

# Superiority, Competition, and Opportunism in the Evolutionary Radiation of Dinosaurs

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The rise and diversification of the dinosaurs in the Late Triassic, from 230 to 200 million years ago, is a classic example of an evolutionary radiation with supposed competitive replacement. A comparison of evolutionary rates and morphological disparity of basal dinosaurs and their chief “competitors,” the crurotarsan archosaurs, shows that dinosaurs exhibited lower disparity and an indistinguishable rate of character evolution. The radiation of Triassic archosaurs as a whole is characterized by declining evolutionary rates and increasing disparity, suggesting a decoupling of character evolution from body plan variety. The results strongly suggest that historical contingency, rather than prolonged competition or general “superiority,” was the primary factor in the rise of dinosaurs.

The rise of the dinosaurs in the Late Triassic and Early Jurassic (230 to 190 million years ago) is a classic example of an evolutionary radiation. During that time, the clade Dinosauria expanded from a single lineage to many dozens of lineages and from one ecological and morphological type to many, and the range of body sizes expanded to include truly gigantic forms (1, 2). Through this expansion in diversity and disparity, dinosaurs became the preeminent vertebrates on land, occupying many ecological roles—especially those at medium to large size—in terrestrial ecosystems worldwide.

The expansion of Dinosauria has long been seen as an example of a “competitive adaptive radiation” in which one group supplants another (3, 4). The dinosaurs were said to have outcompeted other terrestrial tetrapods (notably basal archosaurs, rhynchosaurs, and nonmammalian synapsids) by virtue of their upright or erect posture, which gave them advantages of speed and maneuverability (5), or because they were endothermic (possessing fully warm-blooded physiology) (6). The alternative, opportunistic model (3) proposes that dinosaurs diversified in the Norian, after a Carnian-Norian extinction event (CNEE) 228 million years ago that saw the demise of rhynchosaurs, dicynodonts, and chiniquodontids; dinosaurian clades were then added through the Late Triassic and Early Jurassic until they reached their full diversity.

Most previous studies have treated the rise of the dinosaurs as a single event, whether competitive or opportunistic (3, 5–8). However, phylogenies and diversity trends suggest that this was a two-step process, with the diversification of herbivorous sauropodomorphs in the Norian

(after the CNEE) followed by larger theropods and armored herbivore groups in the Early Jurassic [after extinction of carnivorous crurotarsans at or near the Triassic-Jurassic boundary (TJEE)]. This two-step model has been supported by recent studies of theropods, which became larger and more common after the TJEE (7), and ornithischians, which are now known to have been rare in the Late Triassic after the reassignment of many supposed ornithischian fossils to non-dinosaurian groups (9).

The critical interval to consider is the Late Triassic, especially the Norian and Rhaetian (Fig. 1), a 28-million-year span between the CNEE and TJEE. The key “competitors” of the early dinosaurs were the crurotarsans, the “crocodile-line” archosaurs, which show a range of morphologies and adaptations during this time: long-snouted fish- and flesh-eating phytosaurs, armored herbivorous aetosaurs, and large to giant carnivorous “rauisuchians.” The crurotarsans even replicated many dinosaurian body plans (large terrestrial predators; small swift predators; mid- to large-bodied low-browsing herbivores; agile bipedal herbivores). Several new discoveries show striking convergences between crurotarsans and dinosaurs (10), and many Triassic crurotarsans were previously erroneously identified as dinosaur ancestors (11) or even as true dinosaurs (12). Such morphological convergence suggests that dinosaurs and crurotarsans were exploiting similar resources in the Late Triassic. In some Norian faunas, crurotarsans were numerically more abundant than dinosaurs (3) and seem to have exploited a wider range of body plans. However, by the end of the Triassic all crurotarsans were extinct, save a few lineages of crocodylomorphs.

The key question is why the major dinosaur lineages survived the TJEE, ushering in the 135-million-year “age of dinosaurs,” while most crurotarsan groups went extinct. One common explanation is that dinosaurs outcompeted crurotarsans in the Late Triassic, and notions of general dinosaurian “superiority” have long pervaded the literature (5, 6). Hypotheses of com-

petition between major clades are often vague, difficult to test conclusively, and prone to oversimplification (4). Rather than focusing on such imprecise terms, it is illuminating to examine macroevolutionary patterns. Here, we compared evolutionary rates and relative morphospace occupation in dinosaurs and crurotarsans, in an effort to shed light on their evolutionary dynamics and to assess long-standing perceptions such as “superiority.”

