

# ON THE ECOLOGICAL ROLES OF SALAMANDERS\*

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■ **Abstract** Salamanders are cryptic and, though largely unrecognized as such, extremely abundant vertebrates in a variety of primarily forest and grassland environments, where they regulate food webs and contribute to ecosystem resilience-resistance (= stability) in several ways: (a) As mid-level vertebrate predators, they provide direct and indirect biotic control of species diversity and ecosystem processes along grazer and detritus pathways; (b) via their migrations, they connect energy and matter between aquatic and terrestrial landscapes; (c) through association with underground burrow systems, they contribute to soil dynamics; and (d) they supply high-quality and slowly available stores of energy and nutrients for tertiary consumers throughout ecological succession. Salamanders also can provide an important service to humans through their use as cost-effective and readily quantifiable metrics of ecosystem health and integrity. The diverse ecological roles of salamanders in natural areas underscore the importance of their conservation.

## INTRODUCTION

Salamanders (Amphibia: Caudata) are ancient vertebrates that have evolved extensive ecological diversification for at least the past 150–200 million years (Gao & Shubin 2001, Schoch & Carroll 2003). They are widely distributed in North, Central, and South America, Europe, and temperate eastern Asia (Duellman 1999), with more than 400 species in 59 genera and 10 families (Zug et al. 2001). Their adaptive radiation of life history traits has resulted in exploitation of moist forest leaf litter, grasslands, underground retreats, tree canopies, talus slopes, headwater streams, riparian ecotones, swamps, caves, ponds, and seasonally inundated pools (Petranka 1998). Within these varied environments, salamanders perform many ecological roles or “key ecological functions” (Marcot & Vander Hayden 2001).

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Key ecological functions refer to the primary ways that species use, influence, regulate, and alter biotic and abiotic environments—a concept recommended for multispecies planning, biodiversity conservation, and management of wildlife-habitat relationships (Johnson & O’Neil 2001). In this paper, we review literature on key ecological functions of salamanders in terrestrial and aquatic environments of North America. We offer suggestions for future research by noting basic gaps in knowledge. Nomenclature follows Collins & Taggart (2002).

This review is particularly timely because natural areas are becoming increasingly modified by destabilizing factors such as habitat alteration, toxic chemicals, loss of wetlands, and introduction of exotic species (Aber et al. 2000). Nearly three fourths of forested ecosystems in North America are considered endangered because of threats to their integrity (Noss 1999). The decline in amphibian species, many associated with forests, is now well documented (Alford & Richards 1999, Houlahan et al. 2000, Kiesecker et al. 2004). Although most attention has been given to anurans, salamander populations also are declining (Welsh 1990, Petranka et al. 1993, Wheeler et al. 2003), with unknown consequences to ecosystem processes. Of the 234 identified salamander taxa in the United States, 67 (29%) have a conservation status rank of “imperiled or critically imperiled” in at least part of their range (NatureServe 2003), yet only 13 species are protected or proposed for protection under the United States Endangered Species Act (Semlitsch 2003a). Habitat modifications are cited most often as the causes for salamander declines (Dodd & Smith 2003), with estimated losses of salamanders in some habitats in the millions (Petranka et al. 1993). In addition, zoogeographic evidence suggests that salamander faunas globally are being impacted (Duellman 1999). It is both disturbing and fortuitous that these declines are being reported at a time when salamanders are increasingly being recommended for use as bio-indicators to assess the ecological health and integrity of natural areas (Parent 1992, Welsh & Ollivier 1998, Simon et al. 2000, Welsh & Droege 2001, Micacchion 2002). Our hope is that this review will serve as a stimulus for much needed additional research on the important ecological roles of these abundant but often neglected vertebrate species.

## PATTERNS OF SALAMANDER STRUCTURAL DOMINANCE

Making predictions about sustainability of ecosystems requires information on how dominant biotic and abiotic structures vary over time and space (Bailey 1996). In this section, we review literature on the structural dominance (e.g., density, biomass, calories) of salamander species in North American ecosystems at different levels of ecological organization.

### Terrestrial Habitats

Numerical dominance of salamanders in the terrestrial landscape was first reported from the southern Appalachian Mountains by Hairston (1949). Consistent results

of long-term observations of high numbers along vertical transects led him to conclude that salamander species from the family Plethodontidae were the numerically dominant members of the forest vertebrate fauna, although no comparative data for other vertebrates were reported.

Burton & Likens (1975a,b) first quantified both density and biomass of a salamander guild at a watershed scale. Working in the Hubbard Brook experimental forest of New Hampshire, they estimated that five salamander species had a combined average density of 2950 salamanders/ha ( $0.29/\text{m}^2$ ) and a biomass of 1770 g/ha wet weight. This value was 2.6 times the combined wet-weight biomass of all birds living in the watershed at the peak of bird breeding season and at least equal to that of small mammals such as shrews and mice. The nutrient pool of phosphorus in salamanders (7.79 g/ha) was greater than that in birds (4.27 g/ha) and small mammals (0.21 to 0.41 g/ha) combined. Burton & Likens (1975a,b) are often cited as evidence that salamanders are the most abundant vertebrates in mature forests; however, it does not follow that salamanders compose the greatest amount of vertebrate biomass. Not included in their biomass calculations are large herbivorous mammals, such as deer, and other vertebrates, such as fish, reptiles, or frogs. Salamanders cannot have the highest vertebrate standing crop in forests because white-tailed deer alone contain on average  $1.30 \text{ kcal}/\text{m}^2$  caloric energy (Ricklefs 1979), more than the  $1.165 \text{ kcal}/\text{m}^2$  estimated by Hairston (1987) for a southern Appalachian salamander guild. Hairston (1987) clarified the issue by suggesting that salamanders are the dominant "vertebrate predators" (e.g., carnivores) in forests, thus linking the ecological relevance of salamander abundance to a critical link in the trophic dynamics of food webs. To put the estimated  $1.165 \text{ kcal}/\text{m}^2$  caloric contribution of these southern Appalachian salamander populations into perspective the annual average human harvest of the world's marine fishery was reported as  $0.3 \text{ kcal}/\text{m}^2$  (Odum 1971).

Numerous studies expand the findings of Burton & Likens (1975a,b). Citing research from an oak woodland/redwood forest in California, Stebbins & Cohen (1995) reported that the combined density of the salamander guild was "close to the values of Burton and Likens." Comparable data were reported for a single species, *Plethodon elongatus*, in a Douglas-fir dominated stand in northwest California (Welsh & Lind 1992). In the southern Appalachian Mountains, Hairston (1987) estimated salamander guild abundance across a mosaic of habitats as  $0.6$  to  $1.0/\text{m}^2$  (5961 to 9935/ha), more than three times the density reported by Burton & Likens (1975a) for New Hampshire. Similarly, Petranka et al. (1993) reported 10,000 salamanders/ha ( $1.0/\text{m}^2$ ), representing 12 species in 34 mature forest stands in western North Carolina.

