

## PREDATOR DIVERSITY AND ECOSYSTEM FUNCTIONING: DENSITY MODIFIES THE EFFECT OF RESOURCE PARTITIONING

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**Abstract.** The link between biodiversity and ecosystem functioning is now well established, but the challenge remains to develop a mechanistic understanding of observed effects. Predator–prey interactions provide an opportunity to examine the role of resource partitioning, thought to be a principal mediator of biodiversity–function relationships. To date, interactions between multiple predators and their prey have typically been investigated in simplified agricultural systems with limited scope for resource partitioning. Thus there remains a dearth of studies examining the functional consequences of predator richness in diverse food webs. Here, we manipulated a species-rich intertidal food web, crossing predator diversity with total predator density, to simultaneously examine the independent and interactive effects of diversity and density on the efficiency of secondary resource capture. The effect of predator diversity was only detectable at high predator densities where competitive interactions between individual predators were magnified; the rate of resource capture within the species mixture more than doubled that of the best-performing single species. Direct observation of species-specific resource use in monoculture, as quantified by patterns of prey consumption, provided clear evidence that species occupied distinct functional niches, suggesting a mechanistic explanation of the observed diversity effect.

**Key words:** BEF; biodiversity; density; ecosystem functioning; food web; predator; resource partitioning; trophic interactions.

### INTRODUCTION

Concerted empirical research over the last decade has shown that species richness can enhance the magnitude of ecosystem functioning in a range of systems (Hooper et al. 2005, Balvanera et al. 2006, Cardinale et al. 2006). Despite this emerging paradigm, the ability to predict the functional consequences of species loss in a given system remains elusive because the strength of species diversity effects has proven highly variable across studies (Balvanera et al. 2006). To transform biodiversity–ecosystem functioning research into a predictive science, a clear mechanistic understanding of observed effects is required (Yachi and Loreau 2007).

Although early seminal research on the effect of biodiversity on ecosystem functioning focused on temperate grassland communities (Naem et al. 1994, Tilman et al. 1996), recognition that species in higher trophic levels are more vulnerable to extinction (Petchev et al. 1999, Duffy 2002) has recently shifted attention onto multi-trophic systems (e.g., Duffy et al. 2007). Despite the obvious differences between primary pro-

ducers and mobile, behaviorally complex predators, theory predicts that both sampling and complementarity effects operate to enhance the magnitude of resource capture, irrespective of trophic level (Ives et al. 2005). The sampling (Huston 1997), or positive selection (Loreau 2000), effect occurs when species with extreme trait values dominate resource acquisition and are more likely to be included in diverse species mixtures by chance. In this case, the functioning of the diverse mixture will not exceed that of the best monoculture. In contrast, where niche complementarity is evident, species differing in resource requirements exploit a wider spectrum of resources and experience reduced interspecific competition, thus potentially enhancing the rate of ecosystem processes beyond that of the best-performing single species (Trenbath 1974, Loreau and Hector 2001). Direct evidence of resource partitioning is rare despite recognition of its importance in mediating species coexistence (Chesson 1991). Instead, functional complementarity is often inferred from diversity effects that exceed those that can be explained by the sampling effect alone (Loreau and Hector 2001, Duffy et al. 2003). In contrast to primary producers, however, the resource use patterns of predators can be readily assessed, potentially enabling tractable studies of the functional consequences of diversity mediated through niche partitioning (Ives et al. 2005).

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PLATE 1. The crabs (from left) *Necora puber*, *Carcinus maenas*, and *Cancer pagurus* are important coexisting predators in rocky intertidal habitats. Photo credit: P. Moore.

A rich history of experiments examining trophic interactions between multiple predators and their prey has identified the complexities of predicting aggregate predator effects on prey consumption (e.g., Losey and Denno 1998, Finke and Denno 2004, Siddon and Witman 2004). Such work has become increasingly integrated with research on the link between biodiversity and ecosystem functioning through experiments that maintain total predator density across gradients of species richness (e.g., Wilby et al. 2005, Straub and Snyder 2006). Due to the strong focus on agricultural pest control, previous studies have typically included very low levels of prey heterogeneity (but see Bruno and O'Connor 2005, Byrnes et al. 2006), thereby limiting the potential for resource partitioning among predators. The role of predator diversity within diverse natural food webs thus remains largely unknown.

