Diffuse competition and continuous niche shifts in size-structured populations of predatory salamanders

W. J. Resetarits, Jr.[1] and J. E. Fauth[2]

[1]*Program in Ecology, Evolution, and Integrative Biology, Department of Biological Sciences, Old Dominion University, Norfolk, VA 23529, USA. E-mail: wresetar@odu.edu. Fax: 757-683-5283, Phone: 757 683-3763.*
[2]*Department of Biology, University of Central Florida, Orlando, Florida 32816-2368 USA.*

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Abstract: Size-specific interactions between predators can affect both species population dynamics and the structure and biodiversity of communities they inhabit. Interactions between size-structured populations of predators, especially those with complex life-cycles, often change with resource-use changes driven by ontogenetic niche shifts. However, if resource use is determined largely by prey size, generalist predators may compete across a wider range of body sizes and life stages resulting in diffuse intra- and interspecific competition. We examined size- and stage-specific interactions between juvenile sirens (*Siren i. intermedia*) and adult newts (*Notophthalmus viridescens dorsalis*) in the context of previous experiments demonstrating competitive equality of larvae and strong effects of adult *S. intermedia* on adult *N. viridescens*. Competition between juvenile siren and adult newts were mutually negative and roughly symmetrical. Two *S. intermedia* reduced growth of three *N. viridescens* by 21%, while three *N. viridescens* reduced growth of two *S. intermedia* by 29%. Together with previous work, this implicates diffuse competition as a critical feature in the ecology of these species across the range of body sizes and suggests that intensity of competition varies more with size than species identity. Competition that varies incrementally with body size expands the realm of possibilities for continuous niche changes and diffuse competition across large size gradients. For generalist predators such as *S. intermedia* and *N. viridescens*, body size, except at the extremes, is not an adequate niche difference either intra- or interspecifically.

Nomenclature: Crother **2000 (2001)**.

Abbreviations: ANOVA - Analysis of Variance, MANOVA - Multivariate Analyis of Variance, SVL - Snout to posterior margin of vent, TL - Total length.

Introduction

Ecologists have become increasingly aware of the importance of size-structure in the dynamics of natural populations (e.g., Ebenman 1987, Ebenman and Persson 1988, Wissinger 1992, de Roos and Persson 2001) and the maintenance of species diversity (e.g., Abrams 1994, Takimoto 2003). Size-structured populations (Werner and Gilliam 1984) are especially common among invertebrates (e.g., Polis 1984 1988, Muotka 1990) and ectothermic vertebrates (e.g., Wilbur 1984 1988, Werner 1986 1988), many of which have complex life cycles and indeterminant growth. Freshwater ecosystems in particular often are dominated by size-structured populations of predators (e.g., Van Buskirk 1993, Persson and Eklov 1995, Resetarits 1995a) where changes in body size are accompanied by niche shifts that (in part) reduce the intensity of intra- and interspecific competition (Mittlebach et al. 1988, Muotka 1990, Fisher Huckins 1997).

Interactions among size-structured populations of predators can be particularly intense in smaller bodies of water because species with large terminal body sizes are forced into close association across a wider range of size classes (Mittlebach et al. 1988, Fisher Huckins 1997, Resetarits and Fauth 1998). If ontogenetic changes in resource use involve continuous rather than discrete shifts, size-structure may not reduce competition resulting in strong diffuse competition across a wide range of body sizes. This may be especially true for many generalist predators whose feeding habits are constrained primarily by prey size; food habits change only gradually with increasing gape (Werner and Gilliam 1984, Werner 1986, Wilbur 1988, Szabo 2002).

Broken-striped newts, *Notophthalmus viridescens dorsalis* (Harlan, 1928) (Caudata: Sirenidae), and Eastern lesser sirens, *Siren i. intermedia* (Barnes, 1826) (Caudata: Salamandridae), have strongly size-structured populations and compete at several different life-stages (Fauth et al. 1990, Fauth and Resetarits 1991). Here we report an experiment examining stage-specific interactions between juvenile *S. i. intermedia* and adult *N. v. dorsalis* in experimental pond communities, and place those results in the context of our previous work.

