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Notes and Comments

Resurrecting the Ghost of Competition Past with Dormant Zooplankton Eggs

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ABSTRACT: A common prediction of evolutionary theory is that the strength of interspecific competition should decline over time among sympatric populations of competing species. Here we provide experimental evidence of historical declines in competition effects among competing zooplankton populations. Using diapausing eggs, we resurrected clones of three species of zooplankton obtained from different periods of community assembly in a single lake. We show that clones of *Daphnia ambigua* obtained from early in assembly when *D. ambigua* was dominant became extinct in competition with clones of *Daphnia pulicaria* and *Daphnia dentifera* (the current lake dominants). In contrast, *D. ambigua* clones obtained from later in the lake's history experienced weaker competition effects and persisted with *D. dentifera*. While we cannot rule out the role of intraspecific competition within *D. ambigua*, our results are in line with the view that natural selection favors reduced interaction strength among co-occurring species, facilitating coexistence and population persistence.

Keywords: community assembly, competition, *Daphnia*, evolution, resurrection ecology.

The view that exploitative resource competition is a potent driver of natural selection has a long history, dating back to Darwin's *The Origin of Species*. While this notion persists, controversy remains as to the extent of competition's primacy in the adaptive dynamics of natural communities (Vermeij 1994; Schluter 2000). Numerous theoretical explorations have shown that selection can, under many cir-

cumstances, drive divergences in resource usage among interspecific competitors, reducing the strength of competition and facilitating coexistence among species (e.g., Slatkin 1980; Taper and Case 1985; Abrams 1987; Doebeli 1996). Thus, the strength of competitive interactions in later stages of a community's history are weaker "ghosts of competition past" (Connell 1980; Pritchard and Schluter 2001). Such reductions in interaction strength should be most evident during periods of active community assembly as novel species invade local sites and resident species adapt to increasing competition pressure. However, the search for competition's stamp on evolutionary patterns has commonly focused on spatial comparisons of sympatric and allopatric populations of competing species (reviewed in Schluter 2000; Dayan and Simberloff 2005). While valuable, such studies cannot directly address historical declines in competition intensity among species. Moreover, prior examinations have rarely measured interspecific competition effects experimentally, relying instead on morphological correlates of competitive ability.

The lack of focus on temporal changes in competition effects is due to the difficulty of tracking adaptive change within populations over adequately long time periods. Fortunately, many major zooplankton taxa produce diapausing eggs that remain dormant and viable within the sediments for decades (Kerfoot et al. 1999; Brendonck and De Meester 2003; Kerfoot and Weider 2004; Cáceres et al. 2005). Thus, representatives of populations from different stages of community assembly can be cultured and compared with species and populations from contrasting stages of community development (e.g., Hairston et al. 1999; Kerfoot et al. 1999; Cáceres et al. 2005). Figure 1 documents community assembly of the dominant zooplankton species in Sportsman's Lake (Illinois) based on diapausing egg cases (ephippia) found in its sediments. The lake was initially dominated by *Daphnia ambigua* but over time was invaded by the larger-bodied *Daphnia pulicaria* and *Daphnia dentifera*. These latter taxa are the current biomass dominants, although *D. ambigua* still persists and has been detected at low densities early in the growing season (Cáceres et al. 2005). The general pattern displayed in figure

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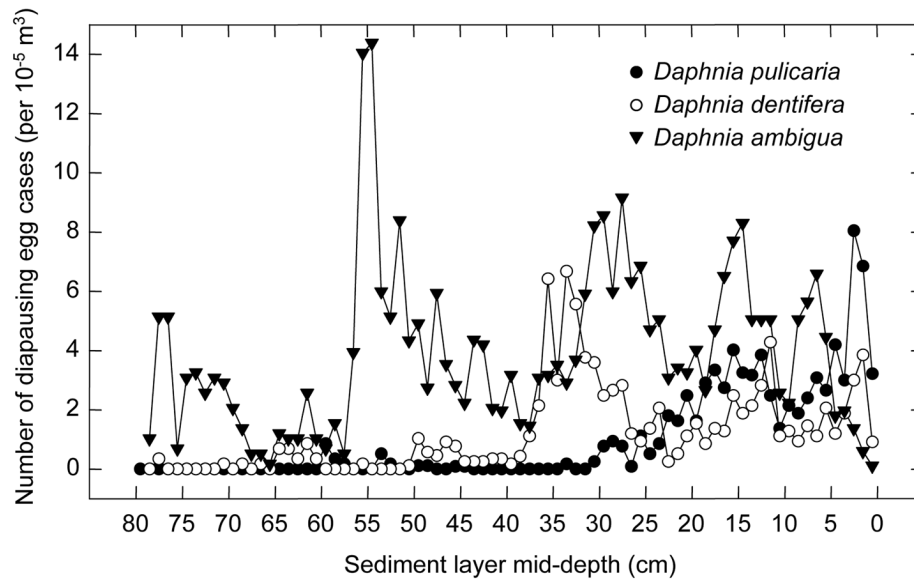