The density of organisms within natural communities is determined not only by resource availability, but by a suite of factors that may act to maintain density below the carrying capacity of the environment. For example physical and biological disturbance (e.g., Sousa 1984), recruitment limitation (e.g., Connolly and Roughgarden 1998), and top down control (including human exploitation) (e.g., Castilla 1999) are all known to influence density independently of local resource availability. Assuming constant resource availability, the density of a species will determine the strength of intraspecific and

interspecific competition, which can in turn influence the effect of species diversity on ecosystem functioning (Cardinale et al. 2004, Weis et al. 2007). Despite the critical role that competition may play in linking diversity and ecosystem functioning, the potential role of density in modifying diversity effects mediated by niche partitioning has yet to be tested empirically.

The efficiency of resource capture by consumers, as measured by the rate of prey consumption, represents an important ecosystem process within complex food webs (Duffy 2002) and allows investigations of multi-trophic interactions within the context of theory linking biodiversity and ecosystem functioning. We conducted a factorial mesocosm experiment to test the hypothesis that predator density modifies the effect of predator species richness on the efficiency of trophic energy transfer between diverse intertidal prey assemblages and three species of predatory crabs. Our results show that clear effects of diversity only occurred at high predator density. Furthermore, our results suggest that predator species exhibited marked differences in the patterns of resource use, representing functional complementarity through resource partitioning.

#### METHODS

We manipulated the diversity and density of three common intertidal predatory crabs, *Cancer pagurus*, *Necora puber*, and *Carcinus maenas* (see Plate 1), in

outdoor mesocosms,  $0.6 \times 0.4$  m in area  $\times$  0.2 m depth, which were subject to a constant flow of fresh filtered seawater at the Marine Biological Association Laboratory in Plymouth, United Kingdom. The predator species are abundant and have overlapping distributions within rocky intertidal habitats on the southwest coast of the United Kingdom. Furthermore, these predators have similar body sizes, enabling the isolation of species identity and diversity effects from those of body size, which can have a strong influence on trophic interactions (Jennings et al. 2001).

We employed a substitutive design, frequently used in biodiversity–ecosystem functioning studies (e.g., Polley et al. 2003, Bruno et al. 2005) including those examining predator diversity effects (Siddon and Witman 2004, Byrnes et al. 2005, Snyder et al. 2006), such that overall density was maintained across a gradient of diversity. We crossed a substitutive gradient of predator diversity with total overall density, allowing the independent and interactive effects of diversity and density to be examined simultaneously (Benedetti-Cecchi 2004). Four different predator assemblages were constructed, three with each species in monoculture and one with all three species combined. Density consisted of two levels: low with three, and high with six predator individuals in total. The high diversity predator community thus contained one and two individuals of each of the three species at low and high density, respectively. These densities are commonly observed in the intertidal at small spatial scales, where crabs aggregate in areas of suitable refugia. We defined a narrow size range for each species to ensure approximately equal masses ( $52 \pm 2$  g wet biomass) of individuals within and among species. Predator-free controls were included to confirm that all reductions in prey were due to consumption. Each treatment was replicated six times in total, but limited space to house mesocosms restricted our experiment to a randomized, temporally blocked design, such that two replicates of each of nine treatments were included in three temporal blocks. The start of each block was separated by two weeks to enable collection of animals during spring tides.