Natural history

Notophthalmus v. dorsalis and *S. i. intermedia* have strikingly different morphologies and life histories. *Notophthalmus v. dorsalis* has the most complex life-cycle of any pond-breeding salamander: it is facultatively paedomorphic but typically retains a complex life cycle with two metamorphic events (see Harris 1987a, Reilly 1987 and references therein). Adult newts are primarily aquatic and court, mate and oviposit in a wide range of lentic habitats, remaining as long as habitats hold water; adult newts effectively colonize new ponds and are relatively tolerant of desiccation (Gill 1978 1979). Newts respond to drying ponds by burrowing into vegetation and debris on the pond bottom or by emigrating (R. Harris et al. 1988, Fauth and Resetarits *personal observations*). When ponds refill, adult newts re-enter the water to feed on a broad range of small aquatic prey, including amphibian eggs and larvae, small insects and zooplankton (Hamilton 1940, Morin 1983b, Taylor et al. 1988).

Siren intermedia is one of the largest salamanders in the Southeastern U.S. and co-occurs with *N. viridescens* in many larger ponds and Carolina bays. *Siren intermedia* is a large (to 380 mm total length [TL]) paedomorphic salamander with the least complex life cycle of any pond-breeding salamander; it is obligately aquatic in both larval and adult stages. Development in *S. intermedia* is relatively continuous with no discrete metamorphosis preceding maturation. Larvae grow rapidly and generally reach maturity in two years at an average TL of 150 mm for females and 180 mm for males (Martof 1973). Adult *S. intermedia* persist in temporary ponds by aestivating in the mud during dry periods (Martof 1969, Gehlbach et al. 1973), a critical adaptation because *S. intermedia* cannot travel overland between isolated aquatic habitats. Survival during estivation is size-dependent (Martof 1969, Gehlbach et al. 1973) so factors that affect growth rate or fat storage (e.g., competition) can directly affect survival. When a pond refills, sirens emerge and feed on invertebrates and larval amphibians (including larval *N. v. dorsalis*) that recolonise the pond (Scroggin and Davis 1956, Collette and Gehlbach 1961, Altig 1967, Fauth and Resetarits 1991, unpublished data).

Sirens and newts both play important roles in the community ecology of temporary ponds (Fauth and Resetarits 1991, Resetarits and Fauth 1998). *Notophthalmus viridescens* is a keystone predator that maintains anuran diversity by reversing the outcome of asymmetric competition among larvae (e.g., Morin 1981 1983a, Wilbur 1987, Fauth and Resetarits 1991). *Siren intermedia* is an opportunistic predator that reduces the intensity of competition among larval anurans by preying indiscriminately on all species (Fauth and Resetarits 1991). Combined, these two predators contribute to the high anuran diversity found in many temporary pond communities in the southeastern United States (Fauth and Resetarits 1991, Resetarits and Fauth 1998).

Materials and methods

We constructed replicate communities (Morin 1983a) in an array of 11 artificial ponds (cattle watering tanks 1.5 m in diameter) at the Duke Zoology Field Station, Durham, North Carolina. We painted the interior of each tank with an inert epoxy enamel to prevent leaching from the galvanized metal and to provide a fresh surface for colonization. Tanks were filled to a depth of 50 cm (approximately 1000 L) with tap water on 25-26 April, and on 27 April 1 kg of dried pond litter was added to each. Two inoculations with 1L of a pond water suspension followed on 28 and 29 April. On 30 April, we added 50 g of rabbit food and 10 stems of the aquatic macrophyte *Myriophyllum* to each experimental pond. We also added six pairs of isopods, 17 snails (both on 30 April), and 100 small larvae of *Hyla chrysoscelis* (on 27 May) to each pond to diversify the prey resources. Tightly fitting lids of fibreglass window screening prevented unwanted colonization by insects and ovipositing treefrogs.

We used an additive design (*sensu* Fauth et al. 1990) with unequal replication to test for competition between the two species. Each experimental pond received either: a) 3 adult male *N. viridescens*, b) 2 juvenile *S. intermedia*, or c) 3 adult male *N. viridescens* plus 2 juvenile *S. intermedia*. Experimental densities roughly equalized initial biomass between the two species and densities of both *S. intermedia* ($1.12/m^2$) and *N. viridescens* ($1.6/m^2$) were within the range of natural densities (Gehlbach and Kennedy 1978, R. Harris et al. 1988, Fauth, unpublished data). Single-species treatments were replicated 3 times, while the competitive treatments had 5 replicates; treatments were randomly assigned to ponds.