Figure 1: Mean number of diapausing egg cases (ephippia) of the dominant zooplankton species found in sediment cores of Sportsman's Lake. Deeper sediment layers were deposited earlier in the lake's history; thus, results represent a chronosequence from early assembly to the recent past. All cores extended to the underlying gravel basin, indicating that the entire sediment column was included in the sample. Results are based on five cores collected using scuba in 2003 and 2004; all ephippia were enumerated per 1-cm sediment layer and ranged from 0 to >100 per species. For detailed methods, see Cáceres et al. 2005.

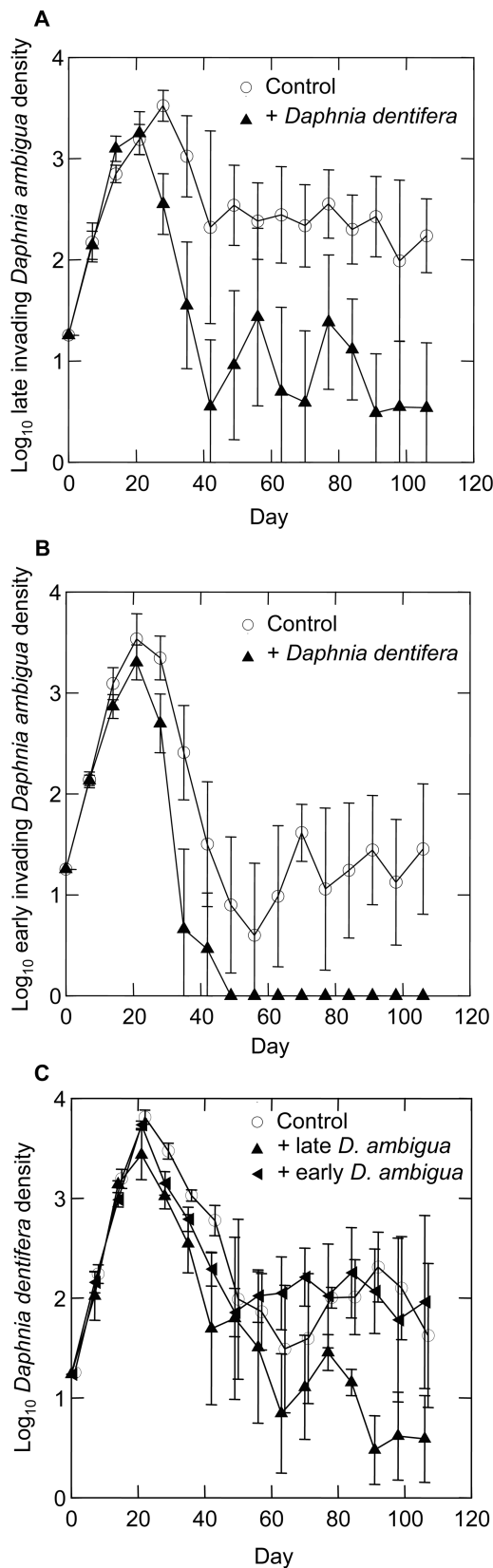
It was corroborated by examining zooplankton body remains preserved in the sediments, and it has also been observed in sediment records from other lakes in the region (C. E. Cáceres, unpublished data). Sportsman's Lake was created in 1953; owing to its recent formation, viable diapausing eggs of the *Daphnia* can be obtained from the entire sediment record. Using clones collected from different periods of the lake's history, we employed a long-term competition experiment to test whether *D. ambigua* (a species that has persisted since early community assembly to the present) has undergone selection for reduced competition effects and enhanced competitive persistence.

