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ARTICLE

Abundance, biomass production, nutrient content, and the possible role of terrestrial salamanders in Missouri Ozark forest ecosystems

R.D. Semlitsch, K.M. O'Donnell, and F.R. Thompson III

Abstract: The transfer of energy and nutrients largely depends on the role of animals in the movement of biomass between trophic levels and ecosystems. Despite the historical recognition that amphibians could play an important role in the movement of biomass and nutrients, very few studies have provided reliable estimates of abundance and density of amphibians to reveal their true importance. Here, we provide robust estimates of abundance and density of a dominant species, the Southern Redback Salamander (*Plethodon serratus* Grobman, 1944), in the oak forest ecosystem of the Ozark Highlands in Missouri. We then use the abundance and density estimates to calculate biomass and nutrient content of salamanders at our study sites in the Ozark forests. Salamanders at the Sinkin Experimental Forest comprise a large amount of protein, energy, and nutrients that greatly exceed estimates derived some 35 years ago in the Hubbard Brook Experimental Forest, New Hampshire. Our estimates (7 300 – 12 900 salamanders·ha^{-1}) are 2–4 times greater than the values reported by Burton and Likens (1975*a*, Ecology, **56**: 1068–1080; 1975*b*, Copeia, **1975**: 541–546). Furthermore, we show that density estimates of other small plethodontid species reported in the literature are nearly an order of magnitude greater than that reported by Burton and Likens. We believe this indicates that previous results have underestimated the importance of salamander biomass, nutrient, and energy flux, and their functional role in regulating invertebrates and carbon retention in forest ecosystems.

Key words: amphibian, biomass, carbon, density, hierarchical models, *Plethodon serratus*, Southern Redback Salamander.

Résumé : Le transfert d'énergie et de nutriments dépend en bonne partie du rôle des animaux dans le mouvement de biomasse entre niveaux trophiques et entre écosystèmes. Même s'il est reconnu depuis longtemps que les amphibiens pourraient jouer un important rôle dans le mouvement de biomasse et de nutriments, très peu d'études ont fourni des estimations fiables de l'abondance et de la densité des amphibiens qui permettraient d'en révéler l'importance réelle. Nous fournissons des estimations robustes de l'abondance et de la densité d'une espèce dominante, la salamandre rayée du Sud (*Plethodon serratus* Grobman, 1944), dans l'écosystème de la forêt de chêne des hautes terres des monts Ozark, au Missouri. Nous utilisons ensuite les estimations d'abondance et de densité pour calculer la biomasse et le contenu en nutriments des salamandres dans les sites d'étude des forêts des Ozark. Les salamandres dans la forêt expérimentale de Sinkin renferment une grande quantité de protéines, d'énergie et de nutriments qui dépasse de beaucoup les estimations obtenues il y a quelque 35 ans dans la forêt expérimentale de Hubbard Brook, au New Hampshire. Nos estimations (7 300 – 12 900 salamandres·ha^{-1}) sont de 2 à 4 fois supérieures aux valeurs rapportées par Burton et Likens (1975*a*, Ecology, **56**: 1068–1080; 1975*b*, Copeia, **1975**: 541–546). En outre, nous montrons que les estimations de la densité d'autres espèces de petits pléthodontidés rapportées dans la littérature dépassent par presque un ordre de grandeur les estimations de Burton et Likens. Nous croyons que cela indique que des résultats antérieurs sous-estimaient l'importance de la biomasse, des nutriments et des flux d'énergie des salamandres et leur rôle fonctionnel dans la régulation des invertébrés et de la rétention du carbone dans les écosystèmes forestiers. [Traduit par la Rédaction]

Mots-clés : amphibien, biomasse, carbone, densité, modèles hiérarchiques, *Plethodon serratus*, salamandre rayée du Sud.