Predators were collected from under boulders within the intertidal zone at Looe, Cornwall, UK. To exclude effects of satiation at the time of collection, crabs were starved for four days prior to experiments in large holding tanks with continuous flowing seawater containing numerous refuges to limit potentially harmful agonistic interactions. Each experimental mesocosm contained a 3-cm layer of coarse sand and gravel upon which rocks of a range of sizes were arranged to recreate a topographically complex, refugium-rich environment mimicking rocky shores (Appendix A). Habitat-forming materials were collected from local shores and rinsed with fresh water to remove macro-biota before introduction to mesocosms. We covered each mesocosm with a tightly fitting fine nylon mesh to ensure animals were

unable to escape. The experiment was conducted between January and March 2007.

Initial prey composition and abundance did not vary among mesocosms (approximately 8.71 g dry mass in total, Appendix B). Five species of prey were used, all naturally co-occurring and collected from the intertidal zone of local rocky shores. Barnacles (*Chthamalus* spp.) could not be transplanted into mesocosms individually, and were therefore transplanted in dense aggregations attached to pieces of rock. Individuals were counted before adding the rock pieces to the mesocosms. For all other prey species we included six individuals within each of two size classes (large and small) to incorporate an element of resource heterogeneity occurring in natural prey populations. Mussels *Mytilus edulis*, periwinkles *Littorina littorea*, topshells *Gibbula umbilicalis*, and limpets *Patella ulysiponensis*, were all added to the mesocosms three days before the start of each experiment.

We used the number and identity of prey absent from each mesocosm upon termination of the experiment to calculate consumption rates for each replicate predator assemblage. We calculated the consumption rate (shell-free dry biomass per day) of each prey type separately to elucidate patterns of prey consumption, and summed these to derive the total rate of prey consumption (Appendix C). We also derived per capita rates to facilitate direct comparisons across density levels. Based on the consumption of each prey type in monoculture, we calculated expected patterns in polyculture and derived proportional deviations from expected (Appendix C). A relatively short experimental duration (five days) was chosen so that extinction of prey types did not occur within mesocosms, which could prompt prey-switching, blurring initial resource use differences between species and potentially weakening the diversity effect (Ives et al. 2005).

Non-transgressive overyielding occurs when the magnitude of an ecosystem process in a diverse mixture exceeds that of the average monoculture value of component species (Fridley 2001). To test for this form of diversity effect, and for the potential interactive effect of total density upon it, we performed a two-way analysis of variance (ANOVA), followed by a priori planned contrasts between the average single-species and the polyculture treatment at both densities. Inclusion of all three species in monocultures facilitated a test of transgressive overyielding, which identifies effects of diversity that could not be produced by the dominance of any single component species. To test for this effect we performed a priori planned contrasts between the best-performing monoculture and the polyculture (Bruno et al. 2005, Duffy et al. 2005) at both low and high densities separately. We conducted a permutated multivariate ANOVA (PERMANOVA [Anderson 2001]) to test for differences in the composition and relative abundances of prey types consumed by the three predator species independently and in combination.

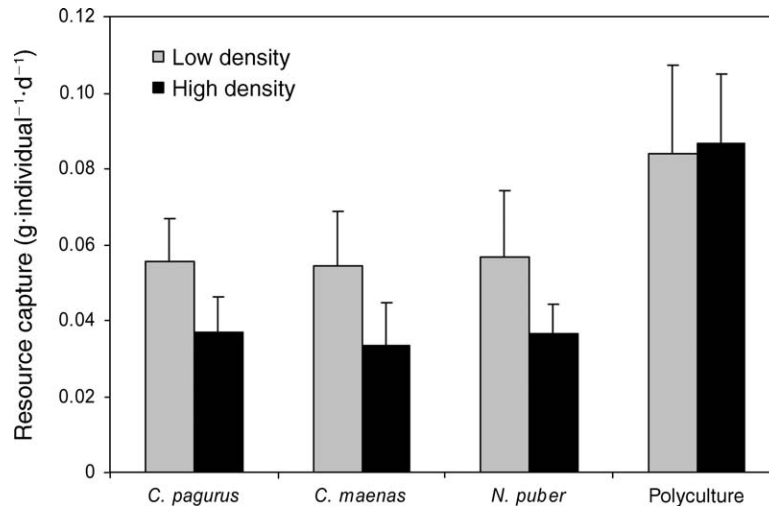


FIG. 1. Aggregate per capita resource capture rate (mean  $\pm$  SE) for all monocultures and the three-species mixture at both low and high densities ( $PC_{\text{Total}}$ ; see Appendix C for calculation;  $n = 6$  replicates per treatment) of the crabs *Cancer pagurus*, *Carcinus maenas*, and *Necora puber*. Significant differences occurred between monocultures and the mixture across high-, but not low-, density treatments. See Results and Appendix E for ANOVA results.