Researchers have often observed that a single salamander species will dominate the terrestrial habitat of a local salamander guild (Table 1). In western North America, this dominance is known to shift between *Ensatina* (*Ensatina eschscholtzii*), two *Plethodon* species (*P. elongatus* and *P. vehiculum*), and *Batrachoseps attenuatus* in relation to region, forest type, and seral stage (Bury et al. 1991; Welsh & Lind 1988, 1991; Cooperrider et al. 2000). The environmental factors

**TABLE 1** Salamander guild species richness and evenness in five forested landscapes with a minimum of 1000 captures (see also Figure 3)<sup>a</sup>

Taxon Rank	Ash 1997	Welsh & Lind 1988	Ross et al. 2000	Mitchell et al. 1997	Ford et al. 2002
1	1234	1097	1967	756	2556
2	69	213	1025	182	626
3	40	72	430	70	392
4	10	38	318	28	184
5	2	21	144	25	59
6	—	20	83	24	45
7	—	5	31	10	30
8	—	4	17	5	21
9	—	1	7	2	17
10	—	1	2	1	7
11	—	—	1	—	—
Total no.	1355	1472	4026	1104	3937
Capture Method	Area search	Pitfall traps	Area search	Pitfall traps	Pitfall traps
Dom. <sup>b</sup> sp.	<i>Plethodon jordani</i>	<i>Ensatina eschscholtzii</i>	<i>Plethodon cinereus</i>	<i>Plethodon cinereus</i>	<i>Plethodon glutinosus</i>
Reg. <sup>c</sup> slope	-1.48 lower diversity	-0.73	-0.72	-0.63	-0.60 higher diversity

<sup>a</sup>Data represent captures across forest stands in varying stages of disturbance.

<sup>b</sup>Numerically dominant species within guild.

<sup>c</sup>Regression slopes from Figure 3, see text for explanation.

responsible for these shifts are mostly unknown. In eastern forests, pioneering surveys by Shelford (1913) identified the Northern redback salamander (*Plethodon cinereus*) as a dominant vertebrate within the leaf litter of late-successional beech-maple stands, and a variety of forest types that converge toward the beech-maple climax state. Contemporary studies confirm that *P. cinereus* numerically dominates salamander guilds in many forest types in the eastern United States (Burton & Likens 1975a,b; Carfioli et al. 2000; see also Table 1). *Plethodon* species other than *P. cinereus* are also known to dominate terrestrial salamander assemblages. For instance, *Plethodon glutinosus* populations dominated four stands of yellow poplar–northern red oak–white oak (15 to >85 years of age) in the Chattahoochee National Forest in Georgia (Ford et al. 2002; see also Houze & Chandler 2002). Jordan’s redcheek salamander (*Plethodon jordani*), which is endemic to a small geographic area of the Blue Ridge Mountains in the southern Appalachians (Petranka 1998), has been shown to be the dominant salamander species in relatively dry terrestrial habitats within its range (Harper & Guynn 1999, Bartman

et al. 2001). These observations suggest that not all narrowly distributed endemic salamander species are necessarily rare as some, such as *P. jordani*, can be numerically dominant and potentially provide important biotic control over ecosystem dynamics within isolated geographic areas.

## Grassland Habitats

Although the vast majority of salamander species in North America are forest specialists and require relatively intact forest stands to complete at least part of their life history, a number of species are known to occupy mostly grassland habitats as adults. The California tiger salamander (*Ambystoma californiense*) is endemic to grasslands and can be the dominant vertebrate predator in ephemeral ponds; densities as high as 325 males and 216 females from a single 3660 m<sup>2</sup> breeding pond have been reported (Trenham et al. 2001). Mammal burrows are critical limited resources for both juveniles and adults of *A. californiense*, and loss of grassland burrow habitat and associated ephemeral breeding ponds have been associated with decline in local populations (Fisher & Shaffer 1996). Other species known to migrate into grassland habitats as adults include the various demic populations of *Ambystoma tigrinum* (see Shaffer & McKnight 1996), the most widely distributed salamander in North America (Petranka 1998), and three species of slender salamanders (*Batrachoseps nigriventris*, *B. attenuatus*, and *B. pacificus*). However, the extent of salamander use of grasslands and adult population density in relation to other habitat types are largely unknown and represent important venues for future research.

## Riparian Habitats

The riparian ecotone between aquatic and terrestrial environments provides unique habitats for salamanders, and some researchers have suggested that this landscape structure has its own ecological identity for amphibians (Bury 1988, Krzysik 1998, Sheridan & Olson 2003). Thirty-five percent of the salamander genera of North America use riparian habitats to complete their life history (Krzysik 1998). Within the Humid-Temperate-Domain ecoregion of eastern North America (Bailey 1996), 47 salamander species use stream or pond riparian corridors for reproduction, foraging, and shelter (Pauley et al. 2000).

Densities of salamanders in riparian areas can exceed those found in upland terrestrial environments. Talus riparian habitats on Vancouver Island support as many as 11,600 *Plethodon vehiculum* salamanders/ha (Ovaska & Gregory 1989), more than three times the salamander density reported by Burton & Likens (1975a) for the entire Hubbard Brook watershed. In the southern Appalachians, salamander density was estimated as 18,486 individuals/ha (1.8/m<sup>2</sup>) from riparian habitats alone (Petranka & Murray 2001), a value 7 times higher than reported by Burton & Likens; biomass was 14 times higher (16.53 kg/ha). Riparian areas along headwater streams in second-growth Douglas-fir forest (southwestern Washington) contained large numbers of salamanders of the genus *Plethodon*, which occurred

adjacent to 93% of streams surveyed (Wilkins & Peterson 2000). In contrast, Waters et al. (2001) studied abundances of amphibians and small mammals along small, intermittent headwater streams in northern California and found the riparian zone to be dominated by small mammals [Allen's chipmunk (*Tamias senex*) and deer mouse (*Peromyscus maniculatus*)], not salamanders. The low numbers of salamanders in these riparian environments may be associated with unpredictable hydroperiods because nearby upland forest habitats supported high numbers of *Ensatina eschscholtzii* (J.R. Waters & H.H. Welsh, unpublished data). Removal of riparian vegetation can have detrimental effects on salamander densities, and is of particular concern for endemic species with patchy distribution (Williams et al. 2002).

## Aquatic Habitats

Numerous studies document that salamanders, not fish, dominate the vertebrate community in the headwater habitats of watersheds (Murphy & Hall 1981, Petranks 1983, Resetarits 1997, Wilkins & Peterson 2000, Lowe & Bolger 2002). For example, giant salamanders (*Dicamptodon*) replace fish as the dominant vertebrate predator in headwater streams from the Pacific Northwest, contributing 99% of the total predator biomass in certain areas (Murphy & Hall 1981). Diller & Wallace (1996) reported populations of the cold water adapted *Rhyacotriton variegatus* in 80.3 % of randomly surveyed headwater streams in Northern California. Conceptually, these low-order stream habitats (sensu Strahler 1964) represent a salamander-dominated region in the upper reaches of the river continuum (Vannote et al. 1980). Salamanders can move higher into headwater streams than fish because physical attributes such as intermittent hydrology, size and depth of pools, and cascades and waterfalls limit the ability of fish to access these areas. Headwater streams likely offered an attractive ecological niche free from fish predation during the lower Paleozoic to upper Mesozoic (360–200 millions of years before present) when fish-tetrapod-salamander evolution occurred (Schoch & Carroll 2003). This hypothesis is evidenced by the widespread adaptive radiation of extant salamander taxa above the species level in headwater regions of watersheds across biomes.