We used a new phylogeny of Triassic archosaurs (Fig. 1) and a data set consisting of 64 taxa and 437 discrete skeletal characters (13) to calculate numerical measures of evolutionary rates [patristic dissimilarity per branch and patristic dissimilarity divided by branch duration (14)] and disparity (morphospace occupation) (13). Note that evolutionary rates analysis approximates the amount of morphologic evolution separating species, whereas disparity analysis approximates the amount of morphologic difference between species (14–17). These are related but separate measures of morphological evolution that together give insights into patterns of macroevolutionary change within and between clades. Disparity analysis does not depend on a specific phylogenetic hypothesis, but evolutionary rates analysis does.

There is no clear evidence for differences in overall evolutionary rates between dinosaurs and crurotarsans during the Triassic as a whole. Dinosaurs exhibit higher mean rates than crurotarsans for all measures (Fig. 2, A and B, and fig. S2, A and B)—as does the entire dinosaur “total group,” Ornithodira (sister taxon to Crurotarsi)—but these differences are generally not significant (tables S1 and S28). A pruned analysis of equal sample sizes for the two clades returns the same result (table S2), as does an analysis restricted to Norian taxa (table S3). There is limited evidence for significantly higher rates in Carnian dinosaurs, but this may be due to small sample size (table S3). Temporal trends do not show a coupled increase in dinosaur rates and decrease in crurotarsan rates, as might be expected under some models of “competition” (Fig. 2, E and F, and fig. S2, E and F). Relative to crurotarsans, dinosaurs exhibit a significantly higher rate of evolution of the appendicular skeleton, but not of the cranial or axial skeleton (table S9). However, there are no significant differences between rates for different regions of the dinosaur skeleton (tables S16 and S17).

Perhaps counterintuitively, the disparity study shows that crurotarsans occupied a larger amount of morphospace than did dinosaurs and ornithodirans as a whole (Fig. 3, A and B, fig. S3, A and B, and tables S21 and S29). Rarefaction curves show that these results are not biased by sample size (fig. S4). The same pattern holds within the Carnian and Norian (table S22), and there are no coupled temporal trends (Fig. 3, E and F, and fig. S3, E and F). Dinosaurs and crurotarsans occupy adjacent areas of morphospace (Fig. 1), which is expected because the analysis is based on cladistic characters.

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Crurotarsans convergent with dinosaurs (poposauroids, “rauisuchids,” and basal crocodylomorphs) occupy an intermediate area between the majority of crurotarsans and dinosaurs. The higher disparity of crurotarsans is borne out by visual examination of Fig. 1, which shows a much larger morphospace than that for dinosaurs. Unexpectedly, this larger crurotarsan morphospace is associated with significantly higher rates of homoplasy (table S18), which suggests that character oscillation is an important factor in body plan evolution.

Archosaurs radiated during the Triassic in the aftermath of the end-Permian mass extinction. Our analysis shows that this radiation was associated with declining evolutionary rates per lineage and increasing morphological disparity throughout the Triassic. One rate metric—dissimilarity calibrated by time interval duration—shows a general decrease through the Triassic, with significantly high rates in the Anisian and low rates in the Norian (Fig. 2D, fig. S2D, and tables S4 and S5). Patterns within Crurotarsi and Dinosauria mirror those of Archosauria as a whole, as both subclades are characterized by decreasing rates (Fig. 2F, fig. S2F, and tables S6 to S8). Similarly, decreasing rates are also seen in cranial, axial, and appendicular character partitions (tables S10 to S15). The significantly high rates of character evolution in early archosaur history are consistent with the hypothesis of elevated rates during major morphological radiations (15, 18–20).