This provided a test of resource partitioning among predator species in terms of the multivariate prey base.

#### RESULTS

We recovered all prey items from predator-free controls upon termination of the experiment, confirming that all prey losses were due to predator consumption rather than other causes of mortality or escapes. All crabs survived the experiment uninjured, showing no evidence of physically harmful agonistic interactions or intra-guild predation. There were no significant differences among temporal blocks or interactions between block and experimental treatments (diversity  $\times$  block,  $F_{6,24} = 0.82$ ,  $P = 0.57$ ; density  $\times$  block,  $F_{2,24} = 0.66$ ,  $P = 0.53$ ; block,  $F_{2,24} = 2.5$ ,  $P = 0.11$ ), hence these data were pooled for subsequent analysis.

The monocultures of the three predator species captured similar prey quantities within density levels (Fig. 1, Appendix D). When species were combined in the polyculture there was significantly greater consumption compared to the pooled single species treatments ( $P = 0.003$ , Appendix E). This diversity effect was, however, dependent upon predator density, with the polyculture significantly outperforming the mean (non-transgressive overyielding) and the maximum (transgressive overyielding) monoculture among the high density treatments only. Specifically, at high density the predator mixture more than doubled the rate of prey consumption, exceeding the average monoculture by 144% ( $F_{1,20} = 10.64$ ,  $P = 0.004$ ) and the best-performing monoculture by 134% ( $F_{1,11} = 6.02$ ,  $P = 0.029$ ). At low density, the effect of diversity was far weaker, with the aggregate rate of resource capture of the polyculture only 52% ( $F_{1,20} = 2.11$ ,  $P = 0.16$ ) above the average monoculture and 48% ( $F_{1,11} = 0.90$ ,  $P = 0.364$ ) above the highest

single species treatment (Fig. 1, Appendix E). The differential effects of diversity between low and high density comparisons can be understood by comparing the effect of density in monocultures and the polyculture. A doubling of monoculture density only marginally elevated total resource capture (Appendix D), resulting in a density-dependent suppression of per capita resource capture efficiency within respective monocultures (marginally significant at an  $\alpha$  level of 0.1,  $F_{1,30} = 3.03$ ,  $P = 0.09$ ). In the polyculture, however, increasing density led to a large increase in total resource capture (Appendix D); density thus had no effect on per capita rates within the polyculture (Fig. 2,  $P = 0.93$ ).

All three predator species in monoculture differed markedly in patterns of prey consumption (Fig. 3). Whilst all predators demonstrated an ability to consume every prey species, clear and consistent differences between species in the patterns of trophic interactions were evident, with particular prey types most heavily consumed by specific predators (Fig. 2). PERMANOVA, with post-hoc pairwise comparisons, confirmed that all the predators exhibited distinct patterns of resource use ( $F_{3,40} = 3.98$ ,  $P < 0.001$ , Appendix F). Moreover, although density significantly affected overall patterns of prey consumption ( $F_{1,40} = 4.14$ ,  $P = 0.01$ ), species-specific differences were robust to changes in total density (interaction  $F_{3,40} = 0.42$ ,  $P = 0.95$ ).