Introduction

The flow of energy and nutrients among organisms has long been recognized as the driving mechanism that maintains ecosystem function (Lindeman 1942; Odum 1971). The transfer of energy and nutrients largely depends on the role of animals in the movement of biomass between trophic levels (Vanni 2002) or translocation of biomass between ecosystems (Polis et al. 1997). Despite the recognition that amphibians could play an important role in the movement of biomass and nutrients within and between ecosystems (Burton and Likens 1975*a*; Davic and Welsh 2004), very few studies have provided any details of standing-crop biomass, energy flow, and nutrient content of amphibians, especially in terrestrial species (Merchant 1970; Burton and Likens 1975*a*, 1975*b*; Seale 1980; Stewart and Woolbright 1996; Petranka and Murray 2001; Beard et al. 2002; Peterman et al. 2008). This lack of information on amphibian biomass, nutrient content, and its flow in ecosystems has limited our ability to understand their role in ecosystem function (Davic and Welsh 2004), and hence to assess the true ecological consequences of their decline or loss (Semlitsch 2003; Wake and Vredenburg 2008), especially among terrestrial woodland salamanders that dominate forest ecosystems in the US (Welsh and Lind 1991; Highton 2005; Welsh and Hodgson 2013).

Salamanders occur in both aquatic and terrestrial ecosystems, can act as both prey for higher trophic levels, and also are predators on aquatic and terrestrial invertebrates at lower trophic

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R.D. Semlitsch and K.M. O'Donnell. Division of Biological Sciences, 105 Tucker Hall, University of Missouri, Columbia, MO 65211, USA.
F.R. Thompson III. USDA Forest Service Northern Research Station, 202 ABNR, University of Missouri, Columbia, MO 65211, USA.
Corresponding author: R.D. Semlitsch (e-mail: SemlitschR@missouri.edu).

levels (Wilbur 1972; Morin 1983; Holomuzki et al. 1994). Furthermore, because of mortality at each stage, dead individuals also provide energy and nutrients to aquatic and terrestrial detritivores (Regester et al. 2006). Salamanders are abundant and comprise a large amount of biomass emerging from wetlands (Gibbons et al. 2006), in riparian habitat adjacent to headwater streams (Peterman et al. 2008), and in deciduous forests (Burton and Likens 1975*b*; Petranka and Murray 2001). Pond-breeding salamanders are thought to be important in controlling the transfer of energy between aquatic and terrestrial ecosystems by the import of eggs into wetlands during reproduction and the export of metamorphosing juveniles that emigrate onto land (Regester et al. 2006). Terrestrial salamanders also generate large amounts of biomass and are purported to exert top-down effects on invertebrate communities, litter decomposition, nutrient recycling, and carbon storage in forest ecosystems (reviewed by Davic and Welsh 2004). However, the role of specific species in ecosystem function has been difficult to elucidate, has yielded contradictory results, and continues to hinder understanding their true ecological value (Wyman 1998; Homyack et al. 2010; Walton 2013; Best and Welsh 2014; Hocking and Babbitt 2014).

Two difficulties are encountered when approaching questions about the role of salamanders in ecosystem function. The first is simply that trophic dynamics are complex, they consist of direct and indirect species interactions, predator–prey relationships are spatially and temporally dynamic, top-down pressure by predators can be context dependent (e.g., litter moisture and season), and prey species often exhibit shorter generation times than predators so they can compensate for losses quickly by density release (Wyman 1998; Walton 2013; Best and Welsh 2014; Hocking and Babbitt 2014). The other difficulty is simply obtaining accurate estimates of salamander abundance needed to calculate biomass, nutrient content, and its associated variance with habitat features or different natural forest ecosystems. Terrestrial salamanders are fossorial, are only surface active on moist cool nights, are seasonally abundant, and have inherently low detection levels (Bailey et al. 2004*a*). Early on, it was determined that as few as 2%–32% of a total population of salamanders reside in the top layer of the forest floor, with the remainder living underground (Taub 1959, 1961). Mark–recapture estimates have since confirmed that only a small fraction of the total population is surface active and detectable during typical field surveys (Kramer et al. 1993; Jung et al. 2000; Bailey et al. 2004*b*). Thus, studies of ecosystem function based on a fraction of the population or a portion of biomass are unlikely to reveal the true importance of salamanders.

