Revisiting Burton and Likens (1975): Nutrient Standing Stock and Biomass of a Terrestrial Salamander in the Midwestern United States

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Animals found in high densities can have significant influence in nutrient cycles of ecosystems. For example, frogs have been known to influence nutrient cycles in tropical forests. However, research understanding the influence of vertebrates in nutrient cycles of North American forest is limited. It has been found that the biomass of terrestrial salamanders (family Plethodontidae) is higher than that of birds, small mammals, and deer in a New Hampshire forest, and recent studies have found prior estimates of terrestrial salamander densities are likely lower than current estimates using sampling and analysis frameworks to account for imperfect detection. A re-evaluation of the impact plethodontid salamanders could have on forest nutrient cycles is therefore justified. We quantified the degree to which a completely terrestrial, lungless salamander (*Plethodon albagula*; Western Slimy Salamander) constitutes a standing stock of limiting nutrients in a Missouri, USA forest ecosystem. We utilized values of whole-body nutrient composition of carbon (C), nitrogen (N), phosphorus (P), calcium (Ca), and magnesium (Mg) of *P. albagula* and spatially explicit density estimates to approximate the contribution of *P. albagula* to forest nutrient cycles. We found that estimates of the standing crop nutrients varied spatially across the landscape and were dictated by density of *P. albagula*. Standing crop estimates were lower than measures for leaf litter, but often were greater than those previously reported for plethodontid salamanders, birds, and in some cases small mammals and deer in North American forests.

FOLLOWING the Fourth Conference on the Biology of Plethodontid Salamanders, a collection of works was published detailing the evolution, systematics, behavior, life history, and general ecology of plethodontid salamanders (Bruce et al., 2000). In hindsight, notably lacking was an investigation into the potential ecological roles of plethodontid salamanders in terrestrial and aquatic ecosystems. Davic and Welsh (2004) detailed some of the ecological roles of plethodontid salamanders, which include measurable predatory effects on lower trophic levels and food webs, and hypothesize other roles, including assistance with chemical transformation of nutrients, regulation of invertebrate diversity, and serving as prey or nutrient pools. One topic in particular that has lacked considerable study is the role of plethodontid salamanders in nutrient cycles. Burton and Likens (1975a) examined the contribution of plethodontid salamanders to metrics of energy flow and nutrient cycling in a New Hampshire forest, but concluded that despite the high biomass attained by this guild of salamanders, they had no measurable influence over energy flow, nutrient standing stock, or nutrient cycling. Since the publication of Burton and Likens (1975a), only two other studies have investigated the influence of terrestrial plethodontid salamanders on nutrient cycles. Hocking and Babbitt (2014) did not find *Plethodon cinereus* (Red-backed Salamander) to have a measurable influence on nutrient cycling in an American beech (*Fagus grandifolia*) New Hampshire forest, while Semlitsch et al. (2014) found *P. serratus* (Southern Red-backed Salamander) was a significant standing stock of several limiting nutrients within a Missouri (Ozark) forest.

In light of large-scale amphibian declines (Stuart et al., 2004; McCallum, 2007; Collins, 2010; Rohr and Raffel, 2010), and projected and reported large scale declines of terrestrial plethodontid salamanders (Rovito et al., 2009; Milanovich et al., 2010), it is important that we critically evaluate the role and contribution of plethodontid salamanders to ecosystem processes, particularly nutrient cycles. Vertebrates have been shown to have measurable influences on nutrient cycles in many ecosystems through consumption, assimilation, or excretion (e.g., Vanni, 2002; Schmitz et al., 2010), and these findings have been extended to terrestrial herpetofauna influencing nutrient cycling in tropical forest floor ecosystems (Sin et al., 2008). Specifically, terrestrial frogs (*Eleutherodactylus coqui*; Common Coquí) have been found to have a measureable influence on several forest floor nutrient processes, such as increasing the pool of available limiting nutrients by increasing elemental concentrations in leaf washes and increasing nutrient availability in decomposing leaf litter, presumably as a consequence of nutrient excretion and population turnover (e.g., carcasses; Beard et al., 2002). However, while plethodontid salamanders comprise over 60% of salamander diversity in the United States alone (Lannoo, 2005), their contribution to nutrient cycles remains poorly understood and understudied.