Methods

Competition was assessed among four groups of zooplankton clones, all obtained from Sportsman's Lake water column samples or sediment cores: *Daphnia pulicaria*, *Daphnia dentifera*, late-invading *Daphnia ambigua*, and early-invading *D. ambigua*. Each group was initially represented by 10 clones chosen haphazardly from lines maintained in the laboratory for numerous generations under common garden conditions. The *D. pulicaria* group was composed of five clones isolated from Sportsman's Lake water column samples taken in spring 2004 and five clones obtained from diapausing eggs extracted from the top 10 cm of sediment cores, representing a

period of co-occurrence of the three species (fig. 1). The *D. dentifera* group was represented by six clones isolated from spring 2004 water column samples and four clones isolated from the top 10 cm of sediment cores. We were unable to isolate *D. ambigua* from water column samples. Thus, late-invading *D. ambigua* clones were all obtained from the top 10 cm of sediment cores. Early-invading *D. ambigua* clones were isolated from sediment core layers between 50 and 60 cm in depth, representing a period of early dominance by *D. ambigua* (fig. 1). Detailed methods for sediment sampling, core processing, and clonal culturing can be found in Cáceres et al. (2005).

Our experimental design consisted of 11 zooplankton treatment combinations: the four zooplankton groups in monoculture, five two-species mixtures (*D. pulicaria* + *D. dentifera*, *D. pulicaria* + early-invading *D. ambigua*, *D. pulicaria* + late-invading *D. ambigua*, *D. dentifera* + early-invading *D. ambigua*, and *D. dentifera* + late-invading *D. ambigua*), and two three-species mixtures (*D. pulicaria* + *D. dentifera* + early-invading *D. ambigua* and *D. pulicaria* + *D. dentifera* + late-invading *D. ambigua*). We did not include any mixtures with early- and late-invading *D. ambigua* together. Early in the experiment, *D. pulicaria* drove all competitors to extinction in all mixtures (data not shown), whereas effects were variable among *D. dentifera* and the *D. ambigua* groups. Hence, we present results only for *D. dentifera*–*D. ambigua* competition;



these included the *D. ambigua*–*D. dentifera* mixtures (*D. dentifera* + early-invading *D. ambigua*, and *D. dentifera* + late-invading *D. ambigua*) and the monocultures of *D. dentifera*, early-invading *D. ambigua*, and late-invading *D. ambigua*. All treatments were replicated four times. Our experimental system consisted of 18-L polyethylene containers filled with 17.7 L of aged tap water. As the phosphorus concentration in the medium was relatively low (total phosphorus = $7.8 \mu\text{g L}^{-1}$), we added phosphorus (as K_2HPO_4) in order to lower the N : P ratio and to boost phosphorus concentrations (final medium concentration = $57.8 \mu\text{g P L}^{-1}$; final N : P atomic ratio = 50.4). Containers were illuminated with fluorescent light fixtures and maintained under constant laboratory conditions in two separate rooms (temperature over the experimental period averaged $24.2^\circ \pm 0.3^\circ\text{C}$, mean \pm SE, comparable to Sportsman's Lake's midsummer, epilimnetic temperatures). We blocked the experiment by room and by container position under the light fixtures (outer vs. inner). However, block effects were not detected in any of our statistical analyses and were removed.

Before the start of the experiment, containers were seeded with an algal inoculum containing *Ankistrodesmus falcatus* (an edible green alga used to culture our zooplankton), seston collected from all zooplankton cultures (filtered through $35\text{-}\mu\text{m}$ mesh to remove *Daphnia*), and 100 mL of Sportsman's Lake seston (collected from the epilimnion in fall 2004 and filtered through $35\text{-}\mu\text{m}$ mesh, which removed macrozooplankton but allowed a diverse assemblage of algae and microzooplankton to enter the inoculum). After 2 weeks, zooplankton were isolated from their cultures and added to their respective treatments (17 randomly chosen adults of each zooplankton group per container). We refer to this date as day 0 of the experiment. Zooplankton were sampled weekly (1.5–2 L total volume) beginning on day 7 and continuing to day 105. Container walls were scrubbed with brushes weekly to remove periphyton growth, and medium was added to counter evaporative and sampling losses.