The purpose of our study was to provide robust estimates of abundance and density of a dominant species, the Southern Redback Salamander (*Plethodon serratus* Grobman, 1944) (Grobman 1944), in the oak forest ecosystem of the Ozark Highlands in Missouri. We hypothesize that abundance and density of woodland salamanders are higher than found previously based on surface counts that do not account for detection. We then use our abundance and density estimates to calculate biomass and nutrient content of salamanders at our study sites in the Ozark forests. We compare our estimates of density and production to those of other species and regions in the eastern US to better understand the importance of terrestrial salamanders across forest ecosystems. Last, we use a GIS model to project our estimates to the broader landscape of the Salem-Potosi District of the Mark Twain National Forest within the Ozark Highlands ecoregion (Nigh and Schroeder 2002).

Materials and methods

Study site and surveys

We conducted our study at the USDA Forest Service, Sinkin Experimental Forest (1666 ha) within the Mark Twain National Forest, Dent County, Missouri, USA (Figs. 1A, 1B). The Ozark Highlands site consisted of mature (80–100 years old), fully stocked, oak-dominated stands (59% of the basal area—white oak, *Quercus alba* L.; black oak, *Quercus velutina* Lam.; scarlet oak, *Quercus coccinea* Münchh.; northern red oak, *Quercus rubra* L.; Kabrick et al. 2014). Leaf fall occurs primarily from mid-October to mid-November each year. The mean annual precipitation was 130 cm, with 61% occurring from April to September. The mean annual temperature was 14 °C, with a mean summer temperature of 24 °C (June–August) and a mean winter temperature of 2 °C (December–February). The soils developed in parent materials derived from sandstone and dolomite layers of the Roubidoux and Gasconade formations and are highly weathered, droughty, strongly acid, and contain a high percentage of rock fragments (Kabrick et al. 2014).

We conducted repeated surveys for terrestrial salamanders on each of 20 rectangular 5 ha experimental units (≥10 m buffer between units; Fig. 1B), which are each oriented on a slope encompassing a mesic-to-xeric moisture gradient (Kabrick et al. 2014). We established two 10 m × 10 m plots within each unit, yielding 40 survey sites. We randomly selected an area to search based on compass direction from the plot center and then surveyed a different 9 m^2 section of each plot five times in each spring and fall season of 2010–2011; surveys were separated by 7 ± 3.7 days (mean ± SE). Plots were selected at the top (dry) and bottom (moist) of the slope to encompass the moisture gradient within each unit. We conducted diurnal area-constrained searches; each of two observers searched half of each plot in 1 m wide transects by crawling through the 3 m × 3 m plot while hand-raking leaf litter and duff. Natural cover objects (rocks, logs–limbs, bark) were flipped when encountered. Surveys continued until the entire 9 m^2 was thoroughly searched (9.1 ± 2.8 min, mean ± SE); we continually replaced leaf litter and cover objects, ensuring plots were reconstructed upon completion. Each round of sampling lasted until each plot was surveyed once (2–4 days per round). We recorded the sex (juveniles were categorized as any individual ≤31 mm snout–vent length (Herbeck and Semlitsch 2000); males when mental gland and (or) swollen nasolabial grooves were present; females when ova were visible), but some were unidentified. We measured snout–vent length (mm) and live mass (nearest 0.01 g) of each salamander captured. We also recorded the capture location of each individual (leaf litter, rock, woody cover object (WCO)), the total number of rocks and WCOs encountered in each plot, and the diameter of WCOs. Soil temperature using Raytek Mini Temp noncontact thermometer gun and leaf-litter depth (measured to nearest 0.5 cm) were also measured on the edge of each plot before searches started. Individuals were held in bags with leaf litter during searches and returned to their point of capture upon survey completion. Cumulative daily rainfall and air temperature data were obtained from the Sinkin Experimental Forest automated weather station located on site within 1–2 km of experimental units.

Population modeling and density estimates

We used binomial mixture models to estimate abundance and detectability parameters per 9 m^2 plot (Kéry and Schaub 2012). We included the following landscape features as covariates of abundance: aspect, slope, soil water-holding capacity, terrain-shape index, landform index as measured in Kabrick et al. (2014). We specified that the abundance intercept vary either among seasons (season-specific) or among sites and seasons (site-by-season). Abundance estimates from season-specific models tend to be lower, but more precise, than estimates from site-by-season models (K.M. O'Donnell et al., submitted and being revised).[1] We included a site-specific

[1]K.M. O'Donnell, F.R. Thompson III, and R.D. Semlitsch. Partitioning detectability components in populations subject to temporary emigration using binomial mixture models. Submitted and being revised.

random effect to account for additional overdispersion in our counts.

