

DENSITY-DEPENDENT EFFECTS OF PREDATOR SPECIES-RICHNESS IN DIVERSITY–FUNCTION STUDIES

GEORGIANNE J. K. GRIFFITHS,^{1,5} ANDREW WILBY,² MICHAEL J. CRAWLEY,³ AND MATTHEW B. THOMAS^{1,4}

¹NERC Centre for Population Biology, Imperial College, Silwood Park, Ascot, Berkshire SL5 7PY United Kingdom

²Department of Biological Sciences, University of Lancaster, Bailrigg, Lancaster LA1 4YQ United Kingdom

³Department of Life Sciences, Imperial College, Silwood Park, Ascot, Berkshire SL5 7PY United Kingdom

⁴Center for Infectious Disease Dynamics and Department of Entomology, Penn State, University Park, Pennsylvania 16802 USA

Abstract. Ecological systems often exhibit a positive but saturating diversity–function curve. Variation in the mechanisms generating this relationship can alter the slope and variance of the curve, with implications for the optimal management of biodiversity for ecosystem services. In biological control, prevalence of selection effects supports augmentation of the most effective natural enemy, but complementarity effects support augmentation of natural enemy diversity. Optimization of biological control strategies from the results of diversity–function studies is limited because few consider changes in function with relative or absolute changes in abundance, and many confound the relative importance of richness and density through experimental designs (additive and substitutive). By manipulating species richness across an abundance gradient we show that effects of species richness are density dependent and indicate how this may be incorporated into experimental designs or models predicting resource consumption in diverse communities. Furthermore, the underlying mechanisms causing an observed diversity–function response, and its associated variation, changed across the richness–abundance gradient. Finally, species-rich assemblages provided higher levels of minimum function than species-poor assemblages, without any compromise on the maximum function possible.

Key words: additive; biological control; complementarity; interference; resource partitioning; selection; substitutive.

INTRODUCTION

Concerns regarding the impact of biodiversity loss on ecosystem services, ecosystem functioning and human well-being are driving conservation and agricultural policy development at national and global levels (Curry 2002, Millennium Ecosystem Assessment 2005). Observational and experimental studies generally indicate a positive, saturating relationship between biodiversity and ecosystem processes, although much of the evidence for this pattern originates from plant-based studies at a single trophic level (e.g., Hector et al. 1999, Hooper et al. 2005). The mechanism underpinning an observed diversity effect can alter the shape of the relationship, and the variability with which maximum function can be achieved at different richness levels (Tilman et al. 1997, Hooper et al. 2005). For example, selection effects (whereby selective processes cause dominance of species with a particular trait [Loreau and Hector 2001]) have a steep diversity–function curve and high variability at low richness levels. By contrast, a diversity–function curve driven by complementarity effects (e.g., resource-use differentiation and/or synergistic interactions) has a shallower slope and lower variability when species

richness is low. Sampling or lottery effects may contribute to selection or complementarity since species-rich assemblages have a greater chance of including a species with traits that lead to dominance (selection effects) or traits that are complementary with other species in the mixture (Loreau and Hector 2001).

Within plant-based studies it is possible to quantify the contribution of individual species toward function (e.g., productivity) in polycultures and thereby partition net diversity effects into contributions by selection or complementarity (Loreau and Hector 2001). Application of this technique in a meta-analysis of biodiversity experiments revealed that while both contribute to net diversity effects, complementarity is more prevalent and more likely to result in positive effects (Cardinale et al. 2007). Unfortunately, elucidating which mechanisms are operating within studies using higher trophic levels is limited by the difficulty of identifying contributions to function of individuals within mixed assemblages.

Prevalence of a particular mechanism driving diversity effects will have important implications for how we manage biodiversity for ecosystem services. For example, to effectively manage natural enemy diversity for pest control function, it is pertinent to know whether it is better to increase the abundance of the single most effective natural enemy or to augment natural enemy diversity per se. These contrasting management options are well illustrated by biological control strategies that

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Corresponding Editor: N. J. Gotelli.

