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References and Notes

1. P. C. Sereno, *Science* **284**, 2137 (1999).
2. D. B. Weishampel, P. Dodson, H. Osmólska, Eds., *The Dinosauria* (Univ. of California Press, Berkeley, CA, ed. 2, 2004).
3. M. J. Benton, *Q. Rev. Biol.* **58**, 29 (1983).
4. M. J. Benton, *Biol. Rev. Cambridge Philos. Soc.* **62**, 305 (1987).
5. A. J. Charig, *Symp. Zool. Soc. London* **52**, 597 (1984).
6. R. T. Bakker, *Evolution* **25**, 636 (1971).
7. P. E. Olsen *et al.*, *Science* **296**, 1305 (2002).
8. R. B. Irmis *et al.*, *Science* **317**, 358 (2007).
9. S. J. Nesbitt, R. B. Irmis, W. G. Parker, *J. Syst. Palaeontol.* **5**, 209 (2007).
10. S. J. Nesbitt, M. A. Norell, *Proc. R. Soc. London Ser. B* **273**, 1045 (2006).
11. Examples include *Ornithosuchus* and *Postosuchus*.
12. Examples include *Poposaurus*, *Revueltosaurus*, *Shuvosaurus*, and *Teratosaurus*.
13. See supporting material on *Science* Online.
14. M. Ruta, P. J. Wagner, M. I. Coates, *Proc. R. Soc. London Ser. B* **273**, 2107 (2006).
15. P. J. Wagner, *Paleobiology* **23**, 115 (1997).
16. M. A. Wills, D. E. G. Briggs, R. A. Fortey, *Paleobiology* **20**, 93 (1994).
17. M. Foote, *Paleobiology* **20**, 320 (1994).
18. J. W. Valentine, *Paleobiology* **6**, 444 (1980).
19. D. Schluter, *The Ecology of Adaptive Radiation* (Oxford Univ. Press, Oxford, 2000).
20. S. J. Gould, *The Structure of Evolutionary Theory* (Harvard Univ. Press, Cambridge, MA, 2002).
21. D. H. Erwin, *Palaeontology* **50**, 57 (2007).
22. The results are unexpected under a null model of diffusive evolution with constant step size over time (*23*).
23. M. Foote, in *Evolutionary Paleobiology* (Univ. of Chicago Press, Chicago, 1996).
24. L. J. Harmon, J. A. Schulte II, A. Larson, J. B. Losos, *Science* **301**, 961 (2003).
25. J. C. McElwain, D. J. Beerling, F. I. Woodward, *Science* **285**, 1386 (1999).
26. D. Jablonski, *Science* **231**, 129 (1986).
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Supporting Online Material

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Materials and Methods
SOM Text
Figs. S1 to S4
Tables S1 to S29
References

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Niche Partitioning Increases Resource Exploitation by Diverse Communities

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Classical ecological theory suggests that the coexistence of consumer species is fostered by resource-use differences, leading to greater resource use in communities with more species. However, explicit empirical support for this idea is lacking, because resource use by species is generally confounded with other species-specific attributes. We overcame this obstacle by co-opting behavioral plasticity in food choice among a group of animal consumers, allowing us to manipulate patterns of resource use while controlling for the effects of species identity and diversity. Within an aphid-parasitoid-radish community, we created a fully factorial manipulation of consumer resource-use breadth (specialist versus generalist) and species diversity (one versus three species) and found that resource exploitation improved with greater specialist, but not generalist, diversity. Therefore, resource partitioning, and not diversity per se, fostered greater overall resource consumption in our multispecies consumer communities.

Early ecological models suggested that relatively strong intraspecific competition paired with relatively weak interspecific competition fosters species coexistence and promotes biodiversity (*1*–*4*). When these conditions exist, new species are able to invade model communities because they can monopolize a subset of the total resource pool. In contrast, when interspecific competition is the predominant force and resource partitioning is absent, only the single consumer species that drives the limiting resource to the lowest level is able to persist (*5*). This leads to the prediction that when species differ in resource-use patterns, adding more species to a community will lead to increased overall exploitation of available resources (*3*, *5*, *6*). It is resource differentiation among consumers at the community level that is expected to lead to more complete resource exploitation and not species diversity per se. However, empirical validation of these ideas has been hindered by the fact that resource-use differences among species typically are inextricably confounded with other species-specific attributes and requirements (such as size, rate of growth, metabolic rate, and fecundity). This lack of empirical support led, until recently, to the deemphasis of resource partitioning as a key driver of community structure (*1*).