We modeled the overall detection probability as two components (K.M. O'Donnell et al., submitted and being revised):[1] (1) the availability of salamanders for capture and (2) the effective detection probability given availability. We expected our effective detection probability to depend on our sampling protocol and the microhabitat complexity of the plot. We set an informative prior for the conditional capture probability intercept term (our exhaustive searches make it unlikely that many surface-active animals were missed) and included the covariates leaf-litter depth, rocks, and WCO to reflect plot complexity. We included days-since-rainfall, soil temperature, time-of-day, and a quadratic effect of time-of-day as covariates on the availability probability. We also included a site-by-season random effect to account for additional variation in availability.

We fit our models in a Bayesian hierarchical framework using JAGS (Plummer 2003) via the R2jags library (Su and Yajima 2012) within the R environment version 3.1.1 (R Core Team 2013). Prior to analysis, all covariates were standardized to promote Markov chain Monte Carlo convergence. We confirmed convergence using the Gelman–Rubin statistic ($\hat{R} < 1.01$; Gelman and Hill 2007) and performed posterior predictive checks (Bayesian P value) to confirm adequate model fit (Kéry and Schaub 2012).

We projected salamander abundance and biomass for the 2755.8 km^2 Salem-Potosi District of the Mark Twain National Forest, which contains the Sinkin Experimental Forest. We used GIS to calculate predicted abundance in forested areas in the district based on aspect, which was the best predictor of salamander abundance. We used the low and high values of the 95% credible interval for the spring 2010 abundance intercepts to generate a range of potential abundance values.

Nutrient analyses

Salamanders used for nutrient analyses were collected on 30 March 2013 from several areas surrounding but 50–100 m outside our survey plots across the Sinkin Experimental Forest. We collected 30 individuals consisting of 10 males, 10 gravid females, and 10 juveniles. Although some variation in nutrient content may be due to date or season of collection, it is likely very small compared with sex, age, or species differences (e.g., Sterner and George 2000). Animals were weighed to the nearest 0.01 g, frozen, and shipped to the Soil, Plant, and Water Analysis Laboratory, University of Georgia, Athens, Georgia, USA, for nutrient analyses. Individuals were oven-dried at 60 °C to a constant mass and ground using a mortar and pestle. Carbon (%C) and nitrogen (%N) content was determined on dried and ground samples using the LECO TruMac CN combustion analyzer (LECO Corporation, St. Joseph, Michigan, USA). Elemental composition (parts per million (ppm) of calcium (Ca), potassium (K), magnesium (Mg), sodium (Na), phosphorus (P), sulfur (S), zinc (Zn)) was determined by digesting ground samples (Environmental Protection Agency (EPA) 200.2) on the Environmental Express Hot Block (Environmental Express, Charleston, South Carolina, USA), followed by analysis on an Inductively Coupled Plasma (ICP_OES) Spectrometer (EPA 6010b). Nutrient data in percentage and ppm were converted to percentage of dry mass and wet mass for each salamander analyzed, and then converted to standing crop by multiplying by the density estimates of salamanders from our field survey plots.

Results

Salamanders collected at the Sinkin Experimental Forest during 2010 and 2011 consisted of three species that were dominated by 98.7% *P. serratus* with only 1.05% Western Slimy Salamanders (*Plethodon albagula* Grobman, 1944) and 0.21% Long-tailed Salamanders (*Eurycea longicauda* (Green, 1818)) out of 1904 captures on our plots. Although other salamanders, including pond- and stream-breeding species occur in Ozark forests that would contribute significantly to the total production of salamander biomass in forest ecosystems, we focused the remaining analyses only on *P. serratus*, thus yielding a conservative estimate of the importance of salamanders across the region.