In this study, we used existing spatially explicit estimates of density derived from binomial mixture models (Peterman and Semlitsch, 2013) and measures of site-specific nutrient content to estimate the contribution of *P. albagula* to the standing stock of carbon (C), nitrogen (N), phosphorus (P), calcium (Ca), and magnesium (Mg) within a Midwestern United States forest. Because they are vertebrates and previous studies showed *Plethodon* spp. can occur at high densities and attain high biomass in forest ecosystems (Burton and Likens, 1975b; Peterman and Semlitsch, 2013; Semlitsch et al., 2014), we hypothesized that terrestrial plethodontid salamanders, such as *P. albagula*, would have high P and Ca content (due to allocation of P and Ca to bone) and constitute large standing stocks of P and Ca. We compared our results with estimates of standing stock from terrestrial vertebrates in North America, and outline future avenues of research needed to better understand the role of plethodontid salamanders in terrestrial nutrient cycles and ecosystems.

MATERIALS AND METHODS

We collected 44 *Plethodon albagula* from 12 sites (based on previous data) within Daniel Boone Conservation Area

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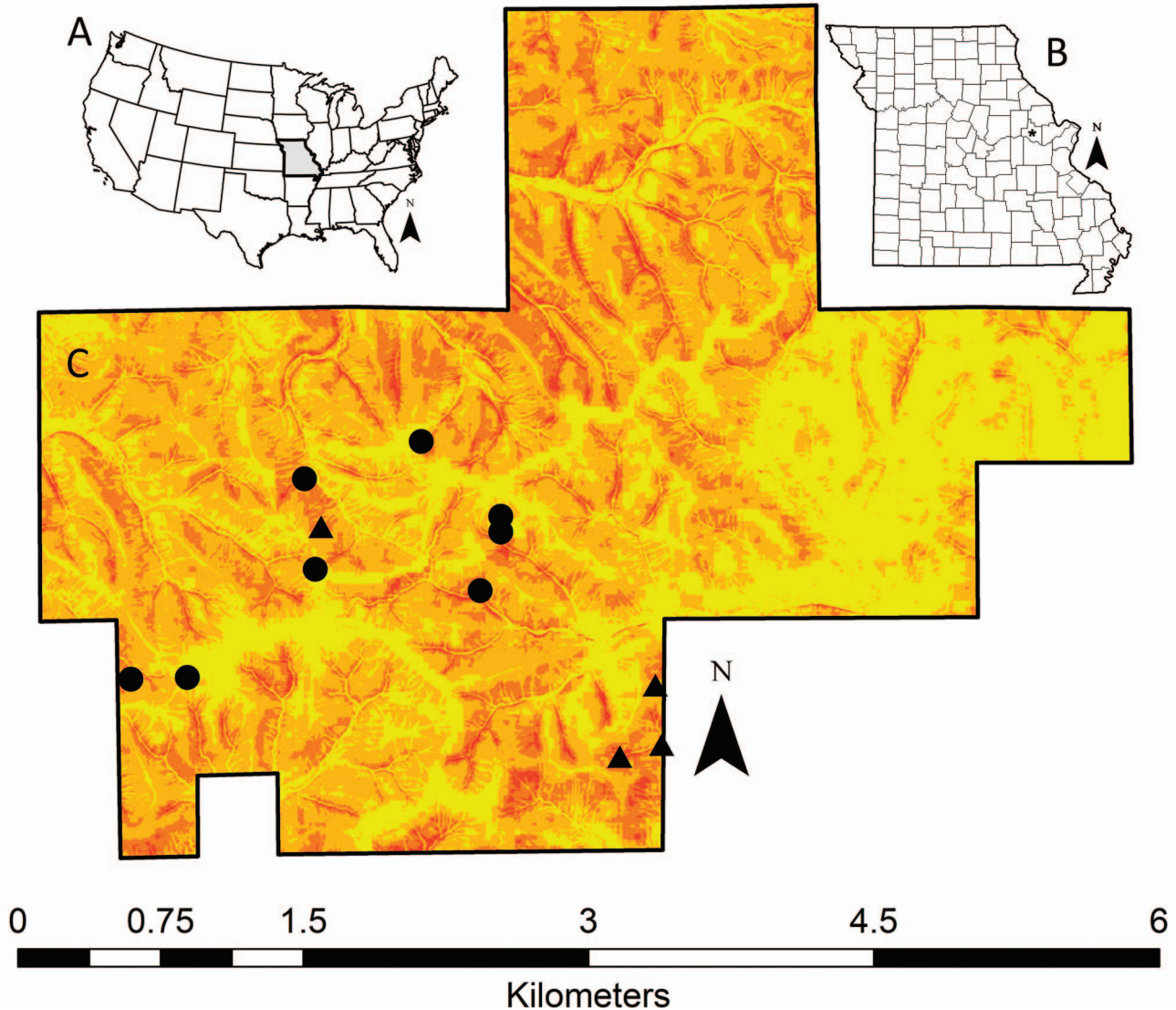
Fig. 1. (A) Outline of Missouri, USA. (B) Warren County, Missouri with dot representing Daniel Boon Conservation Area (DBCA). (C) Spatial values of estimated standing stock (mg·m^{-2}) of biomass, carbon, calcium, magnesium, nitrogen, and phosphorus of *P. albagula* at DBCA and locations of sampling sites for salamander nutrient (black triangles) and salamander nutrient and leaf litter (black dots).