Recent experimental manipulations of species richness have revealed, across a broad range of real-world ecological communities, a general pattern of greater resource exploitation when more species are present (*7*–*9*). However, the role of resource-use partitioning as a mechanism underlying this pattern, if any, has resisted empirical documentation (*10*–*16*). Progress has been hindered again by the seeming impossibility of entirely isolating the impacts of resource partitioning from those of other species attributes (*12*, *14*, *17*).

Here, we report an empirical test of the idea that resource partitioning leads to a net increase in resource exploitation by consumer communities. Our work was conducted in a model system in which plastic prey-choice behavior by natural enemies was exploited to manipulate overlap in resource use, independent of consumer species identity and thus of other species-specific traits. The system consisted of radish host plants, aphid herbivores, and parasitoid natural enemies. Radish (*Raphanus sativus*) plants in the Pacific Northwest of the United States are consumed by a variety of phloem-feeding aphid species, including green peach aphids (*Myzus persicae*), cabbage aphids (*Brevicoryne brassicae*), and turnip aphids (*Lipaphis erysimi*). These aphids are attacked by a diverse community of parasitoid wasps in the family Braconidae, including the species *Diaeretiella rapae*, *Aphidius colemani*, and *A. matricariae* (*18*). Insect parasitoids deliver natural pest control in agricultural systems worldwide, an ecosystem service of great economic and environmental value to humans (*19*).

We manipulated the resource use of individual consumer species by taking advantage of the natural host fidelity exhibited by these otherwise generalist parasitoid wasps (*18*, *20*). Although each parasitoid species is capable of attacking and completing development in all three aphid species, when given a choice, individual female wasps prefer to deposit eggs in hosts of the same species from which they themselves emerged (*20*) (fig. S1). This host fidelity is most likely expressed through associative learning. Upon emergence as adults, wasp parasitoids use the chemical cues associated with the natal host and its environment to direct their searching (*20*). As a result, parasitoids are more likely to locate and oviposit in hosts of the same species as their natal host. Such host fidelity behavior gave us an opportunity to manipulate the breadth of resources exploited by different populations of a single species and also across communities including several wasp species (*21*). We reared wasps of each of the three species on each of the three species of aphids, for a total of nine different wasp/aphid species associations. Then, by combining individual wasps from these source colonies, we could experimentally construct wasp communities differing in intraspecific and/or interspecific resource-niche breadth (fig. S2). By doing so, we were able to isolate the effects of competition on a well-defined resource, the aphid community, from the effects of other parasitoid species attributes.

Wasp communities were assembled that differed in all combinations of species identity, resource-use overlap ("specialists" that partition resources

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versus "generalists" that completely overlap in their resource use), and the potential for intraspecific and/or interspecific competition (with a parasitoid species richness of one versus three) (*21*). We did this in field cages containing all three aphid species and measured the resulting impacts on the percentage of aphid parasitism and on aphid abundance. The manipulation of resource-use overlap and competitive interactions among parasitoids resulted in four parasitoid treatments: (i) a single specialist parasitoid species (36 individual parasitoids of the same species, all reared from the same aphid host); (ii) three specialist parasitoid species, each of which prefers to attack a different aphid host (12 individuals of each of the three parasitoid species, with each species reared on a different aphid host); (iii) a single generalist parasitoid species (36 parasitoids of the same species, with 12 individuals reared from each of the three aphid hosts); and (iv) three generalist parasitoid species that completely overlap in their resource use (l2 individuals of each of the three parasitoid species, with 4 individuals of each parasitoid species reared from each of the three aphid species). Every possible parasitoid/host species combination was included within each treatment, and these compositions constituted replicates within that treatment (table S1). Including all parasitoid/host species combinations ensured that our results could not be unduly influenced by any single parasitoid species or by any parasitoid/aphid species pairing (*22*, *23*). Total parasitoid abundance at the time of release was held constant at 36 adult females (9 females/m^2) across all treatments. This experiment was conducted under real-world conditions in large field cages at the Washington State University Research Station in Othello, Washington.