We found that effective detection probability of *P. serratus* was low across all seasons (0.42) and sites (0.39). Density of salamanders per 9 m^2 plot, after accounting for detection, was significantly related to aspect and ranged from 4.98 salamanders in southwest-facing plots to 7.56 salamanders in northeast-facing plots (Table 1). Other habitat covariates used in the models did not account for significant amounts of variation in density. We also found that density estimates varied among seasons from 0.51 m^{-2} in fall 2011 to 0.87 m^{-2} in fall 2010 (Table 1). Finally, we found differences in salamander density based on the two models; using a season-specific abundance intercept yielded densities between 0.51 and 0.87 m^{-2}, while using a site-by-season abundance intercept predicted densities between 0.91 and 1.56 m^{-2} (Table 1).

Overall, salamanders contained high amounts of C (47.3%), N (11.0%), Ca (2.99%), and P (2.16%) (Table 2). Nutrient content of salamanders varied among sex and age classes (Table 2). Generally, males and females were different; males were higher in Ca, K, Na, P, S, Zn, and K, lower only in N, but the same in C and Mg. Juveniles were generally intermediate in nutrient content between adult males and adult females. However, males, females, and juveniles all varied significantly in K and Na, with juveniles having higher content of these nutrients than either adult males or adult females (Table 2).

Using the range of densities reported in Table 1 and based on mean wet biomass of *P. serratus* (0.79 g, n = 718), we calculated standing-crop biomass and nutrients for salamanders. The relationship between snout–vent length (mm) and wet and dry body masses (g) is highly predictive and can be used to convert snout–vent length data ($\text{mass}_{\text{wet}} = -0.59 + 0.036 \cdot \text{SVL}$; $R^2 = 0.64$). We show that wet biomass varies from 0.58 to 1.02 g·m^{-2}, dry biomass from 0.18 to 0.32 g·m^{-2}, and protein from 0.529 to 0.934 g·m^{-2} for salamanders (Table 3). These values were then extended to hectares with wet biomass varying from 5.77 to 10.20 kg·ha^{-1}, dry biomass varying from 1.79 to 3.16 kg·ha^{-1}, and protein varying from 5.29 to 9.34 g·ha^{-1} in the Sinkin Experimental Forest (Table 3). We determined that salamanders contained, on average, 69% ± 1.95% water (n = 30) and yielded a mean dry body mass of 0.245 g per salamander (Table 2). Using this value for dry mass per salamander, we then calculated the standing-crop biomass, which ranged from 0.18 to 0.32 g·m^{-2}, for salamanders at the Sinkin Experimental Forest (Table 3). Salamanders also contain fairly large amounts of N (0.020–0.035 g·m^{-2}), C (0.085–0.149 g·m^{-2}), Ca (0.005–0.009 g·m^{-2}), and P (0.004–0.007 g·m^{-2}), especially when extrapolated to amounts per hectare (Table 2). Salamanders contained other nutrients in measurable but lower amounts (Table 2).

A literature review indicated that density estimates varied greatly and depended on location and survey methods for other plethodontid salamanders comparable in size with *P. serratus* (Table 4). As expected, surface counts that did not account for detection probability were generally low (mean = 0.676 m^{-2}, range = 0.0496–2.82 m^{-2}). Density estimates based on mark–recapture or population models accounting for detection probability were generally much higher (mean = 4.51 m^{-2}, range = 0.73–18.46 m^{-2}) (Table 4).

Abundance estimates for the Salem-Potosi District (2755.8 km^2; Fig. 1A) ranged from 1.88×10^9 to 2.65×10^9 salamanders for the area that is 85.4% forested and 14.6% nonforested. These values correspond to density estimates of 0.798–1.125 m^{-2} in the forested areas.

Discussion

Salamanders at the Sinkin Experimental Forest contain a large amount of protein, energy, and nutrients that greatly exceed estimates derived some 35 years ago in the Hubbard Brook Experimental Forest, New Hampshire (2950 salamanders·ha^{-1};

Table 1. Density estimates for Southern Redback Salamanders (*Plethodon serratus*) at Sinkin Experimental Forest, Missouri, USA.