(DBCA) in Warren County, Missouri, USA between 7–8 May 2014 (Fig. 1). The study site is predominantly mature (80–100 yrs. old), second-growth oak (*Quercus* spp.) and hickory (*Carya* spp.) dominated overstory forest with varying amounts of sugar maple (*Acer saccharum*) and red cedar (*Juniperus virginiana*) in the understory (Semlitsch et al., 2008). Salamanders were captured by overturning rocks and logs within an approximately 100 × 100 m area at each site. All salamanders captured were placed in plastic containers with a moist paper towel and kept on ice until processing. Coinciding with salamander collections, we collected leaf

litter samples at eight sites across DBCA by randomly placing a 0.25 m^{-2} area of PVC pipe at four plots within each of the eight sites ($n = 32$ total leaf litter samples). All leaf litter within each of the four plots was collected and placed in a large plastic bag to accumulate 1 m^{-2} of leaf litter at each leaf litter site.

Salamander and leaf litter samples were transported to Loyola University Chicago for further processing. Salamanders were euthanized by wrapping them in a paper towel saturated with a 1.0% solution of pH neutral-buffered MS-222 (ethyl m-amino-benzoate methanesulfonate) solution,

Table 1. Mean (±1 SD) and percent of C, N, P, Ca, and Mg, mean individual dry mass (mg) and mean estimated biomass (mg/m²) of *P. albagula* and leaf litter in this study compared to *Plethodon cinereus*, birds, and small mammals at Hubbard Brook Experimental Forest, New Hampshire and *P. serratus* from Missouri.