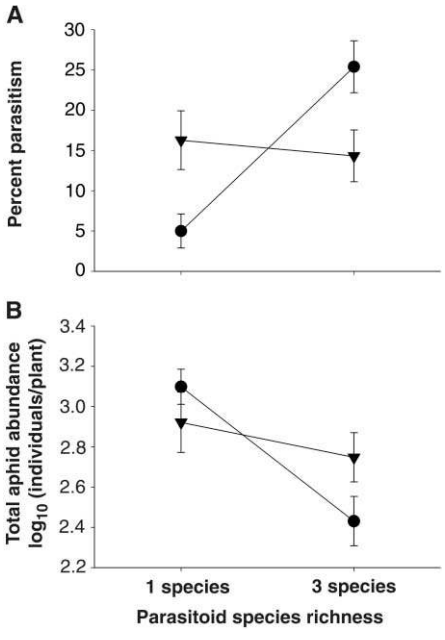

Fig. 1. Interactive effect of interspecific competitive interactions (with a parasitoid species richness of one versus three) and parasitoid resource-use differentiation on aphid population suppression. Population suppression by specialist parasitoids that partition their resource use (circles) is compared to that of generalist parasitoids with completely overlapping resource use (triangles) at two levels of species richness. At a species richness of one, only intraspecific interactions are possible, whereas both intraspecific and interspecific interactions are possible at a species richness of three. (**A**) Percent of total aphid population that is parasitized. (**B**) Total aphid abundance (log-transformed). Data are least squares means ± SEM obtained from repeated measures of analysis of covariance.

We found that parasitism success among wasp communities was affected by a strong interaction between the degree of resource-use overlap and consumer species richness (significant species richness times resource-use overlap interaction, $F_{1,32} = 12.56$, $P = 0.0013$; Fig. 1A). When parasitoids were generalists and any single species had access to all resources, increasing species richness did not affect the parasitism of the aphid community (*t* test of the difference between two means, $t_{32} = 0.40$, $P = 0.6934$; Fig. 1A). In contrast, when consumer species were specialists that used different resources, the percentage of parasitism increased dramatically when three species were present as opposed to one ($t_{32} = 5.25$, $P < 0.0001$; Fig. 1A). Comparing the two treatments including multiple consumer species, the percentage of parasitism was significantly greater when consumer species were specialists than generalists ($t_{32} = 2.40$, $P = 0.0224$; Fig. 1A). Aphid densities did not differ among treatments during the early course of the experiment (fig. S3), suggesting that parasitism rates were not indirectly affected by confounding differences in resource abundance among treatments.

Differences in the percentage of parasitism across treatments resulted in concordant differences in aphid densities. Parasitoid species richness and resource-use overlap interacted to determine total aphid abundance (significant species richness times resource-use overlap interaction, $F_{1,32} = 3.98$, $P = 0.0550$; Fig. 1B). Suppression of aphids was unaffected by the presence of multiple consumer species when parasitoids were generalists that completely overlap in their resource use ($t_{32} = 0.90$, $P = 0.3765$; Fig. 1B), suggesting equitability in the magnitude of intraspecific and interspecific interactions. Such competition among parasitoids is often chemically mediated, with parasitoid females being capable of recognizing the presence of both intraspecific and interspecific competitors (*24*). However, for specialist parasitoids, aphid consumption was greater and thus aphid abundance was lower, with greater parasitoid species richness ($t_{32} = 4.40$, $P = 0.0007$; Fig. 1B). Consistent with these results, per capita impacts on aphids of specialist parasitoids but not generalist parasitoids were higher with greater parasitoid species richness (fig. S4).