⁵ E-mail: g.griffiths@imperial.ac.uk

can be highly polarized in their approach such as classical biological control (which assumes that selection effects dominate by releasing what is hoped to be the single most effective natural enemy) and conservation biological control (which assumes a diverse community of natural enemies will reduce the opportunity for a prey refuge in space or time). However, optimization of biological control techniques from the results of natural enemy diversity–function studies is limited because most empirical studies explicitly consider only the functional change of increasing species richness, without incorporating alterations in interaction strengths attributable to relative or absolute changes in abundance (with some notable exceptions; e.g., Vance-Chalcroft et al. 2004, Vance-Chalcroft and Soluk 2005, Griffin et al. 2008). This is important since predator assemblages may have emergent or non-linear effects on herbivore suppression resulting from the net effect of a range of non-exclusive mechanisms operating between individuals of the same or different species. For example, risk enhancement for the prey population may result from resource-use differentiation and synergistic interactions, while risk-reducing effects may be caused by antagonistic interactions such as intra- or interspecific interference, intra-guild predation, or cannibalism (Casula et al. 2006).

Furthermore, many diversity experiments implicitly confound the relative importance of richness and density through their experimental designs. The additive and substitutive experimental designs (both originating from the plant competition literature where they have enjoyed a similarly contentious history [Jolliffe 2000]) may be used to detect the net effects of species interactions in community competition experiments. A recent review of predator diversity studies revealed an almost equal divide in the use of additive (48.5%) and substitutive (51.5%) experimental designs (Schmitz 2007). The additive design maintains the abundance of individual species in single and multiple species assemblages, while the substitutive design maintains the same overall abundance in single and mixed assemblages. The additive design therefore confounds increases in richness with increases in overall density and tests whether emergent effects due to interspecific interactions occur, relative to a null model of expected performance based on single species treatments (thereby ignoring intraspecific effects). Meanwhile, the substitutive design effectively reduces density of individual species as richness increases and tests for emergent effects of species richness by examining interspecific interactions relative to intraspecific interactions (Jolliffe 2000, Griffen 2006).

In this study, we explicitly test the relative contributions of natural enemy richness and abundance on pest control function, in order to compare the accumulation of net effects between con- and heterospecifics. We identify possible mechanisms by comparing our observed patterns with those predicted by the additive- and multiplicative-risk model (hyphenation is used to distinguish the additive design from the additive-risk

model) and their associated biological assumptions (Soluk and Collins 1988, Sih et al. 1998). The additive-risk model describes independent predator effects and an additive (linear) predator response in the absence of prey depletion. The multiplicative-risk model describes a positive, saturating response of predation against predator abundance that assumes perfect resource consumption where prey depletion occurs (such that no prey may be consumed more than once). Since predictions from the multiplicative-risk model incorporate resource competition for diminishing prey it represents a more accurate model at high predator densities where prey are limited. Our experimental design is then used to compare emergent effects of species richness according to the additive and substitutive designs, and to compare differences in mean, maximum and minimum function of species-poor and species-rich assemblages. This study is conducted using the natural enemy community associated with cereal aphid pests as a model system.

MATERIALS AND METHODS

Experimental set up

The survival of 60 nymphs of the rose-grain aphid *Metopolophium dirhodum* was compared between experimental units with low, medium, and high predator abundance treatments within which low richness (single species) and high richness (three species) of natural enemies were fully nested. Four experimental units were established as no-predator controls. Four single species and four three-species combinations of predator were used in each low and high richness treatment respectively, so that composition was a subset of richness (Appendix A). The four predator species used are abundant and ubiquitous in arable cropping systems and include *Adalia bipunctata* second-instar larvae (Coccinellidae), *Anthocoris nemoralis* adults (Anthocoridae), *Chrysoperla carnea* second-instar larvae (Chrysopidae), and *Tachyporus chrysomelinus* adults (Staphylinidae). *A. nemoralis* combines aerial and foliar foraging in the upper part of the plant, *A. bipunctata* and *C. carnea* are foliar foragers and *T. chrysomelinus* is predominantly a ground active predator. Predator numbers were standardized across treatments to account for differences in body size using allometric scaling of metabolic rate (B) to body mass (M) of $B = M^{3/4}$ (West et al. 1997, Wilby et al. 2005). A single predator unit was therefore composed of one *A. bipunctata*, one *A. nemoralis*, four *C. carnea*, and one *T. chrysomelinus*, and predators were added in units of three (low abundance), six (medium abundance), and nine (high abundance). Experimental units consisted of individual mesocosms (perspex cages $30 \times 30 \times 60$ cm with an opening on one side covered with a fine 0.5 mm mesh) housed within a controlled environment chamber (18°C, 60% relative humidity, 16 h:8 h light:dark) with the experimental design blocked through time. Six wheat plants (*Triticum aestivum*, var. Ashby), grown in