Nutrient	*P. albagula*	*P. cinereus*[a]	*P. serratus*[b]	Birds[c]	Small mammals[a]	Leaf litter
C	46.93 (2.71)	—	47.3 (0.40)	—	—	45.56 (6.11)
N	11.53 (0.61)	9.06	11.0 (0.12)	31.4 (4.4)	4.98	0.78 (0.14)
P	2.48 (0.44)	2.28	2.16 (0.07)	19.2 (0.04)	0.05	0.05 (0.02)
Ca	1.34 (0.27)	3.43	2.99 (0.13)	31.1 (1.0)	3.06	1.83 (0.43)
Mg	0.14 (0.02)	0.13	0.13 (0.003)	1.12 (0.04)	0.13	0.28 (0.14)
Individual mass (mg)	641 (352)	—	245	8600 (1300)	—	—
Biomass (mg/m²)	75.67 (67.23)	39.04	180–320	1.5–22.2		829,000 (336,111)

[a] Burton and Likens (1975a)
[b] Semlitsch et al. (2014)
[c] Sturges et al. (1974)

weighed (wet mass; mg), and measured (snout–vent length [SVL] from the tip of the snout to the anterior portion of the vent; mm). Next, we removed the stomachs and intestinal tracts, dried each salamander sample at 60°C for five days, weighed (dry mass; mg), and homogenized to a powder consistency. Leaf litter samples were dried at 60°C for five days and weighed (mg). Subsequently, whole-body %C and %N of all samples were determined using a Carlo Erba NA 1500 CHN analyzer (Carlo Erba, Milan, Italy). For Ca, Mg, and P analysis, samples were acid-digested (aqua regia double acid; Jones et al., 1991) and analyzed spectrophotometrically (ascorbic acid method). Five random whole leaf litter samples from each of the four unique plots were also analyzed as detailed above. All samples were sent to the University of Georgia Analytical Chemistry Laboratory for analysis.

Previous research at DBCA described the spatial distribution of *P. albagula* abundance across the landscape, finding that abundance was greatest in moist ravines with high canopy cover and low solar exposure (Peterman and Semlitsch, 2013). Spatial abundance estimates were made using binomial mixture models following seven surveys of 135 plots (3 m x 3 m) between 8 April and 28 May 2011. See Peterman and Semlitsch (2013) for full details of sampling and spatial estimation of abundance. Based on 407 unique field measurements of *P. albagula* at DBCA, collected using digital calipers (0.01 mm precision) and a portable digital balance (0.01 g precision), we determined that length was related to mass using the following equation:

$$\log(\text{wet mass}) = -3.288 + 2.869 * \log(\text{SVL}), \qquad (1)$$

which has an adjusted $r^2 = 0.941$. Next, we determined the relationship between wet mass of live *P. albagula* and dry mass from the 44 *P. albagula* collected for the current study using the equation:

$$\text{dry mass} = -88430 + 0201 * \text{wet mass}, \qquad (2)$$

which has an adjusted $r^2 = 0.971$. Abundance estimates from Peterman and Semlitsch (2013) were then converted to densities (salamanders•m⁻²). Using the mean SVL of 407 DBCA *P. albagula* (50.74±SD = 14.90 mm) and equations 1 and 2, we determined the wet and dry mass of an average DBCA *P. albagula*. We then used the dry mass estimate to calculate the amount of each standing stock nutrient (C, N, P, Ca, and Mg) and then extrapolated these per salamander values across the landscape based on the predicted number of salamanders in each 9 m² spatial pixel cell using ArcMap

version 10.1. All spatial analyses were conducted in R (R Core Team, 2014) using the 'raster' package (Hijmans, 2014).

Estimates of standing stock of C, N, P, Ca, and Mg of *P. albagula* were compared to established values of standing stock of *P. serratus* in Missouri (Semlitsch et al., 2014) and plethodontid salamanders, birds, small mammals, and deer from Hubbard Brook Experimental Forest (HBEF) in New Hampshire, USA (Sturges et al., 1974; Burton and Likens, 1975a; Pletscher et al., 1989). Standing stock of C, N, P, Ca, and Mg of leaf litter and *P. albagula* (leaf litter dry mass across all eight plots) were compared using a two-sample *t*-test. All statistical analysis were performed using STATISTICA 12.0 (Statsoft, Inc., Tulsa, OK).