We independently manipulated resource-niche breadth and consumer species richness and found that resource exploitation was strengthened by a complex interaction between these two factors. Among our treatment combinations, the most substantial parasitism of aphids, and thus the lowest aphid densities, were recorded in communities combining multiple species of specialist parasitoids. In contrast, wasp performance was relatively weaker in diverse communities of generalists. With species richness held constant, the key difference between these two treatments is that we would expect intraspecific competition to be relatively intense and interspecific competition relatively weak for diverse communities of specialists as compared to generalists (*25*). Thus, our results closely match the preconditions for species coexistence predicted by classic early niche models (*2*, *3*). Additionally, our results match more recent assertions that it is differences in resource use among species, rather than diversity per se, that intensifies resource exploitation at higher levels of consumer diversity (*6*, *16*, *26*–*28*). Thus, we found empirical evidence that resource-niche partitioning may be both a factor encouraging greater biodiversity and an underlying cause of efficient resource extraction by species-rich communities, once assembled. Our results also support the argument that it is the conservation of species that fulfil specialized functional roles, rather that greater diversity itself, that is needed to preserve ecosystem function (*14*, *29*, *30*).

Studies focusing on predaceous animal consumers can be particularly enlightening, because resources (prey) in such systems are easily identified and the effects of resource capture (prey suppression) are readily observable (*13*, *16*, *25*, *31*, *32*). Further, when foraging behavior is plastic, differences in resource use among species can be experimentally manipulated, a powerful technique for testing the predictions of theoretical models related to resource partitioning, species coexistence, and biodiversity.

References and Notes

1. J. M. Chase, M. A. Leibold, *Ecological Niches: Linking Classical and Contemporary Approaches* (Univ. of Chicago Press, Chicago, 2003).
2. G. E. Hutchinson, *Am. Nat.* **93**, 145 (1959).
3. R. MacArthur, *Theor. Popul. Biol.* **1**, 1 (1970).
4. R. B. McKane *et al.*, *Nature* **415**, 68 (2002).
5. P. Chesson, *Annu. Rev. Ecol. Syst.* **31**, 343 (2000).
6. R. M. May, *Stability and Complexity in Model Ecosystems* (Princeton Univ. Press, Princeton, NJ, 1973).
7. P. Balvanera *et al.*, *Ecol. Lett.* **9**, 1146 (2006).
8. B. J. Cardinale *et al.*, *Nature* **443**, 989 (2006).
9. B. Worm *et al.*, *Science* **314**, 787 (2006).
10. M. E. S. Bracken, J. J. Stachowicz, *Ecology* **87**, 2397 (2006).
11. J. D. Fridley, *J. Ecol.* **91**, 396 (2003).
12. A. Kahmen, C. Renker, S. B. Unsicker, N. Buchmann, *Ecology* **87**, 1244 (2006).
13. W. E. Snyder, G. B. Snyder, D. L. Finke, C. S. Straub, *Ecol. Lett.* **9**, 789 (2006).
14. D. Tilman *et al.*, *Science* **277**, 1300 (1997).
15. A. V. Tiunov, S. Scheu, *Ecol. Lett.* **8**, 618 (2005).
16. A. Wilby, M. B. Thomas, *Ecol. Lett.* **5**, 353 (2002).
17. H. R. Lambers, W. S. Harpole, D. Tilman, J. M. H. Knops, P. Reich, *Ecol. Lett.* **7**, 661 (2004).
18. K. Pike *et al.*, *Proc. Entomol. Soc. Wash.* **102**, 688 (2000).
19. J. E. Losey, M. Vaughan, *Bioscience* **56**, 311 (2006).
20. T. C. J. Turlings, F. L. Wäckers, L. E. M. Vet, W. J. Lewis, J. H. Tumlinson, in *Insect Learning: Ecological and Evolutionary Perspectives*, D. R. Papaj, A. C. Lewis, Eds. (Chapman & Hall, New York, 1992), pp. 51–78.
21. See supporting material on *Science* Online.
22. M. A. Huston, *Oecologia* **110**, 449 (1997).