compost (John Innes No. 3; Westland Horticulture Ltd., County Tyrone, Ireland) to Zadok growth stage 37 (stem elongated and flag leaf visible), were introduced to each mesocosm and five wingless adults added (from cultures kept at Silwood Park). Adult aphids were removed after five days and nymphs were counted after a further two days and reduced to 60 where necessary. Nymphs only were used in the experiment to control for variability in aphid reproductive rates. Predators were added to the plants 24 hours later: *A. bipunctata*, *A. nemoralis*, and *C. carnea* were purchased from Syngenta-Bioline (Telstar Nursery, Essex, UK), *T. chrysomelinus* were collected from Sonning Farm (University of Reading, Berkshire, UK). After four days, predators were recovered and aphids counted. New predator, prey and wheat were used for each of the six experimental blocks.

Analyses

Generalized linear mixed-effects models (GLMMs) with a binomial error structure and logit link were used to partition the variability deriving from random effects of experimental blocks, from variability in the fixed (treatment) effects of predator abundance, richness, and composition (using the lme4 package by Douglas Bates in the open source software R 2.5.0). A quasibinomial error structure was used to account for overdispersion in the data where necessary (Crawley 2007). GLMMs were fit using the Laplace method, that provides an accurate approximation to the log-likelihood (Bates and DebRoy 2004), and the goodness-of-fit of competing models (model simplification) was compared using Akaike information criteria (AIC). AIC is the most suitable test if overdispersion is present or when the degrees of freedom (i.e., the difference in the number of parameters between competing models) is low (Piniero and Bates 2002). Minimum adequate models (MAM) were selected based on their Akaike weight (w_i); this statistic gives the relative weight of evidence in favor of a model i , given other models (<10 AIC points above minimum model). Similar to a probability, higher w_i (closer to one from zero) indicates stronger support for the model being considered (Burnham and Anderson 2002). In addition, the significance of model parameters was tested using Markov chain Monte Carlo simulations to calculate confidence intervals and probability estimates (MCPC) (Boon et al. 2007). Binomial measures of predation and predation per predator unit (nymphs predated, nymphs surviving) in treatment cages were corrected by the mean nymph survival in control cages within each block (to describe predation without background mortality) and are bounded above by 1 and below by 0 to account for prey depletion (such that each prey can only be consumed once). Analysis of nymph predation was used to test the relative contributions of natural enemy abundance \times richness, and abundance \times composition (where \times indicates two main effects plus an interaction term). Analysis of predation per predator unit ($1 -$

(nymphs surviving) $^{1/PU}$, where PU is the number of predator units), calculated according to the multiplicative-risk model (since mean predation in single and multiple species most closely fit this model) was used to examine intraspecific interactions in single species, and inter- relative to intraspecific interactions in multiple species assemblages.

Log response ratios ($\ln[\text{observed/expected}]$) were calculated to detect emergent species richness effects from the additive (P_A) and substitutive (P_S) experimental designs. Expectations were calculated according to the multiplicative-risk model (since observed mean predation most closely fit this model) of proportional nymph survival S from predator species i in monoculture. One comparison was possible for the additive design (using nymph survival for single predator species at low abundance to predict multiple species predation at high abundance), and three comparisons for the substitutive designs (using single species to predict multiple species predation rates at the same abundance level for low, medium, and high abundance):

$$P_A = 1 - (S_i \times S_j \times S_k)$$

$$P_S = 1 - (S_i^{1/3} \times S_j^{1/3} \times S_k^{1/3}).$$

Log response ratios (LR) were also calculated to compare differences in mean, maximum and minimum function of multiple species and single species assemblages ($LR = \ln[\text{multiple species/single species}]$; Cardinale et al. 2007). LR_{net} represents the proportional difference between the mean mortality of all multiple species assemblages and mean mortality of all single species; LR_{trans} represents the proportional difference between the mean mortality of all multiple species assemblages and mean mortality of the best performing single species (positive values indicate transgressive overyielding where diverse assemblages have higher function than the best performing single species); LR_{max} and LR_{min} describe the proportional difference between the best (max) and worst (min) performing multi-species composition and single species.

