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Salamanders in forest-floor food webs: Environmental heterogeneity affects the strength of top-down effects

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Summary

Terrestrial salamanders have been hypothesized to play an important role in the regulation of invertebrate communities on the forest floor. Previous studies testing this hypothesis have used field enclosure or laboratory microcosm methods that may bias outcomes, and no studies have addressed the extent to which environmental heterogeneity affects the strength of salamander effects. In the present study, the effects of the red-backed salamander, *Plethodon cinereus*, on forest-floor invertebrates were examined in open field plots in which neither the movements of salamanders nor invertebrates were impeded. This 2-year study assessed the influence of the bottom-up effect of leaf-litter mass by comparing salamander effects in the spring when litter was abundant to autumn, just prior to leaf fall, when litter thickness was low. *Plethodon cinereus* was found to exert top-down effects on several mesofaunal taxa, but no effects on macrofauna were detected. Salamander effects varied among sampling periods. Leaf-litter mass and, to a lesser extent, litter moisture were the determinants of invertebrate density in spring and fall 2003, whereas salamanders were the single significant factor influencing mesofaunal density in spring 2004, when both leaf-litter mass and litter moisture were especially high. Leaf-litter mass and salamanders in combination influenced mesofaunal densities in fall 2004. The results suggest that the top-down effects of salamanders are strongest in spring when hydric conditions and availability of moisture-retaining cover enhance salamander foraging success, and when salamanders affect initial, rapid stages of mesofaunal population growth.

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Introduction

Terrestrial amphibians have been hypothesized to play pivotal roles in the regulation of invertebrate communities of the forest floor (Hairston, 1987; Petranka, 1998; Davic and Welsh, 2004). Recent experimental studies seem to support this idea. In field enclosure and laboratory microcosm studies, amphibians have been found to exert top-down effects on invertebrate species composition (Wyman, 1998; Rooney et al., 2000; Beard et al., 2002, 2003; Walton and Steckler, 2005). These interactions include direct effects of amphibian predators that reduce the density of macrofaunal invertebrates (Wyman, 1998; Beard et al., 2002, 2003; Walton and Steckler, 2005) and indirect effects that promote increases in mesofaunal taxa (Rooney et al., 2000; Walton and Steckler, 2005).

In addition, several studies also indicate that terrestrial amphibians may influence ecosystem processes, such as decomposition rates and nutrient cycling (Wyman, 1998, 2003; Beard et al., 2002, 2003), although no general pattern of effects has emerged. Wyman (1998) found that decomposition rates of beech leaf litter were reduced in field enclosures with red-backed salamanders, *Plethodon cinereus*, in comparison to salamander-absent control enclosures, a finding attributed to predation on macrofaunal detritivores by salamanders. In contrast, Beard et al. (2002, 2003) reported that the terrestrial frog, *Eleutherodactylus coqui*, accelerated decomposition rates and enhanced nutrient cycling within enclosures in a dry, subtropical forest. Beard et al. (2002) attributed their findings to the conversion of arthropod tissue, which is relatively recalcitrant, to more readily decomposed frog feces, waste products, and frog carcasses. However, Walton and Steckler (2005) reported that *P. cinereus* had no effect on leaf-litter decomposition rates in laboratory microcosms. Walton and Steckler (2005) posited that the effects of salamander-mediated reductions of macrofaunal detritivores on decomposition rates were offset by increases in mesofaunal detritivores in the presence of salamanders.

Some differences among findings are likely to derive from methodological differences among studies, as well as variability in biotic and abiotic factors influencing amphibian activity, invertebrate community dynamics and decomposition rates among studies, species, and environments (Walton and Steckler, 2005). In addition, all previous studies of amphibian-mediated effects used enclosures of some sort, preventing either the movement of the amphibian predator (Beard et al., 2002, 2003) or preventing the movement of both amphibians and invertebrate prey (Wyman, 1998; Rooney et al., 2000; Walton and Steckler, 2005). These closed studies have been useful for demonstrating the *potential* for top-down effects, and this approach can enable tightly controlled experiments exploring specific mechanisms or variables that influence food-web interactions (Walton and Steckler, 2005). However, such studies may not be sufficient to demonstrate the actual importance of predator-mediated effects in a natural setting or at scales larger than that of the enclosure. Enclosures may prevent migration of invertebrates into plots that would offset losses or imbalances in predator–prey or competitive relationships. Enclosures may disrupt behavioral mechanisms that would otherwise limit interactions between predators and prey or between competitors in space and time, and may affect nutrient cycling by concentrating consumer waste products and carcasses within a small space. Further, enclosure size can influence experimental outcomes, such that soil/litter fauna effects observed within small enclosures may be different (e.g., Heneghan and Bolger, 1998) or not detected (e.g., Beard et al., 2003) at larger spatial scales.

Environmental heterogeneity is another factor that has not been investigated adequately with regard to terrestrial amphibian–food-web interactions, but which can be an important determinant of the strength of top-down effects in terrestrial food webs (Hunter and Price, 1992). Predator effects in terrestrial food webs can vary with soil nutrient supplementation or soil fertility (e.g., Schmitz, 1994; Letourneau and Dyer, 1998), rainfall (e.g., Spiller and Schoener, 1995; Dawes-Gomadzki, 2002), or prey density (Spiller and Schoener, 1994; Carter and Rypstra, 1995). In addition, top-down effects may be important only when environmental conditions permit high levels of predator activity (Power, 1992). These issues are likely to be especially important with regard to the role of amphibians in terrestrial, detritus-based food webs. Surface density, foraging times, and foraging success of terrestrial salamanders are strongly dependent upon appropriate thermal and hydric conditions (Jaeger, 1980a, b, 1990; Feder, 1983; Feder and Londos, 1984; Grover, 1998) and similar constraints apply to the activity of invertebrate prey as well. Further, seasonal patterns of leaf fall and changes in litter-nutrient quality due to decomposition may influence relative importance of top-down and bottom-up effects. For example, Rooney et al. (2000) found that *P. cinereus* enhanced Collembola numbers in spring but not fall. Walton and Steckler (2005) found that *P. cinereus* had stronger indirect effects on invertebrate densities in newly fallen leaf litter than in