Seven salamander genera in North America are specifically adapted to conditions found in headwater streams, including *Desmognathus*, *Dicamptodon*, *Eurycea*, *Gyrinophilus*, *Pseudotriton*, *Rhyacotriton*, and *Stereochilus*; some *Ambystoma* and *Taricha* species also breed in low-order stream environments (Petranks 1998, Corn et al. 2003). When larval age classes are included in the tally, total salamander density and biomass in headwater streams can be high compared with average densities of approximately 1.0/m<sup>2</sup> reported in terrestrial habitats. For example, Nussbaum & Tait (1977) estimated densities of *Rhyacotriton* populations from 12.9/m<sup>2</sup> to 41.2/m<sup>2</sup> in Oregon. Davic (1983) reported high seasonal density and biomass for a complete aquatic salamander guild, including larvae (*Desmognathus*, *Eurycea*, *Gyrinophilus*), from a fishless stream in North

**TABLE 2** Seasonal changes in the density and biomass of an aquatic salamander guild from a fishless and spring-fed headwater stream in North Carolina (1980)

	June #/m <sup>2</sup> (g/m <sup>2</sup> )	August #/m <sup>2</sup> (g/m <sup>2</sup> )	October #/m <sup>2</sup> (g/m <sup>2</sup> )
<i>Desmognathus quadramaculatus</i>			
Larvae	2.8 (5.6)	2.3 (4.0)	1.7 (1.2)
Juveniles	1.0 (1.6)	1.6 (3.7)	1.4 (2.9)
Adults	0.2 (0.1)	0.55 (0.7)	0.45 (1.0)
<i>Eurycea wilderae</i>			
Larvae	4.7 (0.25)	10.1 (1.3)	8.6 (0.9)
Adults	0.1 (0.15)	0.0 (0.0)	0.08 (0.01)
<i>Gyrinophilus porphyriticus danielsi</i>			
Larvae	0.4 (0.1)	0.2 (0.05)	0.08 (0.01)
Salamander Guild Totals	9.2 (7.8)	14.7 (9.75)	12.3 (6.1)

Source: Unpublished data from Davic (1983) with corrected biomass values.

Carolina (Table 2). Little variation in salamander guild structure was noted over seasonal time in this study, likely because of the stable environmental conditions provided by a spring-fed environment. Huang & Sih (1991a) reported exceptional densities of *Ambystoma barbouri* larvae in fishless headwater stream pool habitats, on average 20–30/m<sup>2</sup> with values as high as 50/m<sup>2</sup>. Biomass of coastal giant salamander larvae in Caspar Creek on the northern California coast reached 10.4 g/m<sup>2</sup> (Nakamoto 1998). Welsh & Lind found a wide range of salamander larval densities in streams throughout northwestern California, ranging from 0.1 to 5.0/m<sup>2</sup> for *Rhyacotriton variegatus* (Welsh & Lind 1996), to 0.03 to 1.61/m<sup>2</sup> for *Dicamptodon tenebrosus* (Welsh & Lind 2002). Ultimate reasons for natural variation in salamander numbers in headwater stream environments are largely unknown; however, strong association between biotic and/or abiotic factors and salamander density has been reported for a variety of species (Petranka 1983; Davic & Orr 1987; Welsh & Lind 1996, 2002; Diller & Wallace 1996; Welsh & Ollivier 1998; Lowe & Bolger 2002; Barr & Babbitt 2002).

Large river systems support large-bodied salamanders from the genera *Necturus* and *Cryptobranchus*. Multi-year (1989–1991) mark-recapture surveys of the common mudpuppy (*Necturus maculosus*) in Ohio resulted in 382 salamanders collected along a 700 × 50 m stream reach (Matson 1998). Petranka (1998) reports *Cryptobranchus alleganiensis* densities as high as six individuals per 100 m<sup>2</sup>. Given the large body size of *Necturus* and *Cryptobranchus* adults, they may rival the biomass of predatory fish species in localized stream reaches, but we are unaware of any studies that quantify salamander density or biomass in relation to other vertebrates in large rivers.

It has long been recognized that salamanders from the genera *Ambystoma*, *Notophthalmus*, and *Siren* are dominant vertebrate predators in seasonal pools and

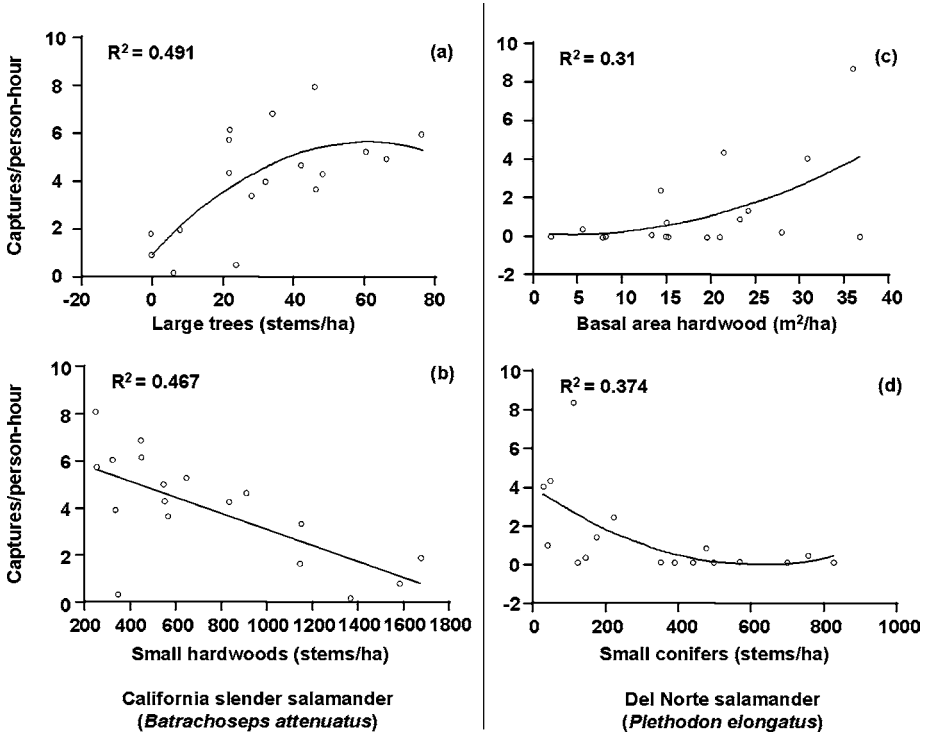
ponds (see reviews in Morin 1983, 1995; Wilbur 1997; Walls & Williams 2001). Salamander densities in these lentic habitats can be extremely high. Adult red-spotted newt densities as high as 10/m<sup>2</sup> were recorded in ponds from south-central Indiana (Cortwright 1998). A study of prairie grassland lakes in North Dakota revealed a maximum density in *Ambystoma tigrinum* of 5000 larvae/ha and a maximum biomass of 180 kg/ha (Deutschmann & Peterka 1988). Even where fish were present, the standing crop of the lesser siren (*Siren intermedia*) in a Texas pond was greater than the combined value of seven fish species (Gehlbach & Kennedy 1978). Likewise, in ponds with fish on the coastal plain of southeastern United States, Means (2000) observed that the dwarf salamander, *Eurycea quadridigitata*, especially the larvae, was the numerically dominant vertebrate predator in 25 of 38 (66%) sampled habitats.

Altering the hydrologic regime can significantly alter salamander dominance in aquatic habitats (Semlitsch 2003b). Herpetofaunal communities inhabiting streams impounded by beaver ponds were compared with unimpounded streams by Metts et al. (2001). Salamanders were dominant amphibians in unimpounded streams (1680 of 2664 captures or 63.1%), but only 8.2% of captures were from habitats impounded by beavers. Snodgrass et al. (2000) reported that wetlands with different hydroperiods contain distinct amphibian assemblages and concluded that short-hydroperiod wetlands are important in maintaining amphibian biodiversity across a landscape because they may support species not found in longer hydroperiod wetlands.

## Succession

A large body of literature indicates that the density of some salamander species is closely associated with forest successional stage, with higher numbers of salamanders in older, more structurally complex systems. The California slender salamander (*Batrachoseps attenuatus*) is 10 times more abundant in old-growth redwood forest than younger regenerating stands (Bury 1983, Cooperrider et al. 2000). Welsh & Lind (1988, 1991) surveyed 54 terrestrial sites in the mixed Douglas-fir/hardwood forests of northern California ranging in age from 30 to 560 years. Three species of terrestrial salamanders were more abundant on old-growth than on younger sites. As reported by Welsh & Droege (2001), salamander abundances tracked closely with several structural attributes that model the forest chronosequence (Figure 1). One of these species, *Plethodon elongatus*, is closely associated with ecological conditions found primarily in the late seral stage of the interior mixed conifer/hardwood forests in California (Welsh & Lind 1995). Old-growth forests are known to support more salamanders than second-growth managed stands on Vancouver Island, Canada (Dupuis et al. 1995). Mitchell et al. (1997) reported significantly more salamanders, especially *Plethodon cinereus* and *Ambystoma jeffersonianum*, from eastern forests 80 to >100 years old compared with forests 2–50 years old. In Georgia forests ranging in age from 15 to >85 years old, both salamander species richness and diversity increased with age (Ford et al.