We analyzed zooplankton densities over the final 6 weeks of the experiment using repeated-measures (rm) ANOVA; this corresponded to a period after which pop-

Figure 2: Temporal dynamics of late-invading *Daphnia ambigua* (clones isolated from 0–10-cm sediment layers; A) and early-invading *D. ambigua* (clones isolated from 50–60-cm sediment layers; B) in monoculture controls and in competition with *Daphnia dentifera*. C, Temporal dynamics of *D. dentifera* in the monoculture control and in competition with either late-invading *D. ambigua* or early-invading *D. ambigua* (results for the control have been horizontally offset to better display the error bars). Shown are mean densities + 1, per container (\pm SE).

ulations peaked in density and attained a quasi-stable state (fig. 2). Zooplankton densities were $\log_{10}(x + 1)$ transformed; a constant was added due to zero values. We expressed densities per experimental container (per 17.7 L) to reduce the influence of the constant. We also measured maximal population growth rates of early- and late-invading *D. ambigua* in their controls and in the presence of *D. dentifera*. Growth rates were calculated as $r = \ln(N_2/N_1)/t$, where N_1 was the initial stocking density, N_2 was density measured on day 14, and t was time (14 days). We did not use day 7 densities to calculate r due to potential short-term culture effects that may have affected initial growth rates. Growth rates were analyzed using ANOVA.

Results and Discussion

Results were consistent with predictions. When in competition with *Daphnia dentifera*, performance of *Daphnia ambigua* clones isolated from early in the assembly of Sportsman's Lake was poor compared to that of clones isolated from later in the lake's history when *D. dentifera* was a more prominent component of the plankton (fig. 2A, 2B). Using rmANOVA and analyzing *D. ambigua* densities in both monocultures and mixtures with *D. dentifera* revealed a significant negative effect of *D. dentifera* on both early- and late-invading *D. ambigua* ($F = 16.87$, $df = 1, 12$, $P = .001$; between-subjects effect); time effects and time interactions were not significant (all $P > .10$). No interaction between *D. dentifera* presence/absence and *D. ambigua* clonal group was detected. Hence, the magnitude of *D. dentifera* effects on *D. ambigua* densities relative to monoculture controls did not differ between early- versus late-invading *D. ambigua* groups ($F = 0.089$, $df = 1, 12$, $P = .77$; between-subjects effect, rmANOVA). Although an interaction was not evident, competitive ability as measured by persistence versus extinction clearly differed between the two *D. ambigua* clonal groups. Early-invading *D. ambigua* was rapidly driven below the limits of detection in competition treatments (fig. 2B); exhaustive sampling at the end of the experiment confirmed that *D. ambigua* became extinct in these containers. In contrast, late-invading *D. ambigua* was able to persist in *D. dentifera* treatments for the duration of the experiment (fig. 2A), indicative of reduced competition effects. Given the rapid competitive exclusion of early-invading *D. ambigua*, it was not surprising that this clonal group had no effects on *D. dentifera* densities in the latter half of the experiment (fig. 2C; all $P > .42$, rmANOVA). In contrast, significant negative effects of competition on *D. dentifera* were detected when comparing *D. dentifera* monocultures to the *D. dentifera* + late-invading *D. ambigua* treatment (fig. 2C;

$F = 8.17$, $df = 1, 6$, $P = .029$; between-subjects effect, rmANOVA); no time effect or time interactions were present ($P > 0.27$, rmANOVA).

In addition to differential competitive outcomes, performance of the two *D. ambigua* groups over the last 6 weeks of the experiment differed, irrespective of *D. dentifera* presence/absence. When averaged across monocultures and competition treatments, late-invading *D. ambigua* attained overall higher average densities compared with early-invading *D. ambigua* (fig. 2A); a significant main effect of *D. ambigua* clonal identity was detected ($F = 6.43$, $df = 1, 12$, $P = .026$; between-subjects effect, rmANOVA). However, this effect was partly driven by zero densities in the early *D. ambigua* competition treatments; when comparing densities averaged over the final 6 weeks in the monocultures alone, differences between early and late *D. ambigua* were weaker ($P = .10$, paired t -test). While our long-term results were indicative of poor performance in competition of early-invading *D. ambigua* clones, short-term maximal growth rates showed that this clonal group can exhibit high performance under high food conditions. When in monoculture, early-invading *D. ambigua* attained higher maximal growth rates compared with late-invading clones (fig. 3). This difference was clear in figure 2, where late-invading *D. ambigua* made a slower approach to peak densities in monoculture, peaking on day 28 (fig. 2A), compared with early-invading *D. ambigua*, which peaked on day 21 (fig. 2B). The opposite pat-