RESULTS

Mean dry mass and nutrient content of *P. albagula* (Appendix 1) and leaf litter collected at DBCA were spatially variable in accordance with the spatial variation in abundance and dry mass (Table 1). Mean estimated dry biomass of *P. albagula* at DBCA was 75.67 (±SD = 69.23) mg•m⁻². Mean estimated standing stock (mg of nutrient•m⁻²) of nutrients of *P. albagula* were spatially variable across DBCA (Fig. 1): carbon: 41.0 (±31.4), range = <0.0000001–1297.8; nitrogen: 10.1 (±7.7), range = <0.0000001–318.7; phosphorus: 2.2 (±1.7), range = <0.0000001–68.6; calcium: 1.2 (±0.9), range = <0.000001–36.8; magnesium: 0.12 (±0.09), range = <0.0000001–3.8 (Table 1). Estimated mean (±SD) leaf litter standing stock of C, N, P, Ca, and Mg was 180,244 (±225,824), 2697 (±3698), 179 (±241), 6493 (±9153), and 974 (±152) mg•m⁻², respectively, and all were significantly greater than *P. albagula* (all two-sample *t*-test *P* values ≤ 0.0001). Mean estimated standing stock of N of *P. albagula* was 2.9, 14.4, 2.3, and 1.7 times greater than those previously reported for plethodontid salamanders in New Hampshire and Missouri, and birds, small mammals, and deer from HBEF, respectively, while mean estimated standing stock of P of *P. albagula* was 3.0–3.1 times greater than plethodontid salamanders at HBEF and Missouri, and 5.1, 54.2, and 1.3 times greater than those reported for plethodontid salamanders, birds, small mammals, and deer from HBEF, respectively (Fig. 2). Standing stock of Ca of *P. albagula* was similar to those previously reported for plethodontid salamanders (1.0 to 1.3 times greater) and 1.7 times greater than birds, but 2.4 and 2.5 times lower than those reported for small mammals and deer at HBEF, respectively (Fig. 2). Standing stock of Mg was similar to reports for small mammals at HBEF and
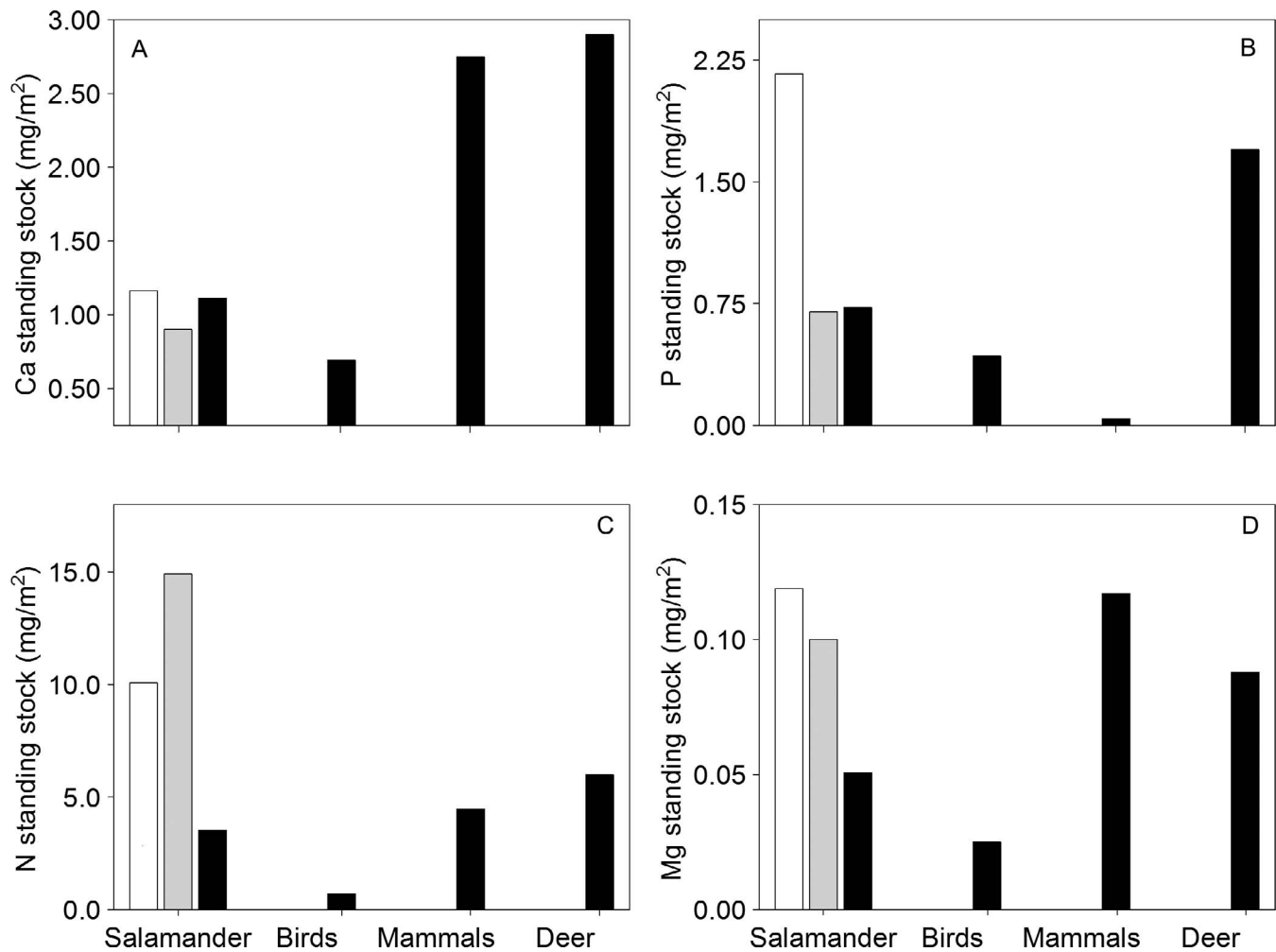
Fig. 2. Estimated mean standing stock of calcium (A), phosphorus (B), nitrogen (C), and magnesium (D) for *P. albagula* in this study (white bars), *P. serratus* from Missouri (gray bars), and plethodontid salamanders (Burton and Likens, 1975a), birds (Sturges et al., 1974), small mammals (Burton and Likens, 1975a), and deer (Pletscher et al., 1989) at Hubbard Brook Experimental Forest in New Hampshire (black bars).