**Figure 1** Bivariate scatterplots and regressions for two Pacific Northwest salamander species showing relationship to structural aspects of forest chronosequence (all coefficients significant at  $p < 0.05$ ). Figure reprinted with slight modification from Welsh & Droege (2001) with permission.

2002). Although salamander diversity did not differ among land use categories in southern Appalachian forests, Hicks & Pearson (2003) also report that overall salamander numbers were greater in older, least altered stands. The observation that woodland salamander density increases during forest succession was verified for *P. cinereus* with a timber-harvest, GIS-based simulator model to predict both abundance and mass per unit area in forests of different ages (Gustafson et al. 2001).

Not all studies report a significant association of salamander abundances with seral stage (see review by deMaynadier & Hunter 1995). The reasons for this lack of association include differences in sampling technique, species tolerances, and/or availability of suitable microhabitat cover. For example, the threatened Cheat Mountain salamander (*Plethodon nettingi*) is most abundant in young red spruce forest stands but is rarely collected in mature forests (Brooks 1948). Metapopulation sizes of red-spotted newts are predicted to decrease as forest succession

cools breeding ponds, making the pools less suitable for adults and production of eggs (Cortwright 1998). Welsh (1990) and deMaynadier & Hunter (1995) both proposed that forest seral stage is an indirect measure of the age-related environmental attributes (e.g., coarse woody debris, foliage height diversity, canopy cover, litter type and depth, and cool, moist, equable microclimatic conditions) that determine whether a site is suitable for a given species. Biotic interactions of predation and competition between species may also be an important causal factor affecting salamander distribution at different stages of seral succession (see review by Hairston 1996).

## PATTERNS OF SALAMANDER FUNCTIONAL DOMINANCE

Ecosystem function refers to direct and indirect interactions of biotic and abiotic components, as well as to their contribution to the performance of the ecosystem as a whole (Müller & Windhorst 2000). The extremely high densities and biomass of salamanders within a variety of discrete forest environments lend credence to a hypothesis that they can regulate ecosystem functions at many different spatial scales and seral stages. Given their low ectothermal energy demands, salamanders would be predicted to affect ecosystem processes more as density-dependent regulators (e.g., process equilibrators or modifiers) or as retentive stores of nutrients than as movers of energy (Chew 1974, Pough 1983). In this section, we review literature on the roles of salamanders as biotic regulators of ecosystem processes and their contribution to resilience-resistance pathways that contribute to ecosystem stability.

### Predatory Effects on Lower Trophic Levels

All the more than 400 salamander species worldwide are obligate carnivores, with most having a polyphagous feeding strategy (Petranka 1998, Zug et al. 2001). Salamanders consume a wide variety of invertebrates and vertebrates within aquatic and terrestrial environments, although aerial prey can also be an important food resource (Davic 1991).

Hairston (1987) calculated that a salamander guild from the southern Appalachians could consume  $5.80 \text{ kcal/m}^2$  annually, which is greater than the estimated  $5.04 \text{ kcal/m}^2$  of all soil invertebrates. These data led Hairston to conclude that “the impact of salamanders on the soil fauna should be taken seriously.” Petranka (1998) suggested that abundant woodland species of the genera *Plethodon* and *Ensatina* would be predicted to regulate the population density of forest floor invertebrates. Other genera (*Ambystoma*, *Amphiuma*, *Cryptobranchus*, *Desmognathus*, *Dicamptodon*, *Notophthalmus*, *Siren*, and *Taricha*) were identified as potential regulators of invertebrate densities in aquatic environments. A number of studies, which we review below (see also Table 3), have now demonstrated through the manipulation of salamander densities that an important linkage exists between

**TABLE 3** Field experiments reporting regulatory effects by salamanders on invertebrate populations in both terrestrial and aquatic environments

Species	Affect/Habitat	Reference
<i>Plethodon cinereus</i> <sup>a</sup>	Invertebrate leaf fragmentors/ Forest floor	Wyman 1998
<i>Plethodon cinereus</i>	Collembola via indirect predation/Forest floor	Rooney et al. 2000
<b><i>Desmognathus quadramaculatus</i></b>	Benthic macroinvertebrates/ Headwater stream	Davic 1983
<i>Dicamptodon tenebrosus</i>	Benthic macroinvertebrates/ Headwater stream	Parker 1992
<i>Ambystoma barbouri</i>	The benthic isopod, <i>Lirceus fontinalis</i> /Headwater stream	Huang & Sih 1991a,b
<b><i>Notophthalmus viridescens</i></b> and <i>Ambystoma</i> spp.	Zooplankton/Artificial tanks	Morin et al. 1983; Morin 1987, 1995; Leibold & Wilbur 1992
<i>Ambystoma maculatum</i>	Isopods, amphipods/ Artificial tanks	Harris 1995
<b><i>Ambystoma tigrinum</i></b>	Benthic invertebrates and zooplankton/Artificial enclosures	Holomuzki et al. 1994
<b><i>Ambystoma tigrinum</i></b>	Caddisfly larvae/Wetlands	Wissinger et al. 1998
<i>Ambystoma tigrinum</i> and <i>Ambystoma laterale</i>	Zooplankton and mosquito larvae/Mesocosms and wetlands	Brodman et al. 2003

<sup>a</sup>Species in bold are identified by authors as potential “keystone species” (sensu Paine 1969).

salamander abundance, prey species diversity, trophic cascades, nutrient cycling, and the detritus-litter food webs of forest, grassland, and associated aquatic environments.

Wyman (1998) experimentally manipulated densities of *Plethodon cinereus* salamanders using leaf litter enclosures and concluded that these abundant salamanders are strong regulators of forest floor invertebrate populations. Rooney et al. (2000) also manipulated *P. cinereus* abundances in forest enclosures and found that salamanders indirectly enhanced the abundance of *Collembola*, a noningested prey item, by regulating the density of invertebrate predators of *Collembola*. Although we are unaware of similar experiments in western forests, the numerical dominance of *Ensatina*, *Plethodon*, and *Batrachoseps* in Douglas-fir forests suggests they also may have significant regulatory effects on invertebrate densities.

The effects of salamander predation on benthic macroinvertebrates in a lotic environment were investigated by Davic (1983) via repeated removal of biomass dominant *Desmognathus quadramaculatus* (adults, juveniles, and larvae—see Table 2) from small stream plots over a 12-month period. The results of this

study showed a significant number of direct (predatory) and indirect (competitive release) impacts on prey species density and biomass where salamanders were removed, but it reported little impact on nonprey species. The collective predation pressure of the aquatic salamander guild was estimated to remove 23 benthic macroinvertebrates/day/m<sup>2</sup> from June to October. Parker (1992) removed *Dicamptodon tenebrosus* larvae for 96 days from a stream pool, which also showed that salamanders can have both direct and indirect effects on benthic macroinvertebrate prey populations. Larvae of *D. tenebrosus* ingested 2.2 g/m<sup>2</sup> of benthic prey compared with a mean standing crop of 3.1 g/m<sup>2</sup> of available prey, which led Parker (1994) to conclude that the regulatory effect by salamanders on invertebrate populations is intense. Huang & Sih (1991a) experimentally added *Ambystoma barbouri* larvae to isolated stream pools and found that the larvae significantly reduced the density and altered the use of microhabitats by the benthic isopod, *Lirceus fontinalis*. Individual *Ambystoma* larvae ingested on average 28.6 isopods/day, indicating that they collectively could remove roughly 5000 isopods/day from pooled areas of the stream. Laboratory experiments showed complex interactions among salamander larvae, isopods, and a top predator, the green sunfish (Huang & Sih 1991b). Subsequently, Sparkes (1996) documented that female isopods mature at larger sizes in stream pools containing *Ambystoma* larvae, thus releasing themselves from intense predation pressure by salamanders.