This experiment focused on juvenile *S. intermedia* and adult *N. viridescens*. Reciprocal treatments using adult *S. intermedia* and juvenile *N. viridescens* were obviated because newts typically have a terrestrial juvenile stage. We used only male *N. viridescens* to prevent the possible confounding effects of reproduction.

We collected sirens and newts from ponds in Scotland County, North Carolina and weighed and measured them (snout to posterior margin of vent [SVL] for *N. viridescens* and total length [TL] for *S. intermedia*) before adding them to experimental ponds on 6 May. Juvenile *S. intermedia* were 101-116 mm TL (± 1 SD; 105 ± 4.88 mm TL) and 1.65-2.51 g (1.90 ± .255 g). Adult *N. viridescens* were 31-43 mm snout-vent length (37 ± 3.20 mm SVL) and 0.99-2.13 g mass (1.52 ± 0.37 g). We destructively sampled ponds on 30-31 October (after 178 days) and anesthetized, weighed and measured (as above) salamanders before preservation.

Statistical analyses

Means of population-level responses for individual ponds constituted the independent units of analysis; survival of both species was 100% so effects on growth were not confounded by differences in survival and thus provide an accurate assay of interspecific competitive effects. We used MANOVA to analyze growth; the multivariate response vector was Δ (final - initial) TL and Δ mass for *S. intermedia* and Δ SVL and Δ mass for *N. viridescens*. We used separate univariate ANOVAs on component variables of growth to interpret overall effects. Wilk's λ was the test criterion for MANOVA analyses, and we used Type III sums of squares. Statistical Analyses used SAS version 6.11.

Results

Overall growth conditions for juvenile *S. intermedia* were favorable; sirens grew rapidly when alone in the experimental ponds, gaining an average of 75.2 mg/day and 0.66 mm/day, attaining a mean final mass of 15.17 g (a 751% increase over initial mass) and a mean final TL of 219 mm (a 115% increase). In both treatments *S. intermedia* grew from small juveniles to mature adults; 7 of 8 females contained at least some mature follicles, whereas the remaining individual contained only vitellogenic follicles. Adult *N. viridescens* grew considerably less than juvenile *S. intermedia* because they were in a more advanced life stage and a different phase of their growth curve. In ponds containing only *N. viridescens* the average gain was 7.1 mg/day and 0.32 mm/day and newts attained a mean final mass of 2.83 g (an 81% increase over

their initial mass) and a mean final SVL of 43 mm (a 15.3% increase).

Despite favorable growth conditions, we detected a highly significant negative effect of *N. viridescens* on juvenile siren growth (MANOVA, $F_{2,5}$=22.45, Wilk's λ = 0.1002, P = 0.0032; Fig. 1). The presence of *N. viridescens* significantly affected both individual components of growth, ΔTL ($F_{1,6}$ = 48.28, P = 0.0004) and Δ mass ($F_{1,6}$ = 15.20, P = 0.008). Mean Δ TL and mean Δ mass were reduced from 117.3 mm and 13.19 g for sirens raised alone to 82.3 mm and 8.62 g for sirens raised with newts (Fig. 1).

There also was a highly significant negative effect of juvenile *S. intermedia* on growth of adult *N. viridescens* (MANOVA $F_{2,5}$=31.49, Wilk's λ = 0.0735, P = 0.0015; Fig. 1). The univariate effect of *S. intermedia* on ΔTL ($F_{1,6}$ = .81, P = 0.404) was non-significant, but the effect on Δ mass was statistically significant ($F_{1,6}$ = 7.05, P = 0.038). Mean Δ TL and mean Δ mass were reduced from 5.67 mm and 1.27 g for *N. viridescens* raised alone to 4.6 mm and 0.74 g for *N. viridescens* raised with *S. intermedia* (Fig. 1).

Discussion

What is the nature of the interactions between these two distinctly different salamanders? In this experiment, interactions between juvenile *S. intermedia* and adult *N. viridescens* were strongly mutually negative and roughly symmetrical. Two *S. intermedia* reduced the mean growth of three *N. viridescens* by 21%, while three *N. viridescens* reduced the mean growth of two *S. intermedia* by 29%. Many small individuals can have a greater impact than fewer large ones, especially if competition is primarily exploitative (Persson 1985, 1988, Norberg 1988, Werner 1994, Claessen et al. 2000, Chalcraft and Resetarits 2004). The slightly greater effect of *N. viridescens* on *S. intermedia* is likely due to the differential effects of competition early in *S. intermedia* development (e.g., early in the experiment).