plethodontids from Missouri, but 2.3, 4.8, and 1.4 times greater than previous reports from plethodontid salamanders, birds, and deer at HBEF, respectively (Fig. 2).

DISCUSSION

Comparisons of biomass and nutrient standing stock.—The spatially variable density of *P. albagula* (mean 0.22 salamanders•m^{-2}; range 0.01–0.87; Peterman and Semlitsch, 2013) resulted in large variation of estimated biomass and nutrient standing stock of *P. albagula* at DBCA, but for many nutrients the mean estimates from across the entire focal landscape exceeded those reported for other terrestrial vertebrates in forest ecosystems. For example, biomass of birds (22.2 mg•m^{-2}), small mammals (44.8 mg•m^{-2}), and deer (74.5 mg•m^{-2}) in a New Hampshire forest were lower than our estimates for *P. albagula* at 75.7 mg•m^{-2} (Sturges et al., 1974; Burton and Likens, 1975a; Pletscher et al., 1989). These estimates of plethodontid salamander biomass also compare to systems with higher biodiversity and primary productivity, as biomass of *P. albagula* is within the range or greater than that of diurnal primates, ungulates, and squirrels in a Gabonese rainforest, which ranged from 3.4 to 114, 0.8 to 5225, and 4.2 to 7.2 mg•m^{-2}, respectively (White, 1994). However, plethodontid salamander biomass and standing stock are considerably less than those reported for living