RESULTS

Models of predator abundance \times richness indicated that retaining both fixed effects and their interaction term produces the best fitting model, accounting for 0.99 Akaike weight compared to simpler models. Predation increased with species richness and abundance and a significant interaction shows that the richness effect is density dependent (Fig. 1a). At low abundance, single and multiple species had similar predation levels but these diverged with increasing abundance. In single species, the relationship between predation and abundance falls well below predictions of the additive-risk model, and increasingly below predictions of the multiplicative-risk model (based on proportional predation in the low abundance treatment where GLMMs

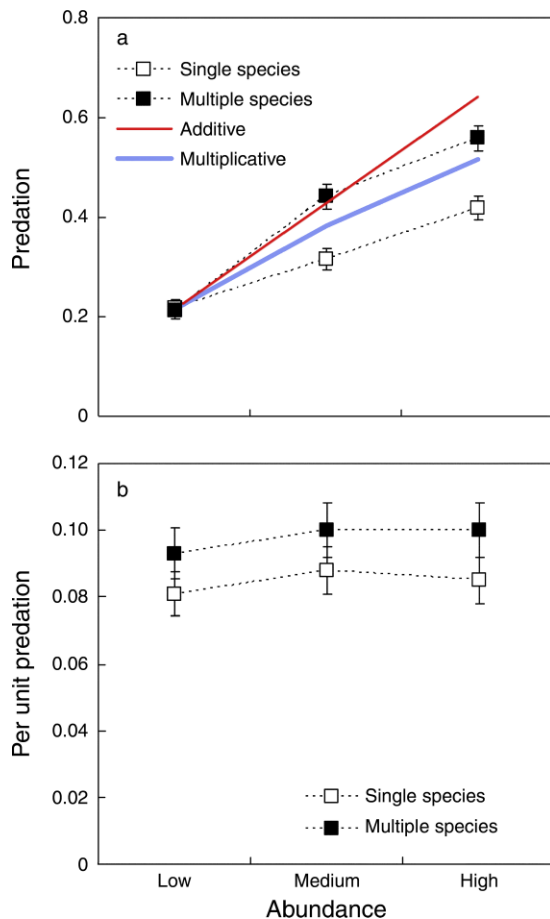


FIG. 1. Predation of *M. dirhodum* nymphs (mean \pm SE, $n = 6$ replicates) by single and multiple predator assemblages at low, medium, and high abundance for (a) observed predation and expected predation according to the additive- and multiplicative-risk models (based on the mean nymph survival in single- and multiple-predator assemblages at low abundance) and (b) observed predation per predator unit, calculated according to the multiplicative-risk model (since mean predation of single and multiple species most closely fits this model).

showed no significant difference between richness levels). This pattern is commensurate with imperfect resource consumption, as may be expected either where only a limited proportion of the total prey is available for predation by a single foraging type, or where intraspecific interference limits predation. Within multiple species, the relationship between predation and abundance is initially additive, and observed predation is consistently above expectations of the multiplicative-risk model. Such high resource consumption may be observed with a number of non-exclusive scenarios; the presence of predator species with different foraging domains may increase the proportion of prey available for consumption through more complete coverage of the total niche space; higher species richness may relax interference between individuals (indicating lower interspecific relative to intraspecific interference); or synergistic interactions may enhance prey availability to one

or more predator species. MCPC probability estimates confirm that abundance and the interaction between abundance and richness had a significant effect on prey consumption, but despite observed trends richness did not describe a significant portion of the variation in nymph predation (Appendix B). However, per unit predation changed minimally with increasing abundance, and multiple species had consistently higher per unit predation than single species (Fig. 1b), consequently only richness explained sufficient variation to be retained in the MAM (as confirmed by Akaike weights and MCPC values, Appendix B).