Calculations based on the resource use patterns of single predator species predicted a relatively even distribution of prey consumption rates in the multispecies treatments (Fig. 3). The observed pattern of trophic interactions was consistent with this prediction (Fig. 3). Deviations from this expected pattern indicated which resources were exploited to a greater degree at high predator diversity (Appendix G). In particular, the

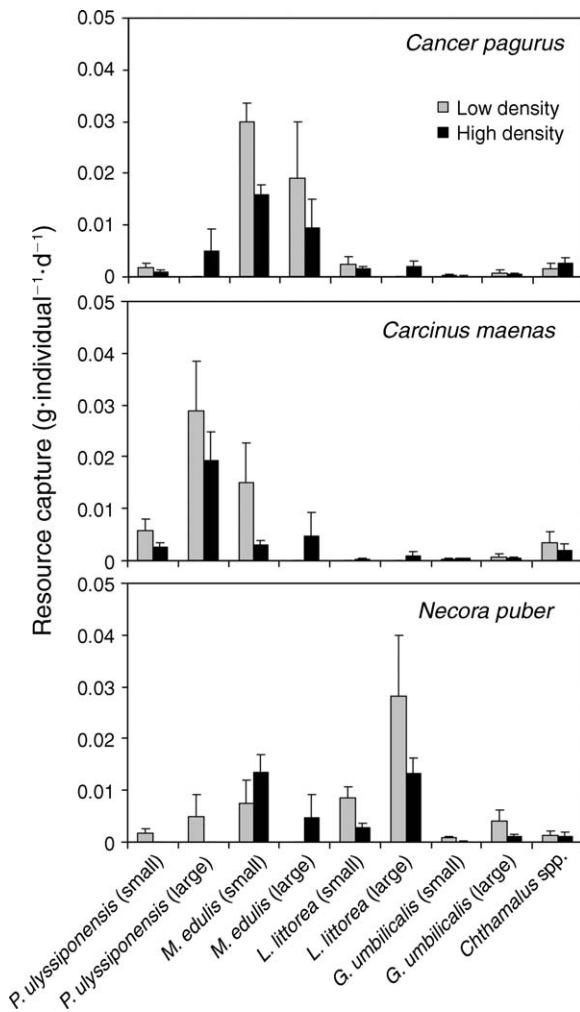


FIG. 2. Observed rates of consumption (resource capture; mean + SE) of each prey type and size for individual predator species ( $PC_{ij}$ ; see Appendix C for calculation) at two predator densities ( $n = 6$  replicates per treatment). Predators exhibited significantly different patterns of prey consumption (Appendix F). Prey are limpets (*Patella ulyssiponensis*), mussels (*Mytilus edulis*), periwinkles (*Littorina littorea*), topshells (*Gibbula umbilicalis*), and barnacles (*Chthamalus* spp.).

consumption of both size classes of *L. littorea* and *P. ulyssiponensis* far exceeded the null expectation at both densities (Fig. 3, Appendix G), consistent with the hypothesis that resource partitioning can enhance the total rate of resource capture by component species.

#### DISCUSSION

Our results show that predator species richness can have a strong effect on the efficiency of resource capture within a model intertidal food web. By crossing diversity treatments with total density, we tested the role of density in modifying the species richness effect, revealing that the loss of diversity leads to a more dramatic drop in ecosystem process rate when predators occur at high density. Furthermore, detailed analysis of species-

specific trophic interactions demonstrated that the three predators occupy distinct fundamental functional niches (sensu Rosenfeld 2002), providing a possible mechanistic explanation of the observed effects.

Our finding that the diversity effect was strongest, and only detectable, at high density (Fig. 1) is not surprising considering the critical role played by competition in the manifestation of the niche partitioning effect. Our analysis identified density-dependent depression of per capita resource capture in single species treatments (at an  $\alpha = 0.1$  level), but no such effect occurred in the polyculture (Fig. 1). This strongly suggests that the strength of negative interactions is less between heterospecifics than conspecifics. Where negative intraspecific interactions are weak or absent in single species contexts, which may be the case at low density in our experiment, individuals gain less, or no, advantage from occurring within a mixed community of consumers (Wilby et al. 2005). The apparent relaxation of negative interactions with increasing species richness thus only produced a clear effect of diversity at high predator density where negative interactions between conspecifics within monocultures were strongest.