In contrast to the above studies, two attempts to exclude the Northern two-lined salamander (*Eurycea bislineata*) and fish predators in streams using mesh cages (Reice 1983, Reice & Edwards 1986) reported no effect on benthic macroinvertebrate prey. However, we view the results of these experiments as inconclusive. The 6.35 mm mesh used for experimental cages by Reice (1983) would not have excluded *Eurycea* larvae and small juveniles. These life stages can be abundant in streams (see Table 2) and are known to ingest a variety of benthic macroinvertebrates (Petranka 1998). In the experiment of Reice & Edwards (1986), adult *E. bislineata* were excluded, but these salamanders are known to feed extensively on terrestrial prey and migrate seasonally well away from flowing water (Petranka 1998); they are unlikely to be strong predators on aquatic benthic macroinvertebrates. However, given their wide-ranging terrestrial dispersal, abundant populations of *E. bislineata* adults may regulate invertebrate species diversity within the riparian stream environment, a hypothesis open to experimentation.

Predatory effects of salamanders are well known to reduce the population density of frog tadpoles and alter coexistence patterns of salamander species in lentic habitats (see Calef 1972, Morin 1995, Wilbur 1997, Kurzava & Morin 1998, Walls & Williams 2001, Brodman et al. 2003). Experiments in artificial ponds led Morin (1995) to conclude that adult *Notophthalmus viridescens* and larval *Ambystoma opacum* show "functional redundancy" in their nearly identical regulatory effects on anuran prey populations. Where salamander predators were abundant, frog density was reduced, leading to increased biomass of primary producers such as phytoplankton. We are unaware of experiments that have tested for indirect effects of salamander predation on macrophyte biomass or diversity.

Predatory effects by salamanders on invertebrates in pond habitats are also well documented (Table 3). For example, Morin (1987) experimentally manipulated the densities of *Notophthalmus viridescens* and *Ambystoma tigrinum* in artificial pools and found that salamander predation significantly altered patterns of seasonal succession of zooplankton. A subsequent experiment revealed that the effect of salamander predation in ponds can cascade through multiple trophic levels to increase algae production (Morin 1995). Similar experiments with *Ambystoma tigrinum* larvae showed both direct and indirect effects on zooplankton and benthic macroinvertebrate abundances in fishless pond enclosures (Holomuzki et al. 1994). Larvae of *Ambystoma tigrinum* also regulate population densities of caddisfly prey in subalpine wetlands of Colorado (Wissinger et al. 1998). Given their tendency to specialize on mollusk prey, *Siren* spp. may play an important role in structuring snail populations in ponds (Petranka 1998). In a more applied vein, Brodman et al. (2003) demonstrated the effectiveness of *Ambystoma* larvae in controlling mosquito larvae populations—mosquito larvae density was 98% lower in wetlands with salamanders compared with salamander-free wetlands.

A variety of field experiments in both terrestrial and aquatic environments have demonstrated that salamander species can function as “keystone predators” (i.e., Morin 1981, Davic 1983, Fauth & Resetarits 1991, Fauth 1999, Wissinger et al. 1998, Wyman 1998). According to the classic concept of Paine (1969), keystone species prevent dominant prey from monopolizing limited resources, thus allowing the coexistence of additional species and/or an increase in the evenness of prey species abundances within a community (see review by Menge & Freidenburg 2001). As discussed by Schulze & Mooney (1993), keystone species as a group have no redundant representation; they exert disproportionate biotic regulation within an ecosystem because their elimination causes changes in community function not performed by other species. Therefore, loss of keystone species such as salamanders could have serious negative effects on ecosystem stability by altering resilience-resistance pathways (Chapin et al. 1997). Davic (2003) proposed a modification of Paine’s (1969) keystone species concept that links the a priori identity of potential keystone species to biomass dominance in ecological functional groups. This view of the keystone species concept is congruent with widespread observations that a single salamander species often dominates multispecies salamander guilds in a variety of habitat types (see Table 1), and its application offers a novel management tool for the a priori identification of potential keystone salamander species in natural areas.

## Regulation of Detritus-Litter Food Webs

More than 90% of the net energy production of a temperate forest is consumed by decomposer organisms and less than 10% by herbivores (Ricklefs 1979). Those invertebrate organisms responsible for most of the decomposition and fragmentation of detritus-litter are well known for both aquatic (Wallace & Webster 1996) and terrestrial environments (Swift et al. 1979). However, the ecological roles of

vertebrate predators as potential regulators of decomposer populations in ecosystems, and ecosystem processes associated with detritus-litter food webs, are poorly known (Bormann & Likens 1979, Konishi et al. 2001).

Some researchers have suggested that salamanders may provide an important indirect regulatory role in the processing of detritus-litter by ingestion of detritivore prey (Burton & Likens 1975b, Hairston 1987, Stebbins & Cohen 1995). Field experiments in lotic (Davic 1983) and terrestrial (Wyman 1998) environments support this hypothesis. Both investigations demonstrated in situ that the presence of salamanders slow the rate of detritus-litter decomposition. These findings are contrary to the suggestion of Hairston (1987) that salamanders feeding on invertebrates, which themselves feed on the bacteria and fungi in the forest floor leaf microflora, would promote a more rapid rate of leaf litter decomposition. Indirect effects on detrital processing have rarely been documented for vertebrates; however, fish predators also have been reported to slow the rate of leaf decomposition in streams (Konishi et al. 2001).

Dominant salamanders in terrestrial environments may serve to maintain resilience-resistance pathways in forests by indirectly dampening the seasonal release of essential micronutrients from leaf litter to the root systems of the flora. Leaf litter decomposes at a rate directly related to the number of invertebrate animals in the litter and the underlying soil (Perry 1994). Wyman's (1998) documentation that *Plethodon* salamanders reduce soil invertebrate numbers and indirectly dampen leaf litter processing has significant implications for the mineralization and immobilization of elements such as carbon, nitrogen, and phosphorus. Results from ongoing experiments by Wyman (2003) suggest an important linkage of *P. cinereus* salamanders to long-term retention of nitrogen compounds from leaf litter and potential regulation of the carbon-nitrogen cycles in forests. By reducing densities of invertebrates that prefer ingesting leaf sections with high nutrient value, salamander predation may allow for longer retention of nutrients in soil over time (Wyman 2003). In a headwater stream, predatory effects of *Desmognathus quadramaculatus* salamanders slow detrital processing (Davic 1983), thus potentially dampening the release of fine particulate organic matter to downstream communities. The downstream movement of organic matter is a central theme of the river continuum concept (Vannote et al. 1980) and resource spiraling (Elwood et al. 1983).

To our knowledge, no experimental studies have investigated effects of salamanders on detrital processing in lentic habitats. However, some evidence suggests that salamanders may play such a role. Wissinger et al. (1998) investigated the predatory effects of *Ambystoma tigrinum* on two species of leaf shredding limnephilid caddisfly larvae. They observed competition between caddisfly species involved in detrital processing, which resulted in strong keystone species effects on prey diversity by salamander predation. Although Wissinger et al. (1998) did not measure decay rate of detritus, their observations suggest that salamanders have the potential to regulate detrital processing in this lentic environment by predatory control of competitively dominant, leaf-shredding invertebrate species. Efford (1969)

estimated the energy budget of Lake Marion, Canada, and found that detritus in the lake bottom represented 86% of the total annual carbon energy storage of 280 g of carbon/m<sup>2</sup>/yr. The detritivore *Hyallolela azteca* reduced detritus content in the bottom of the lake by 40% to 45% in one season and was a highly selected prey of the salamanders *Taricha granulosa* and *Ambystoma gracile*.