Models of abundance \times composition on predation and per unit predation indicated that retaining both fixed effects and their interaction term produces the best fitting model (Appendix B). Strong species identity effects were observed, some of which were highly density dependent resulting in considerable variation in the contributions of different species compositions, especially in single-species assemblages (Fig. 2a). At low

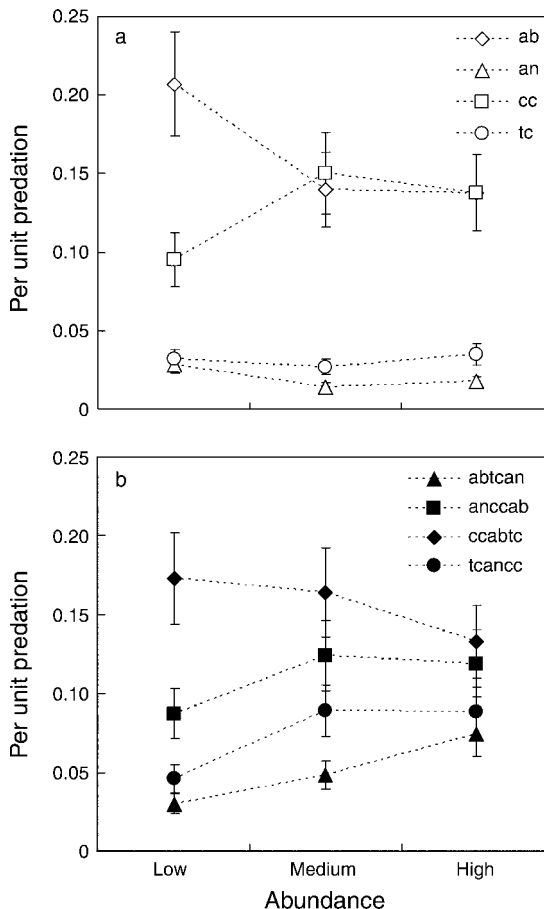


FIG. 2. Per unit predation of *M. dirhodum* nymphs (mean \pm SE, $n = 6$ replicates) at low, medium, and high abundance for (a) single-species compositions and (b) multiple-species compositions. Species codes are: ab, *Adalia bipunctata*; an, *Anthocoris nemoralis*; cc, *Chrysoperla carnea*; and tc, *Tachyporus chrysomelinus*.