An ability to predict the consequences of species loss requires an understanding of the factors that modify diversity effects (Cardinale et al. 2000). Our experiment demonstrates that density should be considered in future

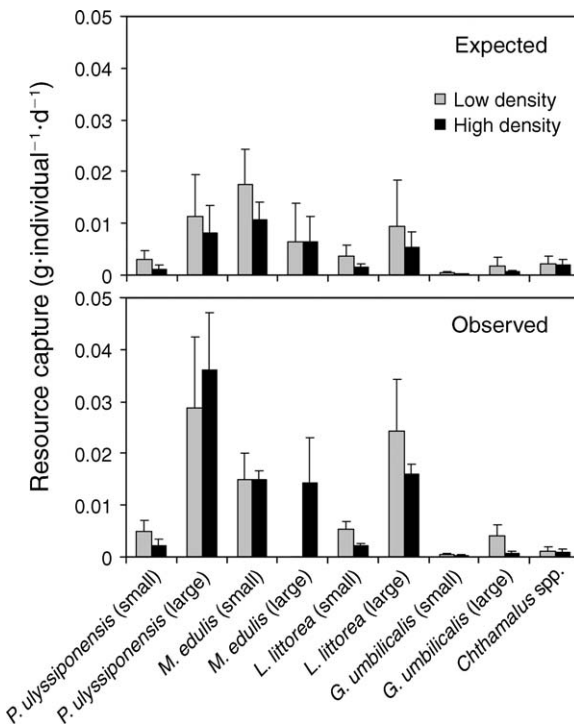


FIG. 3. Expected ( $Pe_{ij}$ ) and observed ( $PC_{ij}$ ) rates of resource capture (mean + SE) for the diverse three-species predator mixture at both high and low density. See Appendix C for calculation of variables, and Appendix G for proportional deviations from expected rates. Prey species are as in Fig. 2.

attempts to understand the functional consequences of biodiversity within both observational and experimental studies. For example, high disturbance systems, and the early successional communities that typify them (e.g., Martins et al. 2007), may not be resource limited, potentially precluding diversity effects (Weis et al. 2007). On the other hand, management activities, such as the provision of protected areas, reduce direct and indirect human impacts on populations, typically increasing the abundance and diversity of predators (e.g., Babcock et al. 2007). The outcome of our experimental diversity manipulation implies that as the density of such predators increases, so too may the value of diversity for ecosystem functioning.

The sampling or positive selection effect (Huston 1997, Loreau 2000), has been credited as the principal mechanism leading to positive diversity effects in both biodiversity–ecosystem functioning (Cardinale et al. 2006) and natural enemy studies (Denoth et al. 2002, Straub and Snyder 2006). However, both theory (Cardinale et al. 2004, Loreau 2004) and experiments (Dimitrakopoulos and Schmid 2004, Gamfeldt et al. 2005, Snyder et al. 2006) suggest that the limited resource heterogeneity typically provided in such studies may preclude resource partitioning, instead highlighting strong effects of particular species (those most suited to the specific conditions, or prey type, provided). We aimed to incorporate the range of prey types, in terms of sizes and species identity, available in the natural environment, thus providing realistic conditions with a high potential for resource partitioning. Indeed, all predators exhibited distinct resource use patterns in monoculture (Fig. 2). We could not provide incontrovertible evidence of resource partitioning, as our experimental setup precluded measurement of species-specific resource use within the diverse treatment. However, the increased consumption of a broad spectrum of prey types in the polyculture (Fig. 3), representing dietary preferences of all three predators, suggests that all species maintained niche differences and benefited from resource partitioning. Moreover, theory and past experiments support the supposition that distinct resource use patterns observed in monoculture would likely have been maintained, or even exaggerated, in the presence of interspecific competition (Odum and Barrett 2005). Our experimental findings thus strongly suggest that resource partitioning can have a marked effect on ecosystem functioning, providing a rare empirical example (but see Bracken and Stachowitz 2006, Kahmen et al. 2006) of a phenomenon that has long been regarded as a key link between species richness and the magnitude of ecosystem functioning (Naeem et al. 1994, Loreau et al. 2001). Although the evidence indicates that all species maintained niche differences in polyculture, the consumption of some prey types deviated disproportionately from expected values (Fig. 3, Appendix G). This suggests that individuals of certain predator species may have benefited to a greater degree