Despite differences in morphology and life history, interspecific competition is a dominant feature of interactions between *N. viridescens* and *S. intermedia* across all body sizes and life stages, except the terrestrial eft stage of *N. viridescens* (this study, Fauth et al. 1990, Fauth and Resetarits 1991, see Resetarits 1995b). Larval sirens and newts compete as equals but there is qualitative asymmetry (*sensu* Resetarits 1997) in competitive responses; competition significantly affects only survival in larval *N. viridescens* and only growth in larval *S. intermedia*. Both responses contribute to population regulation but de-

creased survival has greater potential to immediately impact population dynamics (Fauth et al. 1990).

Competition between juvenile sirens and adult newts has important consequences for interacting populations of these two species. Although we used only male newts, the effects of juvenile *S. intermedia* on adult female *N. viridescens* should be similar and translate directly into reduced fitness, because fecundity is correlated with body size in salamanders (Verrell 1986). Juvenile *S. intermedia* likely reduce the reproductive rate of *N. viridescens* and alter the size-structure of newt populations. Previously, we demonstrated that adult sirens affected newt fecundity in a complex manner (Fauth and Resetarits 1991). Adult *N. viridescens* also should decrease fitness of juvenile *S. intermedia*; fecundity is correlated with body size so reduced growth should affect clutch size as well as age and size at first reproduction The ability of *S. intermedia* to survive aestivation is also size dependent (Martof 1969,

Gehlbach et al. 1973), so mortality may be directly affected by reduced growth and lower fat reserves.

We know how adult *S. intermedia* affect adult newts and newt reproduction, but have little direct evidence of how *N. viridescens* affects large adult *S. intermedia*. Fauth and Resetarits (1991) focused on the keystone predator effect of *N. viridescens* and (due to logistical constraints) lacked an independent estimate of the responses of adult *S. intermedia*. Sirens grew to maturity in the present experiment, suggesting these two species continue to compete as *S. intermedia* grow larger. The effect of *N. viridescens* likely decreases as adult *S. intermedia* grow because of decreasing prey overlap. Adult *S. intermedia* reduced growth of adult *N. viridescens* by approximately 60% across newt densities, but strongly affect *N. viridescens* survival (via competition not predation) only at high adult newt densities (a 21% reduction) (Fauth and Resetarits 1991). How effects on adult growth and sur-
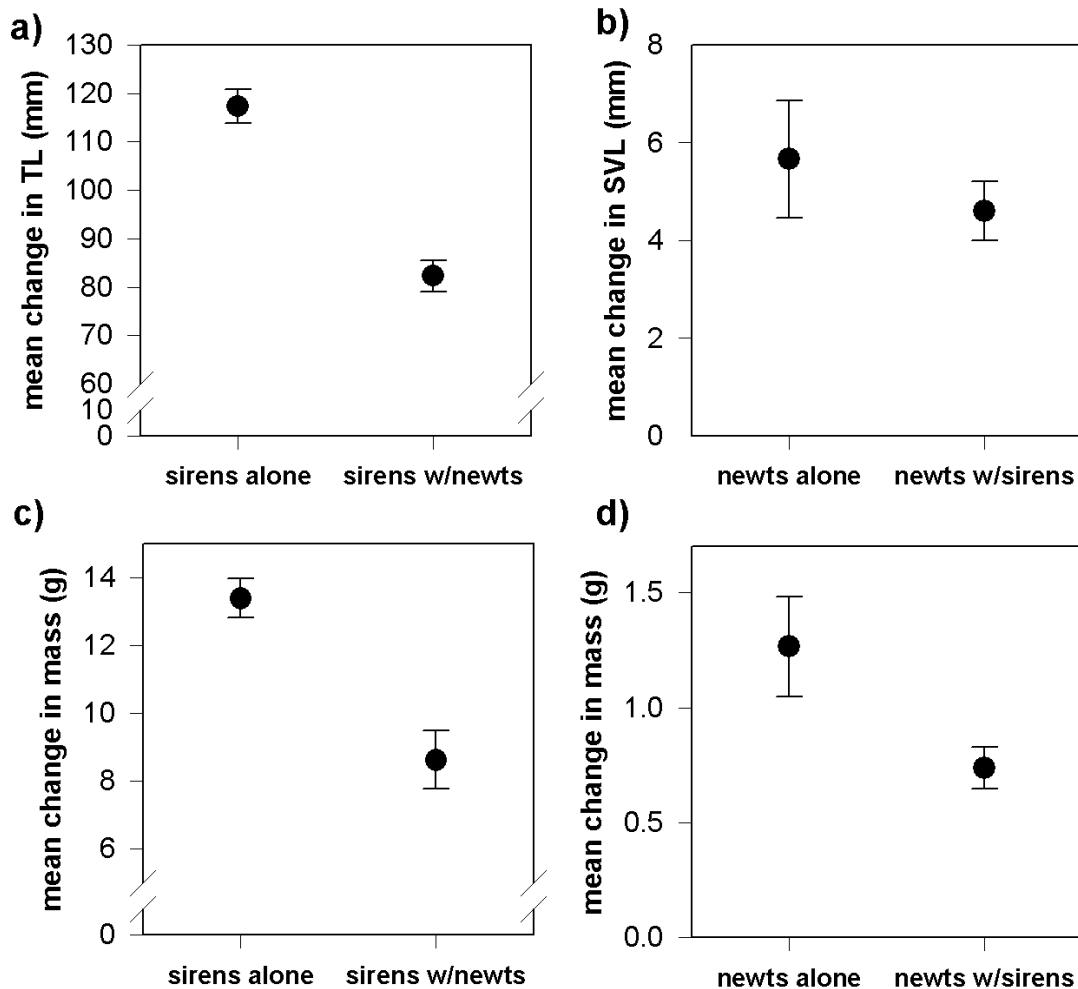