The role of salamanders in damping litter decomposition, with possible global significance, has been discussed by Wyman (1998, 2003). Forests are estimated to contain approximately three fourths of all carbon contained in living terrestrial vegetation, and a little less than one half of that is stored in soils (Perry 1994). Wyman calculated that an 11% to 17% reduction in the rate of forest floor leaf decomposition (because of the estimated regulatory effect of salamander predation) would result in 261 kg to 476 kg of carbon/ha not being released into the atmosphere annually. This cybernetic feedback between salamanders and leaf litter processing suggests that reported declines in salamander densities may be causing an increase in rate of leaf litter decomposition and concomitant increase in CO<sub>2</sub> release to the atmosphere. Wyman (1998, 2003) speculated that this process may contribute to global warming, but he cautions that this idea has too many assumptions to be taken as anything other than a testable hypothesis that warrants further investigation.

## Coupling Aquatic and Terrestrial Habitats

By migrating between environments, consumers can affect food webs of communities at several spatial scales (Polis et al. 1996). Biological coupling of aquatic and terrestrial landscapes has only recently been investigated as this coupling relates to ecosystem integrity. Fisher et al. (1998) propose a conceptual “telescoping ecosystem model,” which suggests that biological cross-links between the aquatic and terrestrial landscapes may enhance the resilience of the ecotone, although flooding is assumed to be the dominant mechanism. For instance, salmon carcasses were found to link the energy and nutrient budgets of both aquatic and terrestrial ecosystems (Cederholm et al. 1999).

Many salamander species are migratory and exhibit both short-term and short-distance movements along landscape corridors or between habitat patches, including migrations of adults to breeding sites. Hairston (1987) and Pauley et al. (2000) cite numerous examples of salamander species that migrate through forests between aquatic and terrestrial landscapes, often at night or during wet periods. Reported distances moved range from 3–1600 m for *Ambystoma* species, 3–60 m for *Desmognathus* species, 100 m for *Eurycea bislineata*, and 800 m for *Notophthalmus viridescens* (Pauley et al. 2000). Disruption of a riparian habitat can significantly alter salamander migrations (Williams et al. 2002), although land-use patterns in the upper watershed may be as important for dispersal of salamander populations as riparian habitat (Willson & Dorcas 2003).

Some salamander species function as dispersal vectors during their migrations. *Ambystoma* salamanders are known to transport mollusks (e.g., pea clam, *Pisidium adamsi*) and achenes of the bur-marigold, *Bidens cernua*, between pooled habitats

during spring migrations (Lowcock & Murphy 1990). Mudpuppies (*Necturus*) serve as a migratory host for the salamander mussel (*Simpsonaias ambigua*), the only North American mussel species known to parasitize a vertebrate host other than a fish (Watters 1995). Metamorphic *Ambystoma* salamanders are responsible for dispersal of fairy shrimp (*Branchinecta coloradensis*) eggs between forest pools by feeding on female fairy shrimp in one pool and defecating in another (Bohonak & Whiteman 1999). These observations suggest a hypothesis that salamander dispersal may provide biotic control of ecosystem processes within both stream and pond ecotones as indicated by the telescoping ecosystem model (Fisher et al. 1998). Experimental verification of this hypothesis would require large-scale removal of salamanders from the riparian, coupled with long-term monitoring of changes in energy flow, nutrient cycling, and population density of salamander prey and predators.

Salamanders also may play an important role in the riparian ecotone via processes of chemical transformation. Amphibians are reported to oxidize ingested aromatic hydrocarbons followed by conjugations to glucuronides and organic sulfates (National Research Council 1981). The high efficiency at which salamanders store lipids and proteins in their tails (Burton & Likens 1975b) suggests that salamanders living within the riparian ecotone could ingest aquatic prey with high body burdens of toxic organic compounds, such as pesticides and chlorohydrocarbons, which could then be oxidized and translocated into the terrestrial environment in less toxic form during salamander migrations. Conversely, Johnson et al. (1999) found that dermal exposure of trinitrotoluene (TNT) and polychlorinated biphenyls (PCBs) resulted in bioaccumulation in tissue of *Ambystoma tigrinum* at concentrations that could affect food-web modeling. Given their relatively long life spans and high numbers in ecosystems, salamanders may be a critical food-web link in the bioaccumulation of persistent chemicals such as mercury and PCBs. Research here would provide useful information on the toxicological role of salamanders as elemental sinks, chemical transformers, and cross-links of organic molecules and heavy metal ions between aquatic and terrestrial environments (see Sparling et al. 2000).

## Regulation of Salamander Diversity

Hairston (1996), Petranka (1998), and Walls & Williams (2001) provide comprehensive reviews of the literature dealing with the ecological role of salamanders as regulators of other salamander species via processes of predation, competition, or both. Studies in which salamander species were either removed from or added to experimental plots indicate that salamanders regulate the distribution and abundance of other salamander species through complex interactions of competition and predation. The studies reviewed by Hairston (1987, 1996) in terrestrial habitats, and Wilbur (1997) in artificial ponds, demonstrate the predictive power of field experiments to address complex ecological questions concerning biotic interactions. Although the relative role of competition versus predation appears to



vary among different salamander guilds and in different habitats, the experimental evidence is now conclusive that both processes are important in the regulation of salamander communities.

## Salamanders as Prey

Many animals are known to consume salamanders, including birds, mammals, snakes, fishes, turtles, frogs, crayfish, predatory insects, and other salamanders (Petranka 1998). The nocturnal habits of salamanders, mimicry, and the toxic skin secretions present in many species indicate that predation pressure is an important selective agent that regulates the distribution and abundance of salamander populations. Burton & Likens (1975a) concluded that salamanders in mature forests “represent a higher quality source of energy and nutrients for tertiary consumers than birds, mice, and shrews.” Given their relatively small size compared with birds and mammals, salamanders can exploit small prey items not selected by larger vertebrates and convert these food sources into biomass that is then made available to larger vertebrate predators (Feder 1983, Pough 1983).

Long-term storage of salamander energy and biomass should have strong stabilizing effects on ecosystem processes. Hairston (1987) suggests that the impact of this storage by salamanders is to dampen stochastic fluctuations in the rate of energy flow. One can extend this line of thinking to the cycling of nutrients. Perry (1994) reported that healthy forests retain nutrients at a similar efficiency regardless of successional stage because trophic pathways exist that allow diversions to “slowly available nutrient pools.” The low energy demand, long life span, slow growth rates, and great abundance of salamanders suggest they may well be the most important slowly available nutrient pools in forests. Margalef (1968) concluded that self-regulating ecosystems tend to conserve information by replacing ecologically equivalent system elements during succession. Salamander life histories and population dynamics fit well this holistic concept of ecosystem function. Different salamander species with similar ecological roles are found across a wide range of environments and seral stages. Given their well-documented numerical dominance in discrete macroenvironments in forests, and the tendency for the density of many species to increase during ecological succession (as herein reviewed), we suggest that salamanders can help maintain the long-term resilience-resistance of trophic pathways by providing abundant biomass and slowly available nutrient pools for top predators, at each seral stage of forest succession.