from occurring within a mixed assemblage, enhancing the consumption of their preferred prey types relative to others'. Further insight into the role of predator diversity could be achieved by documenting the division of resource acquisition rates among species within mixtures. This would provide a more direct test of resource partitioning and facilitate application of statistical techniques to distinguish between complementarity and selection effects (Loreau and Hector 2001, Fox 2005).

The appropriate experimental design to test the effect of species richness on ecosystem functioning continues to be debated (Balvanera et al. 2006, Weis et al. 2007), primarily because species richness cannot be manipulated without a concurrent change in either total density or the density of component species. To clarify interpretation of experiments, the specific questions addressed by alternative designs need to be clearly defined. The substitutive design, used here, equalizes total density across single and multiple species treatments, testing whether, given density-compensation, local extinction of species will influence the magnitude of an ecosystem process. In effect, species which are lost through local extinction are experimentally replaced with individuals of those remaining, thus intraspecific and interspecific interactions are directly compared (Jolliffe 2000, Griffen 2006). Where resource partitioning occurs, as in this experiment, replacing heterospecifics with conspecifics will reduce the breadth of resources exploited, increasing competition and depressing the rate of resource acquisition. We thus suggest that the substitutive design is an effective approach to detect the functional consequences of resource partitioning.

Our experiment identifies the potentially strong effect of resource partitioning among predators in nature, but is only the first step. Species richness remains the most commonly used measure of diversity in experimental tests. However, resource partitioning results from species' differential resource use, and is thus an effect of functional diversity (*sensu* Petchey and Gaston 2002) as opposed to species richness *per se*. The field might thus increase its predictive capacity by shifting the emphasis of biodiversity–function research from species diversity to functional diversity. Multiple predator–prey systems such as the one described here, provide an ideal opportunity to test the theoretical prediction that ecosystem processes will increase with functional diversity independently of species richness (Petchey and Gaston 2006). Furthermore, in order to gauge the possible cascading effects of predator extinction we need to couple theory with longer-term and larger-scale manipulative and observational studies that incorporate predator and prey dynamics, adaptive morphological and behavioral prey responses, as well as indirect interactions. Future experiments should also represent natural systems as we have, incorporating environmental and resource heterogeneity that allows both stable

coexistence and the enhancement of ecosystem processes through niche partitioning.

To increase the relevance and applicability of biodiversity–ecosystem functioning research, we must develop a capacity to predict the consequences of extinction based on measurable properties of both natural and managed ecosystems. We show here that a fundamental property of communities, the density of consumers in relation to their resources, can modify the effect of diversity as mediated by resource partitioning. By explicitly examining mechanistic links between diversity and ecosystem functioning we can develop a predictive capacity, enabling us to quantify the expected loss of ecosystem functioning under scenarios of global and local environmental change.

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#### APPENDIX A

Image of a mesocosm used in the experiment (*Ecological Archives* E089-018-A1).

#### APPENDIX B

Description of prey assemblage (*Ecological Archives* E089-018-A2).

#### APPENDIX C

Calculation of resource capture efficiency (*Ecological Archives* E089-018-A3).

#### APPENDIX D

Total resource capture rate within all treatments (*Ecological Archives* E089-018-A4).

#### APPENDIX E

Analysis of predator diversity and density effects (*Ecological Archives* E089-018-A5).

#### APPENDIX F

Analysis of species-specific resource consumption (*Ecological Archives* E089-018-A6).

#### APPENDIX G

Comparison of prey consumption patterns between monocultures and the polyculture (*Ecological Archives* E089-018-A7).