Figure 1. Growth responses of juvenile *S. intermedia* to the presence of adult *N. viridescens* in terms of change in total length (**a**) and change in mass (**b**). Corresponding growth responses (**c**) and (**d**) of adult *N. viridescens* to the presence of juvenile *S. intermedia*. Values are treatment means (± 1 standard error). Survival was 100% for both species.

vival impact reproductive output depends on adult newt density, complicating predictions about potential effects on newt population growth (Fauth and Resetarits 1991).

Our understanding of interactions between *N. viridescens* and *S. intermedia* now encompasses virtually the entire range of body sizes and co-occurring life stages (Fauth et al. 1990, Fauth and Resetarits 1991, Resetarits and Fauth 1998) **(Fig. 2)**, and includes intraguild predation, in addition to the competitive interactions discussed here. Thus, our understanding of interactions across all life stages is unusual for any pair of size-structured species (Fig. 2).

Because these species function as generalist predators and compete at all sizes and life stages despite differences in morphology, life history, foraging mode, etc., their interactions provide insights into how generalized prey habits can affect the role of size structure, complex life cycles, and even morphological similarity in competitive interactions and species coexistence. Niche shifts at the boundary between life stages are a widespread phenomenon, especially in species with complex life cycles (Wilbur 1980, Werner and Gilliam 1984). Such niche shifts underlie the concept of the ontogenetic niche and ecological species (Polis 1984, Werner and Gilliam 1984). Documentation of competitive interactions that vary only incrementally
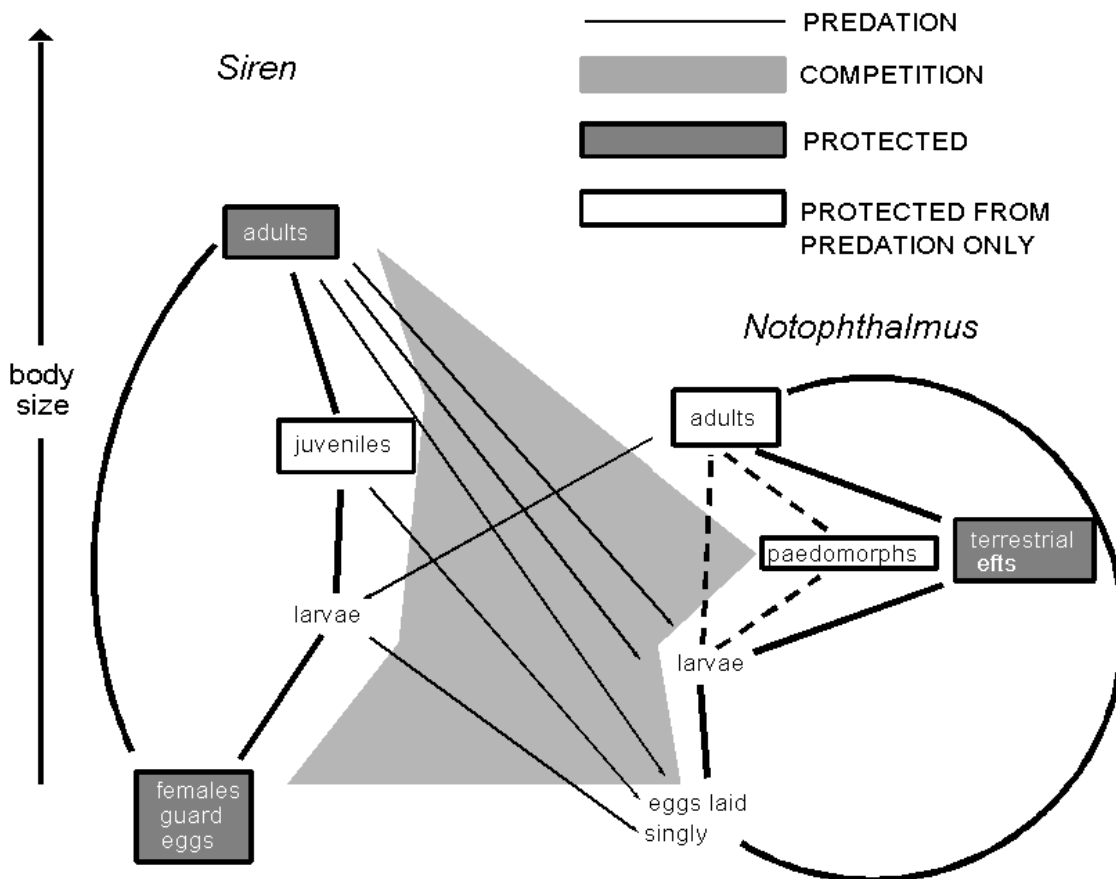

Figure 2. Life cycles including several alternative pathways for *Notophthalmus* and a summary of interspecific interactions including both competition and intraguild predation between *S. intermedia* and *N. viridescens*. The stippled gray area indicates the range of body sizes at which the two species compete through size-specific and diffuse competition. Intraguild predation (Polis and McCormick 1987) between these two species has been documented for adult *Siren* preying on larval *Notophthalmus* (see text), but there is strong potential for intraguild predation between several life stages of these species. Newt eggs are laid singly on aquatic vegetation or pond debris and are vulnerable to