## Underground Retreats

The environmental impact of underground retreats is well known and extensively reviewed (Meadows & Meadows 1991, Butler 1995). Burrows and underground passageways have ecosystem level functions beyond the increased fitness they incur to the species that make and use them. A large number of salamander species are known to occupy underground retreats (Petranka 1998). This mode of life is widespread across numerous families and genera, with obvious adaptive value to

organisms susceptible to desiccation and predation (Semlitsch 1983). Although the density of salamanders in subsurface soil habitats is mostly unknown, a census of *Plethodon cinereus* in Michigan (Test & Bingham 1948) found that successive removals of salamanders from plot-strips yielded captures of 118, 146, 131, and 101 individuals over time. Failure to reduce salamander densities after repeated removals led Test & Bingham (1948) to suggest that a large percentage of the salamander population was underground in burrows and not directly beneath cover objects in the forest floor. Taub (1961) experimentally documented that *P. cinereus* spends significant time in burrows at least 12 inches deep. The availability of small mammal runways and burrows are thought to limit the population density of some *Ambystoma* species (Faccio 2003). Recently, a three-year study of *Plethodon* salamanders from the Great Smoky Mountains verified that significant proportions of terrestrial populations are subterranean (Bailey et al. 2004a).

Although use of underground retreats by salamanders is well documented, a long-standing controversy exists as to whether salamanders create their own burrows or merely take residence in burrows constructed by other animals. According to Dunn (1926), two *Desmognathus fuscus* left in a terrarium for over a year were found with many well-formed soil burrows. Dunn (1928) subsequently argued that *Desmognathus* and *Plethodon* salamanders have the ability to make their own burrows and do not merely follow crannies made by other animals as implied by Nobel (1927). A number of salamander genera have now been reported to either create or modify soil burrows including *Plethodon* (Brooks 1946, Heatwole 1960), *Ambystoma* spp. (Gruberg & Stirling 1972, Semlitsch 1983, Jennings 1996), *Siren* (Etheridge 1986), and *Phaeognathus hubrichti* (Hale & Guyer 2000). Stebbins (1951) noted that captive *Dicamptodon ensatus* are “good burrowers” and dig in gravel in an attempt to bury themselves. Marcot & Vander Hayden (2001) list 9 of 21 salamander species from the Pacific Coast that either create or modify soil burrows. Within the lungless salamander family, genera from the subfamily (Desmognathinae) retain basal morphological characters that are associated with burrowing and wedging between rocks (Titus & Larson 1996), including heavily ossified skull, flat wedge-like head, atlanto-mandibular ligaments, enlarged dorsal spinal muscles, and hind limbs relatively larger than forelimbs.

Organisms that modulate the availability of resources to other species by causing either physical or chemical changes to habitats have been referred to as “ecosystem engineers” (Jones et al. 1994). The above citations, although somewhat circumstantial, allow for a hypothesis that salamander species may serve an important ecological role in forests as ecosystem engineers of soil dynamics by creation, modification, and long-term occupancy of underground burrow systems. Regardless of how it is accomplished, either by creating burrows or using existing passages, the long-term residence of salamanders below ground suggests a number of significant ecosystem level effects: (a) translocation of nutrients, fungi, and other microorganisms from the forest floor to subsurface plant root systems; (b) deposition of excretory nutrients and organic matter for use by bacteria and fungi; and (c) increased dispersal of gases (e.g., dissolved oxygen, nitrogen, carbon dioxide) through the

soil matrix. We are unaware of any experimental studies of these ecosystem processes, which represent an important area for future investigation in forest soil dynamics. Migrations by abundant salamanders into underground retreats during catastrophic events such as forest fires (Pilliod et al. 2003) and volcanos (Zalisko & Sites 1989) may help reset the chronosequence of forest ecosystem recovery, with surviving salamanders acting as biological legacies, both as a source of high energy prey and as predators that regulate invertebrate prey populations.

## SUMMARY AND DISCUSSION

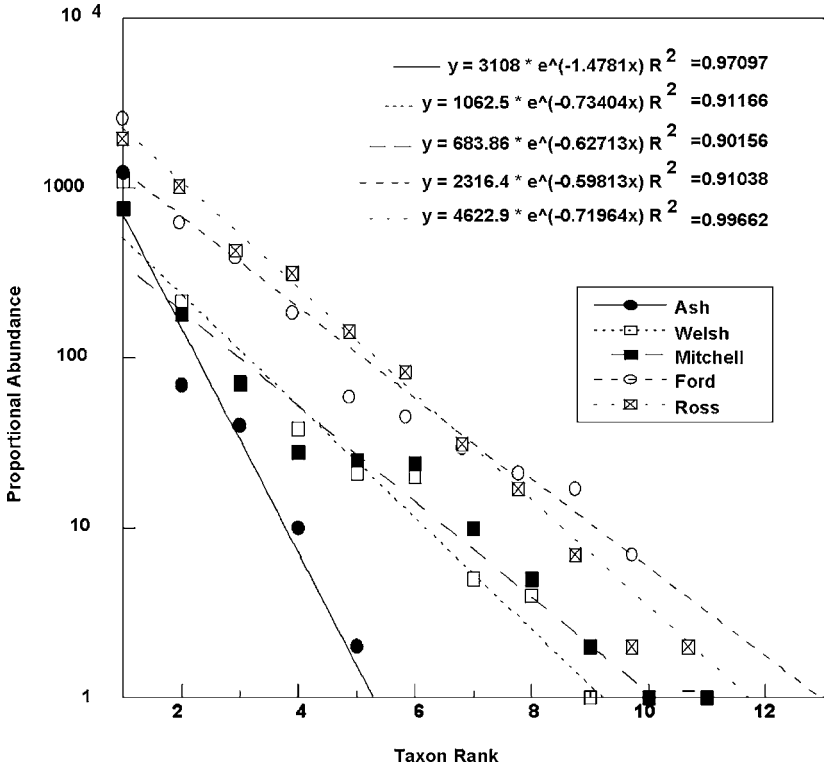
This review considers the key ecological functions (Marcot & Vander Hayden 2001) of salamanders in terrestrial, riparian, aquatic, and subterranean environments within North America ecosystems (Figure 2). The compiled evidence supports a hypothesis that salamanders help provide fundamental biotic control of numerous ecosystem processes: (a) They furnish an abundant source of energy and nutrients for both terrestrial and aquatic consumers such as birds, fish, reptiles, mammals, and decomposers; (b) as predators of invertebrate species associated with the decomposition of organic matter, they modulate energy pathways and the release of essential minerals; (c) as keystone predators (*sensu* Paine 1969), they decrease the abundance of competitively dominant prey, thereby increasing taxa diversity in lower trophic levels; (d) through their complex life cycles they serve as connecting pathways for energy and matter between aquatic and terrestrial landscape elements; (e) by occupying and modifying underground refugia, they serve as facilitators of soil dynamics; and (f) by converting and storing large amounts of secondary production in the form of salamander biomass, they enhance forest resilience-resistance (= stability) throughout ecological succession.

Salamanders can also provide an important service to humans as sentinels of ecosystem integrity through their use as cost-effective and readily quantifiable metrics of ecosystem resilience-resistance. Welsh & Droege (2001) report that the coefficient of variation (CV) associated with statistical sampling trends for forest dwelling plethodontid salamanders (CV = 27%) is significantly lower than other vertebrates, such as passerine birds (57%), small mammals (69%), and other amphibians (37%–46%). These numbers imply that population trends for terrestrial salamanders can be detected more quickly and with fewer years of monitoring effort than other vertebrate species. Up to 20 years of stability in local population density has been reported for some plethodontid species (Hairston 1996). Population densities for migratory pond-breeding ambystomatids and salamandrids are known to vary by an order of magnitude depending on the rain-year, making these salamander species less attractive for use as long-term quantitative sentinels of ecosystem resilience and resistance (Pechmann et al. 1991, Trenham et al. 2000, Semlitsch 2003b), although Cortwright (1998) statistically demonstrated no broad shifts in density of red-spotted newts over a 10- to 11-year period from 36 breeding ponds.