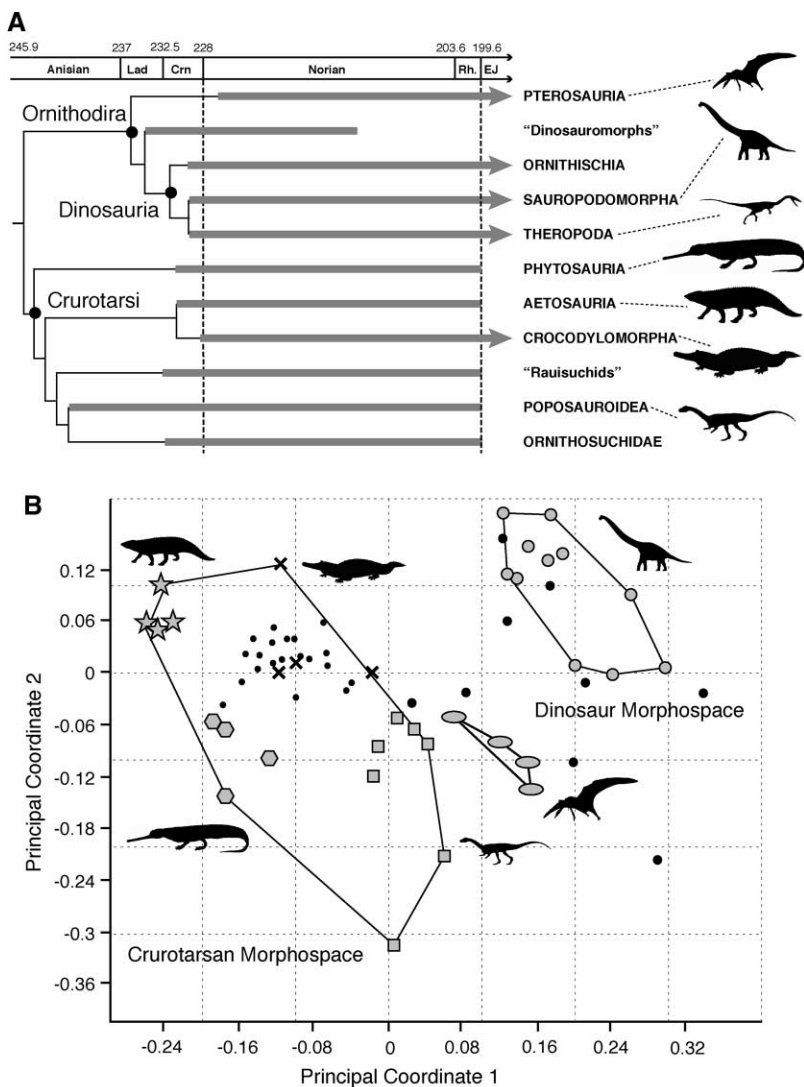
In contrast, archosaurs show increasing disparity throughout the Triassic, with a significantly high peak in the Norian (Fig. 3, C and D, and tables S23 and S24). Both crurotarsans and dinosaurs show a general increase in disparity across the Triassic, except for a Ladinian drop for crurotarsans that may be due to small sample size, but the differences between time bins are not significant (tables S25 and S26). This pattern differs from the findings of several paleontological studies, which have shown that disparity often peaks early in the history of major clades (15–17, 21).

Unexpectedly, these results indicate a decoupling of character evolution and morphological disparity in Triassic archosaurs (22, 23). The inverse relationship indicates that, apparently, the burst of character evolution in early archosaur history did not translate into a wide range of body plans. Only later, when evolutionary rates decreased and homoplasy increased (tables S19 and S20), did a slower rate of character change result in the development of several new body plans (phytosaur, aetosaur, crocodylomorphs, pterosaurs, and dinosaurs), all of which are first known from the Carnian or Norian. Decoupling of lineage diversification and disparity has been noted before, but only in the context of within-subclade disparity among extant lizards (24). Further work is needed to determine what, if any, broad generalizations characterize evolutionary radiations across a