predation by *Siren*. Juvenile (efts) and adult *Notophthalmus* are invulnerable to siren predation because of the powerful tetrodotoxin contained in their skin (Brodie et al. 1974). Terrestrial efts also are protected from all interaction with sirens because all siren life stages are obligately aquatic. Adult *Notophthalmus* likely prey on small larval *Siren* because adult newts readily consume prey items of similar size (including other larval salamanders) (e.g., Harris 1987b). However, because female sirens brood their eggs, eggs may be relatively invulnerable to newt predation (Godley 1983). Other siren life stages enjoy a size refuge from newt predation. Thus, despite strong interactions, each species also possesses a life stage relatively unaffected by the other species that can serve as reproductive storage potential (Warner and Chesson 1994).

with body size in two competing, generalist predators expands the realm of possibilities for continuous niche changes across large gradients of body sizes, and identifies the potential for diffuse intercohort competition within and between entire populations of competing species (Werner 1986, Persson 1985, 1988, Szabo 2002). Such diffuse competition suggests that, for species such as *N. viridescens* and *S. intermedia*, body size is not an adequate niche difference either within or between species to alleviate competition and facilitate coexistence (Wilson 1975). As a consequence, competitive effects may alternatively cascade up or down the size distribution, both within and between species. Instantaneous competitive superiority depends on the relationship between intrinsic characteristics of a species at a given size and the current profile of resource availability. If patterns of resource distribution are fixed (and barring mitigating factors such as disturbance), diffuse competition between and among species and size classes could destabilize populations and affect species coexistence. If resource profiles are spatio-temporally variable, such diffuse intra- and interspecific competition should promote population stability and prevent competitive exclusion by constantly shifting the asymmetry of the competitive interaction between species and among size-classes. Thus, coexistence between competing species may be facilitated not by distinct niche differences between species and size classes, but by diffuse competition and shifting patterns of competitive superiority.

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