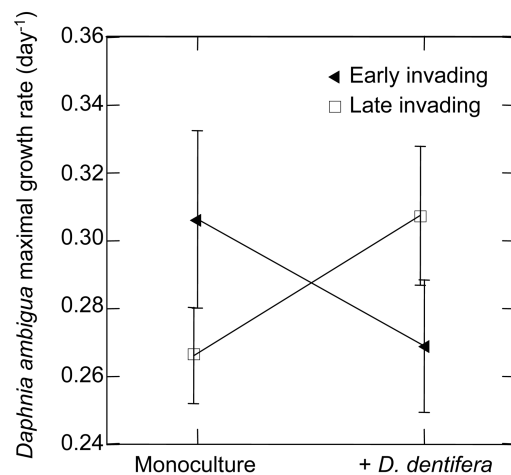


Figure 3: *Daphnia ambigua* maximal growth rates (r) for both clonal groups (early invading vs. late invading) measured over the first 14 days of the experiment. Shown are mean values (\pm SE) in the monoculture controls and in competition with *Daphnia dentifera*. Data for late-invading *D. ambigua* have been horizontally offset to better display the error bars.

tern emerged in treatments with *D. dentifera*. Late-invading *D. ambigua* showed higher maximal growth rates in competition treatments compared with early-invading clones (fig. 3), further supporting the conclusion that this clonal group experiences reduced effects of competition. When analyzing growth rates in both *D. ambigua* monocultures and in treatments with *D. dentifera*, a significant interaction between *D. ambigua* population identity and *D. dentifera* presence/absence was detected, using two-way ANOVA ($F = 5.26$, $df = 1, 12$, $P = .041$; main effects were not detected, all $P > .10$).

Population growth rate results (fig. 3) are consistent with a trade-off in competitive ability and maximal growth rate in *D. ambigua*. Sometimes referred to as the gleaner versus opportunist trade-off, this trait structure has been shown to operate interspecifically in a diversity of taxa, from protists to invertebrates (Sommer 1985; DeMott 1989; Schmitt 1996; Tessier et al. 2000; Steiner 2005). Our study indicates that this trade-off may function intraspecifically in addition to among species. Moreover, theory shows that high maximal growth rates can allow species to persist in heterogeneous landscapes through rapid utilization of newly opened (low-density, high-resource) habitats (Bolker and Pacala 1999). Hence, it is plausible that high growth rates allowed early-invading *D. ambigua* clones to invade and flourish in Sportsman's Lake before establishment of more dominant competitors.

The existence of a growth rate-competition trade-off raises an important question as to whether shifts in *D. ambigua* competitive ability over time arose purely as a by-product of selection via interspecific competition (following invasion by *D. pulicaria* and *D. dentifera*) versus intraspecific competition. Evidence from subsequent laboratory life-history experiments indicates that a simple shift in competitive ability or R^* (sensu Tilman 1982) has not occurred between our early- and late-invading *D. ambigua* clones. Using juvenile growth rate assays to quantify minimum resource levels needed to sustain positive growth (a relative measure of competitive ability; Tessier et al. 2000), we found no mean difference between the early- and late-invading *D. ambigua* groups when using a single edible alga, *Ankistrodesmus falcatus*, as a resource (C. F. Steiner and C. E. Cáceres, unpublished data). As temperature conditions from these assays matched the mean in our long-term experiment, this suggests that differential competitive outcomes and monoculture performance observed in our study were probably due to the presence of a diverse algal assemblage and late-invading *D. ambigua*'s greater efficiency at utilizing these resources (a resource quality effect rather than a pure quantity effect). This is consistent with general models of character displacement and the evolution of competitive interactions in which interspecific competition drives intraspecific