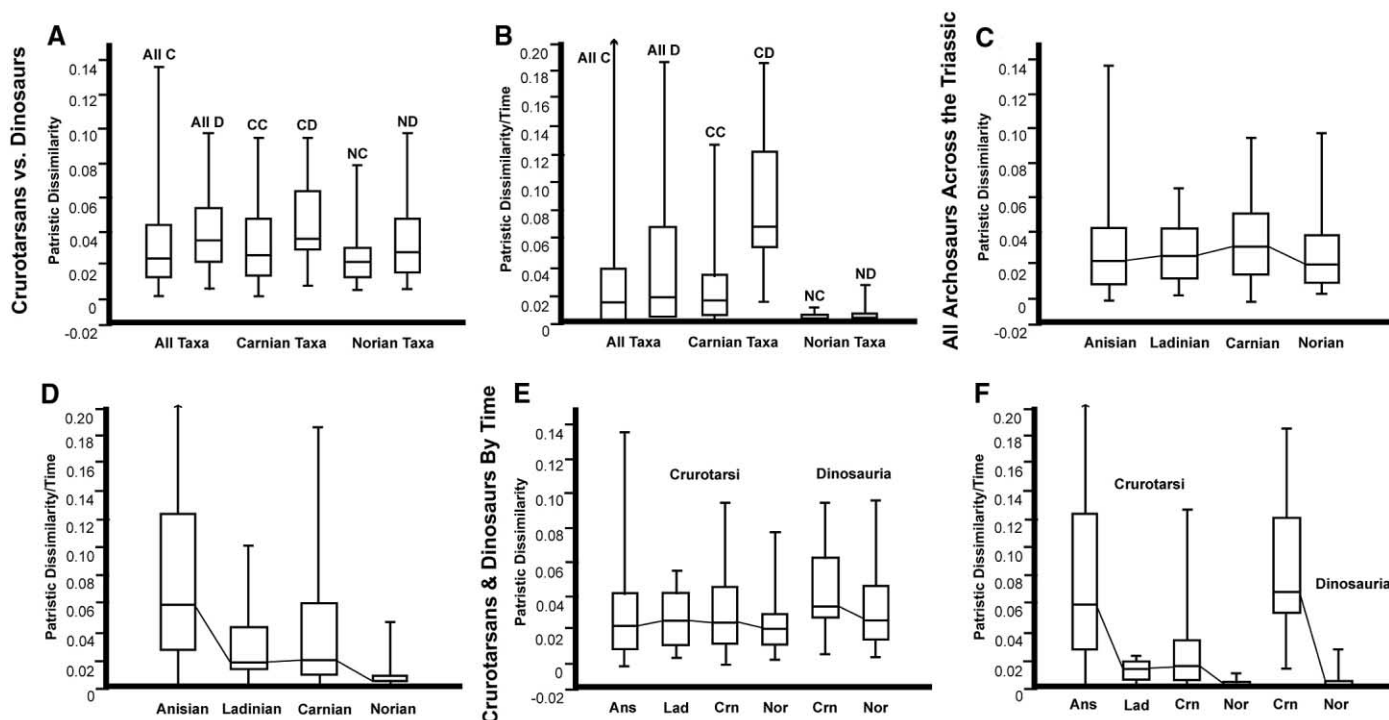
wide range of organisms, time scales, and clade dimensions.

For the first 30 million years of their history, dinosaurs lived alongside and shared niches with another major clade (Crurotarsi) that occupied more morphospace and evolved at indistinguishable rates. These patterns seriously contrast with general notions of dinosaurian “superiority” and the long-standing view that dinosaurs were preordained for success (5, 6). It is difficult to explain why crurotarsans and not dinosaurs went extinct at the TJEE, which may have been a catastrophic event (7) or an ecologically drawn-out affair triggered by eruption and elevated CO<sub>2</sub> levels (25). Either way, as in most mass extinction events, the death of species is often more random than eco-

logically selective (26), and so the relative proportions (or relative success) of two groups during normal times may reverse during a sudden crisis. Nonetheless, our results are consistent with at least two explanations: (i) Crurotarsans died out by chance, despite their larger range of morphospace and similar evolutionary rates to dinosaurs; (ii) dinosaurs prevailed because of one or several key adaptations. The second suggestion is difficult to entertain because dinosaurs and crurotarsans lived side by side for 30 million years, and crurotarsans occupied more morphospace and were often more abundant and diverse than dinosaurs. It is likely that dinosaurs were the beneficiaries of two mass extinction events—and some good luck.