arthropods of the southeastern United States, which range from 1,150 to 3,560 mgBiomass•m^{-2}, 17 to 497.5 mgCa•m^{-2}, and 2.6 mgMg•m^{-2} (Fig. 1; Seastedt and Tate, 1981) and are also less than reports of leaf litter values in this study and Seastedt and Tate (1981). Few studies exist for comparison of nutrient standing stock of vertebrates in terrestrial systems, but those studies from HBEF in New Hampshire and a Missouri Ozark forest show standing stock of many limiting nutrients are comparatively greater in *P. albagula* than deer, birds, small mammals, and *P. cinereus* and *P. serratus* (terrestrial plethodontid salamanders).

Significance of standing stock of P. albagula ***in forest ecosystems.***—Our results suggest *P. albagula* represent a standing stock of nutrients known to limit global plant and algal growth (e.g., Bigelow and Canham, 2007; Elser et al., 2007; Lebauer and Treseder, 2008). Retention of N and P in forest ecosystems is imperative, as P is lost through leaching and N primarily accumulates through biological N fixation largely dictated by P availability (Güsewell, 2004)— and both are limiting nutrients for forest ecosystems. Deposition of strong acids from atmospheric pollution have strong effects on terrestrial ecosystems (Driscoll et al., 2001), and Ca and Mg depletion are considered primary predictors of forest declines in North America (e.g., Horsley et al., 2000; Schaberg et al., 2001; Juice et al., 2006); thus, any

retention of Ca and Mg in forest ecosystems could represent an important link. Vertebrate contributions to nutrient cycles of detrital ecosystems can be significant due to highly labile liquid and solid wastes, and carcasses (e.g., Ruess and McNaughton, 1987). Insect carcasses are more easily decomposed than leaf litter (Seastedt and Tate, 1981) and can subsidize terrestrial nutrient cycles (Polis et al., 1997; Yang and Gratton, 2014), and we suspect plethodontid carcass decomposition is faster than insects due to a lack of chitin. Although plethodontid biomass is lower than invertebrates in North American forest (e.g., Seastedt and Tate, 1981; King et al., 2013), their biomass and nutrient standing stock is greater than many forest-dwelling vertebrates of North America (Fig. 1; Table 1) and could represent a significant portion of forest nutrient cycles.

The spatial heterogeneity of the standing stock of nutrients within *P. albagula* is also of note (Fig. 1). As described in Peterman and Semlitsch (2013), the density and subsequent biomass of *P. albagula* is greatest in ravine habitats. This suggests plethodontid influence on nutrient cycles in ravine habitats could be greater than adjacent habitats. Assimilation rates of *P. cinereus* are between 80–90% and are significantly higher at lower temperatures (Merchant, 1970; Crump, 1979; Bobka et al., 1981). Furthermore, the probability of nutrient retention by *Plethodon* differs across life stages. For example, average daily energy intake day (ingestion) of juvenile *P. cinereus* is 1.8 times greater than daily energy intake in adults, but energy intake is 2.3 times less than energy excretion in juveniles (Crump, 1979). These findings suggests that *Plethodon* inhabiting cooler habitats are likely assimilating more and excreting fewer nutrients, and adult *Plethodon* may play a more prominent role in nutrient retention than juveniles. Considering that ravine habitats have both the highest density of *Plethodon* across DBCA (and predictably have a greater number of adults) and are cooler in temperature compared to the surrounding upland habitat, the heterogeneous distribution of *Plethodon* across DBCA could have greater implications for the spatial heterogeneity of nutrient retention in terrestrial forests with hotspots of nutrient retention being patchily distributed among cool ravine habitats (Fig. 1).