shifts in resource usage, facilitating species coexistence (Slatkin 1980; Taper and Case 1985; Doebeli 1996; Dayan and Simberloff 2005). Within filter-feeding *Daphnia*, this could involve shifts in multiple feeding traits; previous studies have shown that these species can vary in their capacity to digest different algal taxa and in their ability to filter resources based on cell size or other aspects of cell morphology (DeMott 1989; Sterner 1989; Tessier et al. 2001). However, we know of no studies that have examined intraspecific variation in algal-resource utilization. Answers to many of these issues await more detailed exploration of clonal variation in *D. ambigua* competitive ability and feeding ecology through the lake assembly sequence, both before and after dominance by *D. pulicaria* and *D. dentifera*. A similar exploration of *D. pulicaria* and *D. dentifera* traits from their early invasion to the present would also shed light on whether these taxa have experienced concomitant changes in their ecology. Theory predicts that clones of *D. pulicaria* and *D. dentifera* isolated from earlier in the lake's history would have had less time to adapt to local competitive interactions and thus would experience stronger negative effects of interspecific competition and exert stronger negative effects on early-invading *D. ambigua* compared with *D. pulicaria* and *D. dentifera* clones from later in the lake's history.

Although our results suggest that resource usage drives differential competitive performance within *D. ambigua*, our experiment was intended only to assess variation in exploitative competition under a constant environmental setting and at a highly localized scale. It is important to note that there are additional mechanisms that may mediate competitive interactions among zooplankton in nature that our design cannot address. These processes may explain why *D. pulicaria* was able to exclude all competitors in our experiment but is able to coexist with both *D. dentifera* and *D. ambigua* in Sportsman's Lake (Cáceres et al. 2005). For instance, zooplankton species can exhibit significant variation in habitat choice and vertical distribution within lake water columns (DeMott 1989; Leibold 1991; Leibold et al. 1994). Species may also segregate temporally, achieving population peaks at different periods of the growing season (DeMott 1989). Finally, predation by fish is known to strongly impact *Daphnia* populations, potentially influencing evolutionary trajectories and community-level organization (e.g., Cousyn et al. 2001; Mittelbach et al. 2006). Sportsman's Lake, from its early history to the recent past, has been repeatedly stocked with a diverse assemblage of planktivorous and piscivorous fish representative of temperate zone lakes (Illinois Department of Natural Resources, unpublished data). Unfortunately, detailed records of fish abundance through time are not available. Yet, it is plausible that variation in planktivory has influenced the pattern of zooplankton assembly

and variable species dominance evident in figure 1. As planktivorous fish generally feed selectively on large-bodied zooplankton (such as *D. pulicaria* and *D. dentifera*) rather than small-bodied taxa (such as *D. ambigua*; e.g., Mittelbach et al. 2006), variation in planktivore abundance could indirectly control the strength of the evolutionary effects of competition on *D. ambigua* through its effects on the abundance of interspecific competitors. However, the strength and direction of such effects could also depend greatly on how predators affect prey habitat choice (Rundle et al. 2003); for instance, competition could intensify if predators induce zooplankton to migrate and aggregate in shared refugia. Finally, predation could also generate intraspecific trait shifts by mediating the strength of intraspecific competition within *Daphnia* species. High planktivory could reduce population densities and select for high maximal growth rates (a tolerance strategy), while low planktivory could lead to high zooplankton densities and selection for stronger competitive ability (Tessier et al. 2000; Tessier and Woodruff 2002). Indeed, this could provide an additional alternative explanation for the trait differences observed between early- and late-invading *D. ambigua*. These points serve to highlight the often dizzying degree of complexity inherent to any natural system. Although we are unable to disentangle and assess the relative importance of these factors at this time, future work will attempt to address these issues through laboratory and field experimentation.

Resource competition is frequently cited as a major organizational force within temperate-zone zooplankton communities (DeMott 1989; Steiner 2003). Despite this recognition, remarkably few studies have experimentally examined the evolutionary role of interspecific competition within zooplankton populations (though see Leibold 1991; Leibold et al. 1994). Although we cannot dismiss alternative drivers of variable competitive ability within *D. ambigua*, including the role of intraspecific competition and the indirect effects of planktivory, we uncovered clear reductions in the impact of interspecific competition on *D. ambigua*. This is consistent with the prediction that natural selection favors reduced interaction strength among competing species that co-occur in local communities. This reduction in competition effects can in turn lead to reduced extinction probability, enhanced population persistence, and species coexistence. Finally, our work provides an important lesson for ecologists attempting to comprehend the temporal dynamics of community assembly and functional diversity within trophic levels; intraspecific trait shifts can occur on relatively short timescales and thus must be considered in addition to the ecological processes governing species-level sorting.

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