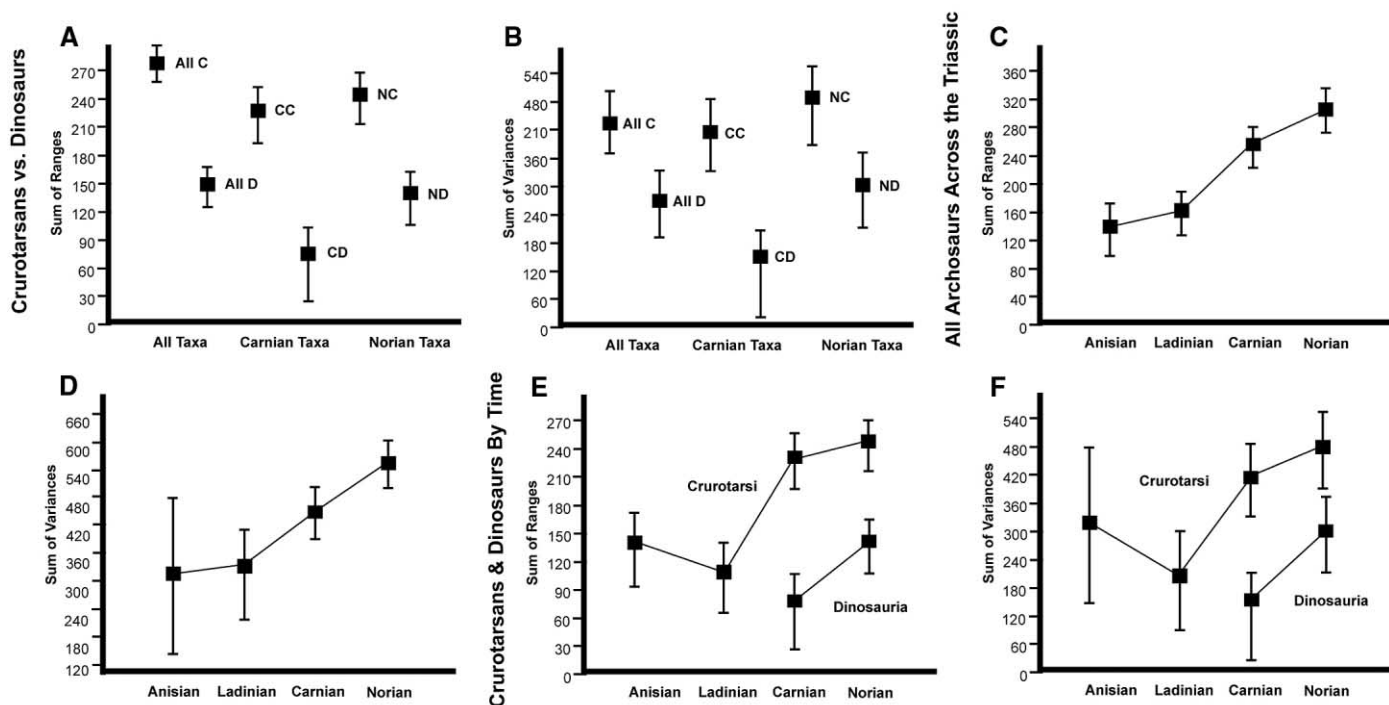


**Fig. 1.** Phylogenetic relationships and morphospace occupation for Triassic archosaurs. **(A)** Framework phylogeny for Triassic crurotarsans (13) scaled to the Triassic time scale (13). Numbers at top refer to millions of years before present; gray bars represent the observed durations of major lineages; vertical dashed lines denote two hypothesized extinction events (CNEE and TJEE); arrowheads indicate lineages that survived the TJEE. Lad, Ladinian; Crn, Carnian; Rh, Rhaetian; EJ, Early Jurassic. **(B)** Empirical morphospace for Triassic archosaurs, based on the first two principal coordinates (13). Large circles, dinosaurs; ovals, pterosaurs; squares, poposauroids; hexagons, phytosaurs; stars, aetosaurs; crosses, crocodylomorphs; smaller solid circles, “rauisuchids”; larger solid circles, nondinosaurian dinosauromorphs, *Scleromochlus*.



**Fig. 2.** Plots of rate of morphological character evolution for archosaurs, based on two metrics: patristic dissimilarity per branch and dissimilarity per time interval (13). Rates are based on ACSTRAN character optimization, but DELTRAN gives nearly identical results (fig. S2). Boxes represent the distribution of real data, with boxes encompassing percentiles 25 to 75 and the whiskers representing percentiles 5 to 95. (A and B) Evolutionary rates of crurotarsans and dinosaurs (All C, all Triassic crurotarsans; All D, all Triassic dinosaurs; CC, CD, NC, and ND, crurotarsans

and dinosaurs subdivided into Carnian and Norian taxa). (C and D) Disparity against time for all crown-group archosaurs. (E and F) Disparity against time for both crurotarsans and dinosaurs. Dinosaurs exhibit higher evolutionary rates than crurotarsans, but these are not significant (table S1). Rates for all archosaurs are either approximately constant (dissimilarity metric) or decrease from an Anisian high to a Norian low (dissimilarity/time metric; see also tables S4 and S5). Patterns within Crurotarsi and Dinosauria mirror the general pattern (tables S6 to S9).



**Fig. 3.** Plots of archosaur morphological disparity, based on two metrics: sum of ranges and sum of variances (13). Squares represent mean values; error bars denote 95% confidence intervals based on bootstrapping. (A and B) Disparity of crurotarsans and dinosaurs (abbreviations as in Fig. 2). (C and D) Disparity against time for all crown-group archosaurs. (E and F) Disparity against time for both crurotarsans and dinosaurs. Crurotarsans exhibit a significantly higher disparity

than dinosaurs when all Triassic taxa (nonparametric multivariate analysis of variance:  $F = 29.89, P < 0.0001$ ) and Carnian ( $F = 13.36, P = 0.0003$ ) and Norian ( $F = 20.59, P < 0.0001$ ) subdivisions are analyzed. Archosaur disparity increases over time and reaches a statistically significant peak in the Norian (tables S23 and S24). Crurotarsan and dinosaur disparity generally increase over time, but differences between individual time bins are not significant (tables S25 and S26).

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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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