23. D. Tilman, C. L. Lehman, K. T. Thomson, *Proc. Natl. Acad. Sci. U.S.A.* **94**, 1857 (1997).
24. C. R. Nufio, D. R. Papaj, *Entomol. Exp. Appl.* **99**, 273 (2001).
25. D. L. Finke, R. F. Denno, *Nature* **429**, 407 (2004).
26. P. Casula, A. Wilby, M. B. Thomas, *Ecol. Lett.* **9**, 995 (2006).
27. A. R. Ives, B. J. Cardinale, W. E. Snyder, *Ecol. Lett.* **8**, 102 (2005).
28. M. Loreau, *Proc. Natl. Acad. Sci. U.S.A.* **95**, 5632 (1998).
29. D. R. Chalcraft, W. J. J. Resetarits, *Ecology* **84**, 2407 (2003).
30. D. U. Hooper, J. S. Dukes, *Ecol. Lett.* **7**, 95 (2004).
31. T. Bukovinszky, F. J. F. van Veen, Y. Jongema, M. Dicke, *Science* **319**, 804 (2008).
32. O. J. Schmitz, *Science* **319**, 952 (2008).

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Materials and Methods
Figs. S1 to S4
Table S1
References

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Degradation of microRNAs by a Family of Exoribonucleases in *Arabidopsis*

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microRNAs (miRNAs) play crucial roles in numerous developmental and metabolic processes in plants and animals. The steady-state levels of miRNAs need to be properly controlled to ensure normal development. Whereas the framework of miRNA biogenesis is established, factors involved in miRNA degradation remain unknown. Here, we show that a family of exoribonucleases encoded by the *SMALL RNA DEGRADING NUCLEASE* (*SDN*) genes degrades mature miRNAs in *Arabidopsis*. SDN1 acts specifically on single-stranded miRNAs in vitro and is sensitive to the 2′-*O*-methyl modification on the 3′ terminal ribose of miRNAs. Simultaneous knockdown of three *SDN* genes in vivo results in elevated miRNA levels and pleiotropic developmental defects. Therefore, we have uncovered the enzymes that degrade miRNAs and demonstrated that miRNA turnover is crucial for plant development.

Plant miRNAs carry a 2′-*O*-methyl group that protects them from a 3′-to-5′ exonucleolytic activity and a uridylation activity that adds an oligoU tail to the 3′ ends of miRNAs (*1*, *2*). Maintaining proper steady-state levels of miRNAs is crucial for plant development (*3*–*7*). The steady-state levels of miRNAs are presumably determined by the opposing activities of miRNA biogenesis and degradation. A conserved exonuclease from *Caenorhabditis elegans* and *Schizosaccharomyces pombe*, Eri-1, specifically degrades small interfering RNA (siRNA)/siRNA* (where siRNA* represents antisense siRNA) duplexes with 2-nucleotide (nt) 3′ overhangs in vitro and reduces RNA interference efficiency in vivo (*8*, *9*). Exonucleases that degrade single-stranded small RNAs have yet to be identified.

To identify enzymes that degrade single-stranded miRNAs or siRNAs, we took a candidate-gene approach. We presume that enzymes involved in miRNA metabolism evolved from enzymes that process structural and/or catalytic RNAs, a view supported by the fact that a number of known players in small RNA metabolism also function in the processing of ribosomal RNAs (rRNAs) (*10*–*13*). We sought for *Arabidopsis* homologs of a class of exoribonucleases in yeast, Rex1p to Rex4p, which participate in 3′-end processing of rRNAs and tRNAs (*14*, *15*). BLAST (*16*) searches using the 4 Rex proteins identified 15 *Arabidopsis* proteins containing an exonuclease domain (fig. S1). At3g15140, which belongs to a clade of 6 proteins (fig. S1), was the most similar to Eri-1 among the 15 proteins. Because we seek enzymes that degrade single-stranded small RNAs, we excluded proteins in this clade from our analysis.