Our estimates of biomass and standing stock of nutrients differs from that of Burton and Likens (1975a), a study that concluded the standing stock of elements in plethodontid salamanders was not large enough to influence intra-ecosystem nutrient cycles in a New Hampshire forest, but are similar or greater than estimates derived in Semlitsch et al. (2014), who show estimates of biomass and standing stock of *P. serratus* in Missouri are significantly greater than those reported by Burton and Likens (1975a). Density estimates and values of percent nutrient content of *P. albagula*, *P. cinereus,* and *P. serratus* are similar (Table 1). However, our estimates of biomass, and standing stock of N, P, Ca, and Mg are 94, 185, 198, 4.5, and 133% greater, respectively, than those reported for *P. cinereus* (Burton and Likens, 1975a, 1975b). Two factors likely contribute to this difference. First, *P. albagula* is a large-bodied plethodontid (Petranka, 1998; Lannoo, 2005) and our mean dry mass values of *P. albagula* are 4.6 and 2.0 times greater than *P. cinereus* from New Hampshire (Burton and Likens, 1975b) and *P. serratus* from Missouri (Semlitsch et al., 2014). Second, Burton and Likens (1975a) used surface counts to estimate population density of *P. cinereus*, which carries the unrealistic assumption that salamanders are perfectly observed (i.e., detection probability = 1). Violation of this assumption leads to an imprecise, often significant underestimation of plethodontid salamander abundance (Bailey et al., 2004; Mazerolle et al., 2007).

Proposed future directions.—To fully understand whether plethodontid salamanders serve important roles in terrestrial nutrient cycles several avenues of research should be explored and combined. We anticipate important opportunities in the following areas: (1) continuing to estimate abundance and density of plethodontid salamanders using methods that account for imperfect detection; (2) expanding our examination of the unique physiological specializations of plethodontid salamanders as proposed by Feder (1983), particularly areas involving the metabolism, energy stores, ingestion, assimilation, and excretion of limiting elements; (3) combining these measures to provide a broader estimate of plethodontid nutrient standing stock in comparison to other vertebrate taxa; and (4) continuing to develop experimental studies to examine ecosystem-level influence of plethodontid salamanders on nutrient cycles (see Hocking and Babbitt, 2014) and compare those estimates to invertebrates and vertebrates in similar systems. In particular, our study and those of Burton and Likens (1975a, 1975b), Semlitsch et al. (2014), and Hocking and Babbitt (2014) were conducted in the Midwestern and Northeastern United States—areas of low plethodontid diversity (Petranka, 1998). Estimates of plethodontid salamander influence on nutrient cycles in the North American Appalachian Highlands, an area considered a global hotspot of plethodontid diversity and abundance, could yield estimates much greater than those reported in our study or other studies involving vertebrate or invertebrates. With the challenges of global climate change and continued land use, plethodontid salamanders will certainly be affected. Ecologists will undoubtedly monitor and track changes to particular species, but examinations into the potential loss of ecosystem functions are important topics that we must continue to examine.

ACKNOWLEDGMENTS

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Appendix 1. Sample size and mean (±1SD) %C, N, P, Ca, and Mg of *Plethodon albagula* at Daniel Boone Conservation Area (Warren County, Missouri) and the linear regression results between *P. albagula* % nutrient content and body mass.

	n	Mean % of dry mass	Linear regression y-intercept	r^2	P
%C	41	46.93 (2.71)	42.635+0.007*dry mass	0.639	≤0.001
%N	41	11.53 (0.61)	12.344−0.001*dry mass	0.460	≤0.001
%P	43	2.48 (0.44)	2.257+0.001*dry mass	0.080	0.066
%Ca	43	1.34 (0.27)	1.102+0.001*dry mass	0.219	0.002
%Mg	43	0.14 (0.02)	$0.136+5.133^{-7}$*dry mass	0.001	0.953