Rolstad et al. (2002) concluded that the use of indicator species to assess forest health should concentrate on species that show long-term population stability and repeatedly occur in distinct habitats within old-forest stands. Many species of salamanders fit well the indicator species criteria of Rolstad et al. (2002); however, monitoring programs will need to consider variation in detection probability to track long-term trends in population density (see Hyde & Simons 2001; Bailey et al. 2004a,b). Observations on the presence-absence of sentinel salamander species also can provide useful information about existing conditions in natural areas. For example, breeding populations of spotted salamanders (*Ambystoma maculatum*) have been associated with wetlands that have high floral diversity and integrity (Micacchion 2002). Numerous Plethodontid species have been suggested to help classify aquatic life use potential under the Clean Water Act for primary headwater streams (Ohio EPA 2002). As aptly coined by Vitt et al. (1990), salamanders can provide an important ecological role as “harbingers of environmental decay” and sentinels of ecosystem condition.

Our review documents widespread observations in which at least one salamander species (rarely two) dominates the local salamander guild in different macroenvironments (see text on structural dominance and Table 1). These findings indicate that current emphasis on protection of rare species of salamanders, although clearly worthy, should be expanded to include those species that are dominant (in numbers and/or biomass) across the landscape and/or that function as keystone predators (sensu Paine 1969). Disturbances that reduce these ecologically dominant salamander species could result in profound alteration of critical ecosystem functions (see Conner 1988, Chapin et al. 1997).

This recurrent pattern of numerical dominance by a single salamander species at the landscape scale may be a fundamental aspect of the “rules-of-assembly” (Wilson 1999) of undisturbed forests. Ecologists have long recognized that closely related taxa in a community are not equally abundant but that their numbers tend to conform to mathematical patterns such as the geometric-series, log-series, log-normal, or MacArthur broken-stick distribution (reviewed by Tokeshi 1993, Brown 1995). A review of salamander abundance data from five North American forests with at least 1000 captures (Welsh & Lind 1988, Mitchell et al. 1997, Ash 1997, Ross et al. 2000, Ford et al. 2002) shows that a geometric-series model, combined with an exponential power-law regression of the semi-log data, provides a good statistical fit (Table 1, Figure 3). The simplicity of the model is appealing because variations in regression slopes (steepness and elevation), coefficients of determination ( $R^2$ ), and intercepts of  $x$ -axis (estimate of species richness) and  $y$ -axis (abundance of the dominant taxon) may be useful diagnostic tools to help predict structural changes of salamander communities between disturbed and undisturbed forests. For instance, the highly negative slope of the regression curve for the salamander community studied by Ash (1997) in Figure 3 suggests that the overall species diversity of the salamander community was disturbed, with disproportional numbers of the dominant ranked species, *Plethodon jordani*. Tokeshi (1993) used geometric-series models to show greater loss of plant community diversity



**Figure 3** Geometric-series plots for salamander communities from five different forested landscapes. Regressions are exponential functions (all coefficients significant at  $p < 0.01$ ). See Table 1 for raw data.

after long-term application of nitrogen fertilizer, and Sponseller et al. (2001) applied geometric-series regressions to study variation in benthic macroinvertebrate communities under stress from different watershed land uses. Future studies are needed to determine precisely how the mosaic pattern of forest habitats might cause deviations from a generalized geometric-series distribution for salamander communities, in a variety of undisturbed and disturbed forest areas, and at various stages of seral succession.

Concern over declining amphibian populations has produced a number of calls for greater conservation of salamander populations and their habitats (Bury et al. 1991; deMaynadier & Hunter 1995; Welsh & Lind 1995, 1996; Petranka 1998; Welsh & Droege 2001; Semlitsch & Rothermel 2003; Wyman 2003). If we view the landscape from the perspective of the salamander, it is the mosaic pattern of microenvironmental conditions present within different types of habitats (e.g., stream, pond, wetland, forest floor) that is critical to the long-term survival of salamander populations. Given the diversity of life history adaptations in salamanders

and the tendency for salamanders to migrate between different habitats, protection of salamander species diversity will require attention to both micro and macrohabitat requirements (Welsh 1990; deMaynadier & Hunter 1995; Welsh & Lind 1995, 1996; Trenham 2001; Semlitsch & Rothermel 2003) in both aquatic and terrestrial environments.

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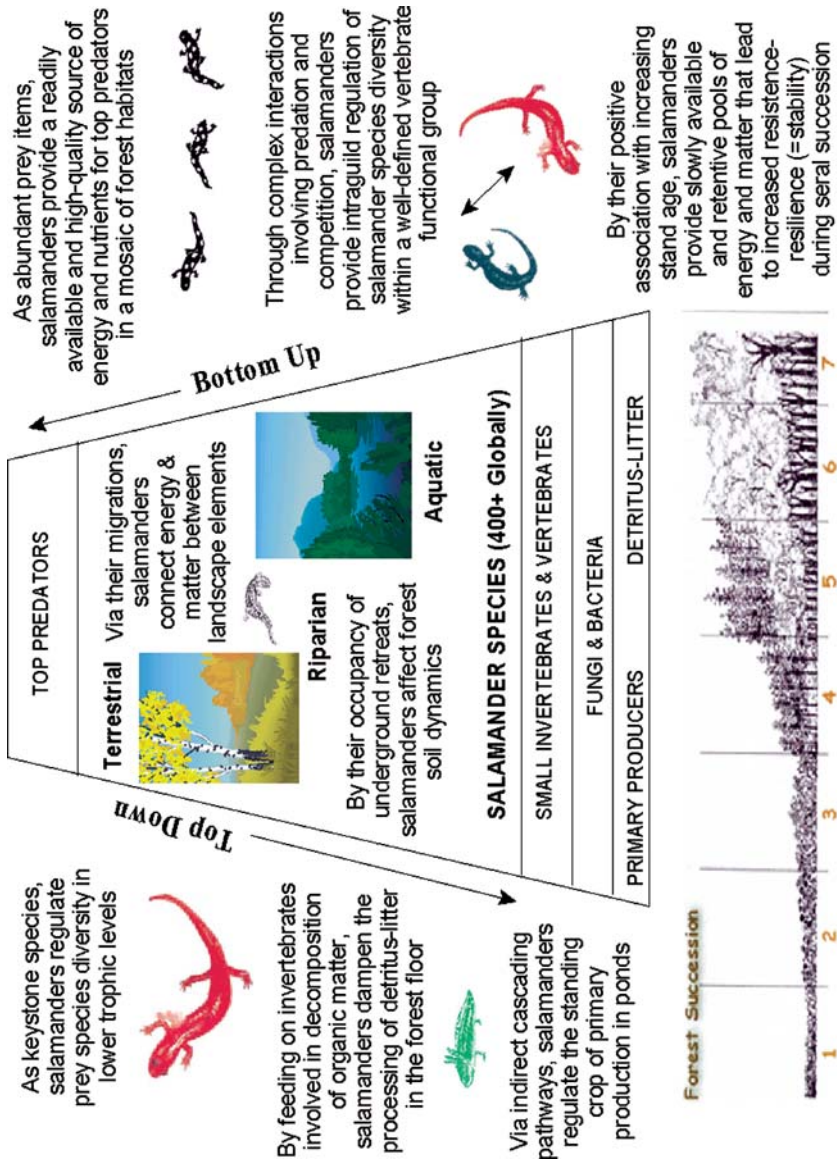
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**Figure 2** Key ecological functions of salamanders in ecosystems. Forest succession image used with permission of the Forest Historical Society. Salamander images courtesy of Travelin' Naturalist, Lenz Design, and US EPA (Mark Erelli, artist).