From the remaining Rex homologs, we randomly chose At3g50100 from the five-member clade and At3g15080 from the outliers (fig. S1), expressed them as glutathione *S*-transferase (GST) fusion proteins in *Escherichia coli* (fig. S2), and tested their activities on miRNAs in vitro (*17*). A 5′ end–labeled single-stranded RNA oligonucleotide corresponding to miR167 in sequence (but lacking a 2′-*O*-methyl group) was incubated with GST-At3g15080, GST-At3g50100, or GST. Whereas GST-At3g15080 or GST did not exhibit any activity on miR167, GST-At3g50100 degraded the full-length miR167, generating a product of ~8 to 9 nt (Fig. 1A; the size of the final product was estimated from Fig. 2D). GST-At3g50100 also acted on miR173 and 2′-*O*-methylated miR173 and generated products of ~8 to 9 nt (Fig. 1A). We refer to At3g50100 as SMALL RNA DEGRADING NUCLEASE1 (SDN1) hereafter.

To determine whether SDN1 is an endonuclease cleaving the RNAs between nucleotides 8 and 9 from their 5′ ends or a 3′-to-5′ exonuclease that cannot process RNAs of 8 nt or shorter, we labeled miR173 with ^{32}pCp at the 3′ end and incubated miR173-^{32}pCp with GST-SDN1. miR173-^{32}pCp was resistant to GST-SDN1, and phosphatase treatment of miR173-^{32}pCp to remove the 3′ phosphate rendered the miRNA susceptible to GST-SDN1 (Fig. 1B). Furthermore, a product of 15 nt, which would be expected if SDN1 were an endonuclease cleaving between nucleotides 8 and 9 from the 5′ end, was not observed on phosphatase-treated miR173-^{32}pCp (Fig. 1B). These data indicated that SDN1 is a 3′-to-5′ exonuclease.

GST-SDN1 did not have any effect on a single-stranded DNA oligonucleotide (Fig. 2B) and is therefore a ribonuclease. Unlike Eri-1 (*9*), GST-SDN1 failed to degrade miR173 in a miR173/miR173* duplex (Fig. 2B and fig. S3). To examine SDN1 substrate size, synthetic RNA oligonucleotides of 17, 18, 20, 21 (miR167), 22 (miR173), 23, 24, and 27 nt (table S2) were incubated with GST-SDN1 separately. SDN1 degraded all tested RNA oligonucleotides and yielded an end product of ~8 to 9 nt, regardless of the length of the substrates (Fig. 2A). However, SDN1 cannot act on longer RNAs. pre-miR167 or a 300-nt RNA from the protein-coding *APETALA1* (*AP1*) gene was not detectably degraded by GST-SDN1 (Fig. 2C). Therefore, SDN1 acts specifically on single-stranded small RNAs in a sequence-independent manner.

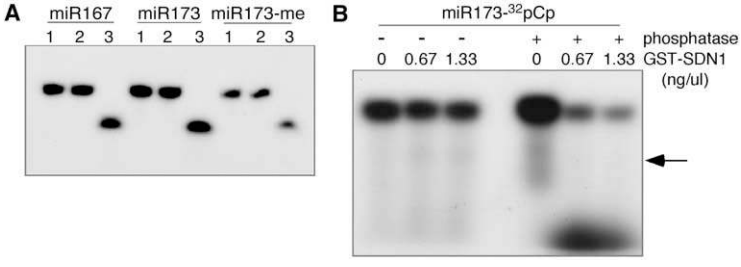

Fig. 1. *Arabidopsis* At3g50100 (SDN1) possesses 3′-to-5′ exonuclease activity on miRNAs. (**A**) Enzymatic activity assays on single-stranded miRNAs in vitro. RNA oligonucleotides were 5′-end labeled, incubated with buffer alone (1), purified GST (2), or purified GST-At3g50100 (3), and resolved on a denaturing polyacrylamide gel. miR173-me is a miR173 oligonucleotide containing a 2′-*O*-methyl group on the 3′ terminal ribose. (**B**) Enzymatic activity of GST-At3g50100 (GST-SDN1) on miR173 labeled at the 3′ end with ^{32}pCp. miR173-^{32}pCp was treated (+) or not treated (–) with phosphatase before incubation with GST-SDN1. The arrow indicates the position of the expected 15-nt product if SDN1 were to cleave the RNA between nucleotides 8 and 9 from the 5′ end. The radioactivity at the bottom corresponds to the position of free nucleotides.

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