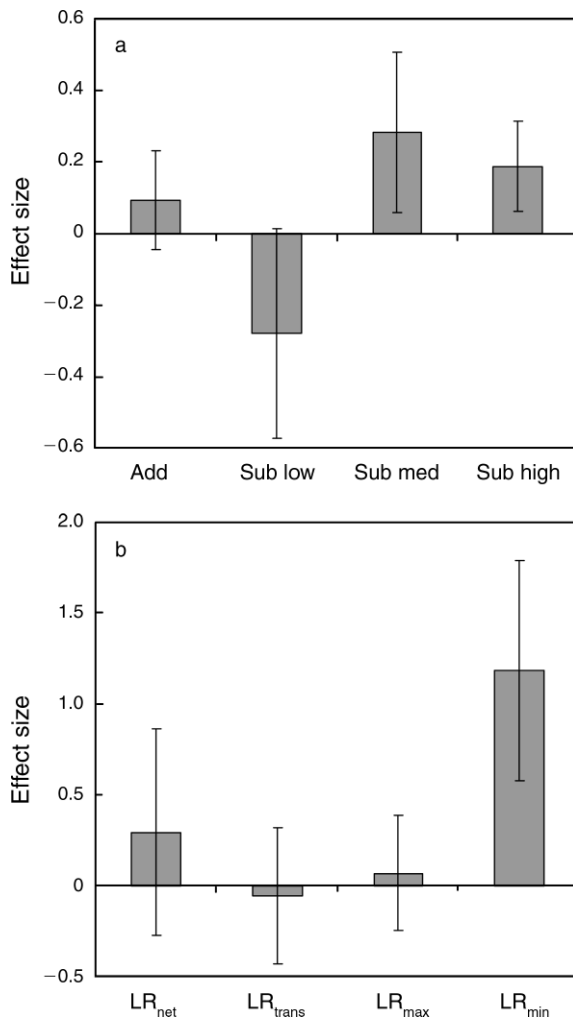


FIG. 3. Log response ratios (mean and 95% CI) to detect (a) effects of species richness according to the additive and substitutive experimental designs where an effect size >0 indicates risk-enhancement and <0 indicates risk-reduction for the prey; (b) effects of species richness measured by LR_{net} (mean predation of species-rich relative to species-poor assemblages), LR_{trans} (mean predation in species-rich assemblages against the best performing single species), LR_{max} (predation of the best performing multiple species composition against the best performing single species), and LR_{min} (predation of the worst performing multiple species composition against the worst performing single species), where a value >0 indicates the multi-species assemblage performs better. All metrics are calculated within experimental blocks and averaged across blocks. Effect sizes differ from zero where 95% CI do not cross the x -axis.

abundance, *A. bipunctata* was the most effective single species, but intraspecific interference appeared to reduce its contribution at higher abundances. Per unit predation by *C. carnea* showed a contrasting pattern with evidence of intraspecific facilitation increasing prey capture at higher abundances. *A. bipunctata* and *C. carnea* formed the two most effective single species at medium and high abundance, and generated highest per

unit predation rates when combined in multiple species assemblages. In multi-species compositions, per unit predation rates started to converge with increases in abundance, though this was possibly driven by increasing abundance of the most effective predators.

According to the additive design or the substitutive design at low abundance, there was no evidence of emergent species-richness effects (i.e., deviation from level of predation expected using the multiplicative-risk model, Fig. 3a). By contrast, the substitutive design at medium and high abundance showed risk-enhancement for prey in the presence of multiple predator species, indicating that species richness effects may be density dependent. Log response ratios comparing function in single and multiple species indicated that mean predation in species-rich assemblages was equivalent to both mean predation in species-poor assemblages and the best performing single species (Fig. 3b). Similarly, no significant effect was found between the best performing single and multiple species treatments. However, mean function was significantly higher in the worst performing species-rich assemblage compared to its species-poor counterpart.

DISCUSSION

Quantifying function within species-rich and species-poor assemblages across an abundance gradient is both integral to the definition of diversity and necessary for its management. Inclusion of an abundance gradient illustrates that effects of species richness on function can be density dependent and that the density of interacting organisms can drive patterns of resource use, an observation also pertinent to aquatic systems (Griffin et al. 2008). Furthermore, this study shows that detecting emergent effects of species richness using single comparisons within an additive or substitutive design can be misleading. This is not to say that either design is incorrect, rather that a single density comparison is inappropriate for tests of interactions in natural communities that are both variable and changeable in their relative richness and abundance. A response surface analysis (Law and Watkinson 1987, Inouye 2001) may be the only comprehensive technique to examine both overall species richness effects and interactions, but this labor-intensive approach can be simplified to address more specific questions. For example, to only test whether species richness has an emergent effect on function, a substitutive series (or replacement series) design will show density dependence of richness effects as illustrated with our data, while an additive series design (based on different densities of single species) will be most appropriate to examine changes in interactions across an abundance gradient (Jolliffe 2000). Alternatively a term describing predator density-dependent interactions (e.g., Beddington et al. 1975) needs to be included in models predicting predation rates in multiple-predator assemblages (Evans 1991, Peckarsky 1991, Vance-Chalcroft et al. 2004).

Ultimately, in order to design and test diversity effects accurately, we require a better understanding of how communities assemble (along a gradient from substitutive to additive) in nature.

In our study, natural enemy species were highly idiosyncratic in their predatory potential, as would be expected given different functional responses, prey specificity, modes of hunting and microhabitat domain (Schmitz 2007). Clearly, predator species identity is an important component to consider for maximizing pest control function (Chalcraft and Reseraris 2003, Wilby et al. 2005, Straub and Snyder 2006), especially when natural enemy species richness is low, since the order in which species accumulate can strongly alter the shape of the diversity–function relationship. This provides support for the sampling effect dominating the relationship between natural enemy diversity and pest control function at low diversity, a corollary of which is greater variability in function as indicated by our data.

