levels that differ significantly from predators. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Sources of variability in the effect of predator richness.—In our final set of analyses, we examined how the type of ecosystem, the spatiotemporal scale of experiments, and taxonomic differentiation among predator species, individually correspond to the diversity effect size. LR_{mean} did not vary consistently with type of study system (i.e., agricultural, freshwater, or marine; $F_{2,37} = 1.661, P = 0.193$). However, LR_{mean} tended to be higher in experiments that included mixtures of predator species that incorporated greater TD ($F_{1,37} = 18.517, P < 0.001$, Fig. 3A) and in experiments that were larger in scale ($F_{1,37} = 5.581, P = 0.024$, Fig. 3B). LR_{max} did not vary with system ($F_{2,37} = 1.269, P = 0.293$), TD ($F_{1,37} = 1.762, P = 0.193$, Fig. 3C) or scale ($F_{1,37} = 0.339, P = 0.565$, Fig. 3D).

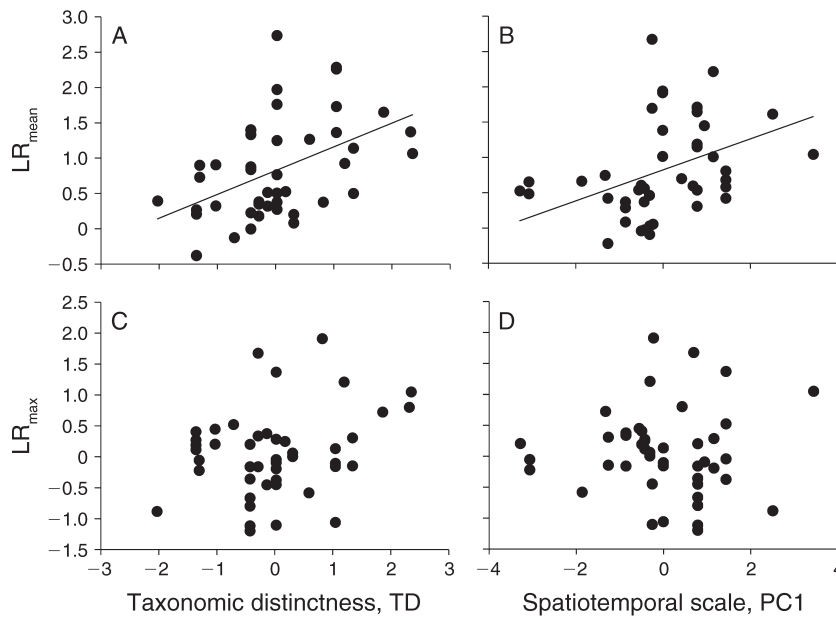


FIG. 3. Sources of variability in the effects of predator richness on prey suppression. Positive effects of (A) taxonomic distinctness (TD, the average taxonomic distance between predator species included in a diverse mixture) and (B) spatiotemporal scale on LR_{mean} , and (C) no significant effects of TD and (D) spatiotemporal scale on LR_{max} . Spatiotemporal scale was calculated from a principal-components analysis including the separate spatial and temporal scales of each experiment (see *Methods* for details). Response variables in panels A and B were corrected for the effect of scale and TD, respectively.

DISCUSSION

Individual studies and former syntheses have suggested that effects of predator richness on prey suppression may be sufficiently variable to defy broad generalizations (Bruno and Cardinale 2008, Cardinale et al. 2012). Individual studies in our analysis certainly spanned the range of possible effects with a mix of positive, negative, and nonsignificant mean richness effects (LR_{mean}). While this variation lends some support to previous conclusions that a single predator-richness-prey-suppression relationship may not exist, it is striking to us that this new meta-analysis, bolstered by a surge of recent experiments, has revealed a general positive mean richness effect on prey suppression. By focusing exclusively on experimental studies in which predator richness was directly manipulated and initial prey density equal across all treatments, our findings complement and broaden those of Letourneau et al. (2009), whose meta-analysis of relationships between predator richness and arthropod herbivore density in terrestrial systems was dominated by correlative studies and therefore open to alternative explanations. Combined with previous meta-analyses of biodiversity experiments focusing on lower trophic levels, our results point toward a general pattern of enhanced ecosystem function with species richness, regardless of trophic level under investigation.

Predator richness did not, however, strengthen prey suppression relative to the single most effective species (LR_{max}), perhaps implying that as long as the single

most efficient predator is conserved, losses of predator richness may not affect prey suppression. For several reasons, however, this absence of a so-called “transgressive overyielding” effect should be interpreted cautiously. First, it has been suggested that a statistical bias may exist in the calculation of this metric (Schmid et al. 2008). Second, the probability of detecting transgressive overyielding appear to increase with temporal and potentially spatiotemporal scale of experiments (Cardinale et al. 2011) and therefore the relatively short-term and small-scale experiments that dominate our data set may underestimate the occurrence of transgressive overyielding in natural communities (see also Duffy 2009). Nevertheless, the fact that individual species have potential to maintain prey suppression at levels equal to, or exceeding, species-rich mixtures highlights how much variability exists among individual species in experiments (species identity effects). It also suggests that the order of predator extinction (and therefore which species remain extant) could have large impacts on the relationship between predator richness and prey suppression in natural systems (Straub and Snyder 2006, O’Connor et al. 2008).