Although species identity effects dominated at low diversity, interactions occurring between multiple species generated a positive richness effect which could be caused by a number of non-exclusive mechanisms. Two of these mechanisms would be able to account for increases in predation relative to rates predicted by the multiplicative risk model, which describes perfect resource consumption: relaxation of intraspecific interference and resource-use differentiation. Both could occur due to the different foraging domains of species in the multiple predator assemblage. For example, by including species that forage aerially, on the plant and on the ground, more of the niche space covered by the prey is susceptible to predation, and there is less predation pressure on a single portion of the niche space that could result in behavioral interference or resource competition (as suggested by reductions in single species per unit predation at high abundance). For predation to exceed levels predicted by the multiplicative risk model however, synergistic interactions must be occurring between species to increase prey availability to one or multiple species. For example, foliar foraging predators may elicit a prey defense mechanism in aphids, causing them to drop from the plant, but this escape response will also make them more available to ground active predators such as carabids (Losey and Denno 1998).

There has been considerable debate in the biodiversity–ecosystem functioning literature regarding the prevalence of two sets of diversity mechanisms, particularly with the publication of two meta-analyses on empirical diversity–function studies that provide contradictory evidence in support of the selection vs. complementarity effects (Cardinale et al. 2006, 2007). What is apparent from the current study is that not only can species richness effects be density-dependent, but the mechanisms driving those species richness effects might also vary along a richness–abundance gradient. Theoretically, processes leading to dominance may be more

likely in species-poor assemblages that lack the range of direct and indirect interactions typical of more complex communities (Downing and Leibold 2002). Furthermore, we can provide support for the hypothesis that where there is a positive diversity effect, the apparent absence of transgressive overyielding (indicated by a nonsignificant LR_{trans} value) does not automatically provide evidence for selection effects (Cardinale et al. 2007). Substitutive comparisons of single and multiple predator species at medium and high abundance showed that predator function in multiple species treatments exceeded function in the single species treatments. As these treatments comprised only one-third the abundance of the most effective species and so were not simply dominated by them, this increased function can only be attributed to complementarity (i.e., resource-use differentiation, synergistic interactions, reduced intraspecific interference relative to interspecific interference, or some combination thereof).

Natural enemy diversity effects (including selection and complementarity) can be observed across multiple time-frames so long as the measure of function (e.g., predation in short-term experiments and predator population in long-term experiments) is appropriate (Petchey 2003). In this experiment, biodiversity effects were based on the set of environmental, physiological and behavioral traits determining predator efficiency within a single prey patch. Consequently, our experiment does not incorporate processes such as immigration and emigration between multiple prey patches or birth and death rates across multiple generations, which impact function over larger spatial and temporal scales (Griffiths et al. 2008a). Ultimately, elucidation of the mechanisms that contribute to net diversity effects at multiple time frames are necessary to enhance our understanding of the relationship between natural enemy diversity and pest control function.

For biological control purposes, the patterns observed in our experiment suggest that where natural enemy abundance is low, substantial increases in function may be achieved by augmenting populations of single, highly effective species, but these must be selected to avoid the limitations of intraspecific interference illustrated by *A. bipunctata*. However, where natural enemy populations are intermediate or high, it may be more advantageous to increase diversity and the representation of functionally complementary species (Petchy and Gaston 2002, Naeem and Wright 2003). This will reduce intraspecific interference between functionally equivalent species, and enable new species to occupy unique and complementary niche space. Additionally, measures of variability are particularly important for ecosystem services such as crop protection which tend to have clear biological and economic thresholds, with reliability and risk often important factors for farmers accustomed to the predictability of agrochemicals (Griffiths et al. 2008b). As such, it is an important observation that minimum function was greater and more reliably achieved with a

species-rich assemblage compared with the more variable single-species treatments, without any compromise on the maximum function possible. Add to this the fact that the most effective predator is likely to be pest-, crop- and context-dependent and this creates a strong argument for retaining or augmenting a diversity of natural enemies for optimum pest control function (cf. the insurance hypothesis [Loreau et al. 2003]).

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APPENDIX A

Units of each predator species included in single and multiple species treatments at low, medium, and high abundance (*Ecological Archives* E089-172-A1).

APPENDIX B

Akaike weights and probability estimates of the minimum adequate models simplified from (a) abundance \times richness and (b) abundance \times composition, on mortality of *Metopolophium dirhodum* nymphs (*Ecological Archives* E089-172-A2).