Our finding that mean richness effects (LR_{mean}) of predators are stronger than those of both plant richness and decomposer richness indicates that species losses may have the strongest effects at higher trophic levels, where they are thought to be most likely to occur, as previously predicted (Duffy 2002, 2003). We tentatively attribute the difference between our findings and those of Cardinale et al. (2006), who reported consistent

PLATE 1. A seven-spot ladybug (*Coccinella septempunctata*) attacking a black bean aphid (*Aphis fabae*). Ladybugs were often among the most effective predators in agricultural biodiversity experiments (e.g., Straub and Snyder 2006). Photo credit: Matt Cole.



effects of richness within different trophic levels on resource depletion, to our greater power to detect differences owing to the recent increase in number of studies, and our more restrictive study selection criteria (i.e., final time point only, substitutive design only) that likely minimized variability. The cause of the differential effect of diversity across trophic levels that we found is currently unclear, but we can speculate about possible explanations. First, actively moving predators may experience more intense intraspecific competition than organisms within lower trophic levels, which might strengthen effects of resource-use complementarity (Griffin et al. 2008, Northfield et al. 2010). Second, the mobility of predators and their prey may also promote synergistic effects due to cooperative foraging and/or conflicted prey escape behaviors (e.g., Losey and Denno 1998). Third, the general decline in richness with trophic level in food webs (Woodward et al. 2005) suggests that species packing and associated niche overlap may decline with trophic level, rendering predator species more functionally unique. These possibilities, and perhaps others, deserve attention in future work since predicting the consequences of extinction will now obviously require that we better understand and account for the potentially differential effects of richness within trophic groups.

Our results suggest that the strengthening of mean richness effects with space and time that has been reported for primary producer studies (Cardinale et al. 2011, Reich et al. 2012) also applies to predator studies. Although, like previous workers, we did not investigate mechanisms underlying effects of scale, we can forward several possible non-exclusive explanations. First, as previously hypothesized, larger spatiotemporal scales tend to provide more heterogeneity in space and time and greater scope for species complementarity (Stachowicz et al. 2008, Duffy 2009). Second, larger temporal scales should allow greater potential for the more efficient resource capture of diverse predator populations to be converted into greater aggregate population size/bio-

mass, as predicted by theory (Ives et al. 2005), potentially further strengthening the effect of predator richness on prey suppression. Unfortunately, few experiments have reported, or have been conducted over sufficient time periods to allow, changes in predator population size/biomass. As such, there is no way to presently assess how predator population sizes vary with richness in experiments. Further experimental work is required before we can assess whether the two mechanisms forwarded above are correct interpretations of increasing predator diversity effects at larger empirical scales. Nevertheless, our findings warn that experiments performed to date likely underestimate effects of predator richness on prey suppression at the larger spatiotemporal scales pertinent to management decisions (Duffy 2009).

The mean effect of predator richness on prey suppression also increased with TD, a taxonomically based proxy of PD. This finding supports the idea that the evolutionary divergence of species can capture important aspects of functional diversity (FD; Cadotte et al. 2009, Flynn et al. 2011, Srivastava et al. 2012; but see Best et al. 2013), which in turn drives effects of predator richness on prey suppression, and suggests that the phylogenetic or taxonomic uniqueness of species relative to others in the same community could be a useful indicator of the functional consequences of its extinction. Elucidation of the specific mechanisms underlying TD effects on prey suppression reported here is not possible given the data that presently exists, but may have included enhanced resource-use complementarity (e.g., Northfield et al. 2010), synergistic prey capture (e.g., Losey and Denno 1998) and even reduced potential for intraguild predation (IGP). Notably, neither spatial scale nor TD explained significant portions of variability in LR_{max} . We speculate that this is because the effect of richness on LR_{max} not only depends on species interactions but also on variability among monocultures and the presence or absence of extreme species, which may not be as clearly positively related to TD/PD.

In apparent contradiction to our findings, previous work on multiple predator (MP) interactions has frequently found that negative interspecific interactions between predators (e.g., IGP) reduces the strength of prey suppression (Sih et al. 1998, Vance-Chalcraft et al. 2007). This can perhaps be reconciled with the biodiversity–ecosystem function (BEF) studies reported here by appreciating that these bodies of literature have had different foci, used different approaches and in many cases asked different questions. First, while MP studies are designed to isolate effects of specific individual interactions, BEF studies (as defined here) include three or more species and therefore reveal the net effects of multiple interactions among predators, potentially reducing variability of effects (by averaging over more interactions) and creating higher potential for negative interactions (i.e., strong interference or IGP) to be counteracted by niche differences among species and/or positive interactions. Second, MP studies have tended to use additive experimental designs and BEF studies substitutive designs, which are not directly comparable (Griffen 2006, Byrnes and Stachowicz 2009). Regardless of these differences, we anticipate that MP studies will continue to provide important insights into the nature and strength of interactions between specific pairs of predators, which can ultimately only aid in the task of understanding effects of predator richness.

In summary, we reported here that, despite moderate variability in effect sizes among individual studies, a general positive mean effect of predator richness on prey suppression is now clear and this effect exceeds analogous richness effects within both plant and detritivore trophic levels. We also found that variability in effect size among individual predator diversity studies can be partially explained by both the scale of the experiments and the degree of predator taxonomic distinctness. While the controlled manipulative experiments synthesized here provide clear evidence of the functional role of predator richness, they were inevitably limited by practical constraints in scope and scale. We look forward to innovative future studies that expand our scales of understanding and begin to consider the cascading effects of predator biodiversity within the context of more complete and complex natural food webs.

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SUPPLEMENTAL MATERIAL

Appendix A

Details of literature search methodology and short discussion of study selection criteria ([Ecological Archives E094-203-A1](#)).

Appendix B

Details of individual studies used in meta-analysis, including data source, experimental treatments, and maximum species richness ([Ecological Archives E094-203-A2](#)).

Supplement

Meta-data used in analyses ([Ecological Archives E094-203-S1](#)).