	2010		2011		
	Spring	Fall	Spring	Fall	Mean density (per 9 m²)
Aspect					
0 (southwest)	5.80 (4.40–7.56)	5.92 (4.52–7.59)	4.77 (3.63–6.17)	3.44 (2.56–4.51)	4.98
0.5	6.42 (5.12–8.03)	6.56 (5.30–8.05)	5.28 (4.26–6.53)	3.81 (2.99–4.77)	5.52
1.0	7.12 (5.82–8.67)	7.27 (6.05–8.65)	5.85 (4.82–7.05)	4.22 (3.39–5.15)	6.12
1.5	7.91 (6.81–11.27)	8.08 (6.65–9.72)	6.50 (5.33–7.86)	4.69 (3.74–5.74)	6.79
2.0 (northeast)	8.80 (6.81–11.27)	8.99 (7.13–11.28)	7.23 (5.71–9.07)	5.22 (4.02–6.63)	7.56
Density (per m²) from the model*	0.85–1.56	0.87–1.52	0.70–1.17	0.51–0.91	0.73–1.29

Note: Values presented are derived from repeated sampling over 2 years and calculation of abundance using a binomial mixture model (see Materials and methods) and represent mean density (per 9 m²) and 95% credible intervals (in parentheses). Estimates of mean density (per m²) are also presented in the last row.

*Lower estimate from the model with season-specific abundance intercept; upper estimate from the model with site-by-season abundance intercept.

Table 2. Nutrient content (percentage of dry mass) of Southern Redback Salamanders (*Plethodon serratus*) collected at Sinkin Experimental Forest, Missouri, USA.

Sex group	C	N	Ca	Mg	K	Na	P	S	Zn
Juveniles	47.1 (0.64) ab	11.6 (0.14) a	2.86 (0.22) ab	0.133 (0.0005) a	0.85 (0.022) a	0.772 (0.040) a	2.13 (0.11) ab	0.638 (0.014) a	0.013 (0.0008) ab
Females	48.8 (0.47) a	10.6 (0.14) b	2.60 (0.12) a	0.119 (0.0024) b	0.725 (0.018) b	0.459 (0.010) b	1.95 (0.059) a	0.564 (0.010) b	0.011 (0.0002) a
Males*	46.0 (0.67) b	11.0 (0.21) ab	3.51 (0.23) b	0.132 (0.0039) ab	0.821 (0.018) c	0.596 (0.019) c	2.39 (0.12) b	0.694 (0.023) a	0.015 (0.0010) b
Mean	47.3 (0.40)	11.0 (0.12)	2.99 (0.13)	0.128 (0.0025)	0.814 (0.017)	0.609 (0.028)	2.16 (0.065)	0.632 (0.014)	0.013 (0.0005)

Note: Values are presented as the mean and SE (in parentheses) of 10 individuals (except C and N that had 9 individuals) for each sex group ($n = 30$ total salamanders). Different letters indicate significant effects of sex group ($P < 0.05$).

*Sex determination of adults outside the breeding season is ambiguous, thus this group may contain both adult males and nongravid females.

Table 3. Standing crop of biomass and nutrients of Southern Redback Salamander (*Plethodon serratus*) populations at the Sinkin Experimental Forest, Missouri, USA, based on analyses in Tables 1 and 2.

		Amount (g·m⁻²)		Amount (g·ha⁻¹)	
	Amount per individual (g)	Lower	Upper	Lower	Upper
Biomass					
Wet mass	0.790	0.58	1.02	5769.35	10195.16
Dry mass	0.245	0.18	0.32	1788.50	3160.50
Protein*	0.724	0.529	0.934	5287.25	9343.23
C	0.116	0.085	0.149	846.0	1494.9
N	0.027	0.020	0.035	196.7	347.7
Ca	0.007	0.005	0.009	53.4	94.4
Mg	<0.001	<0.001	<0.001	2.29	4.05
K	0.002	0.001	0.003	14.6	25.7
Na	0.001	0.001	0.002	10.9	19.2
P	0.005	0.004	0.007	38.6	68.2
S	0.002	0.001	0.002	11.3	20.0
Zn	<0.001	<0.001	<0.001	0.23	0.41

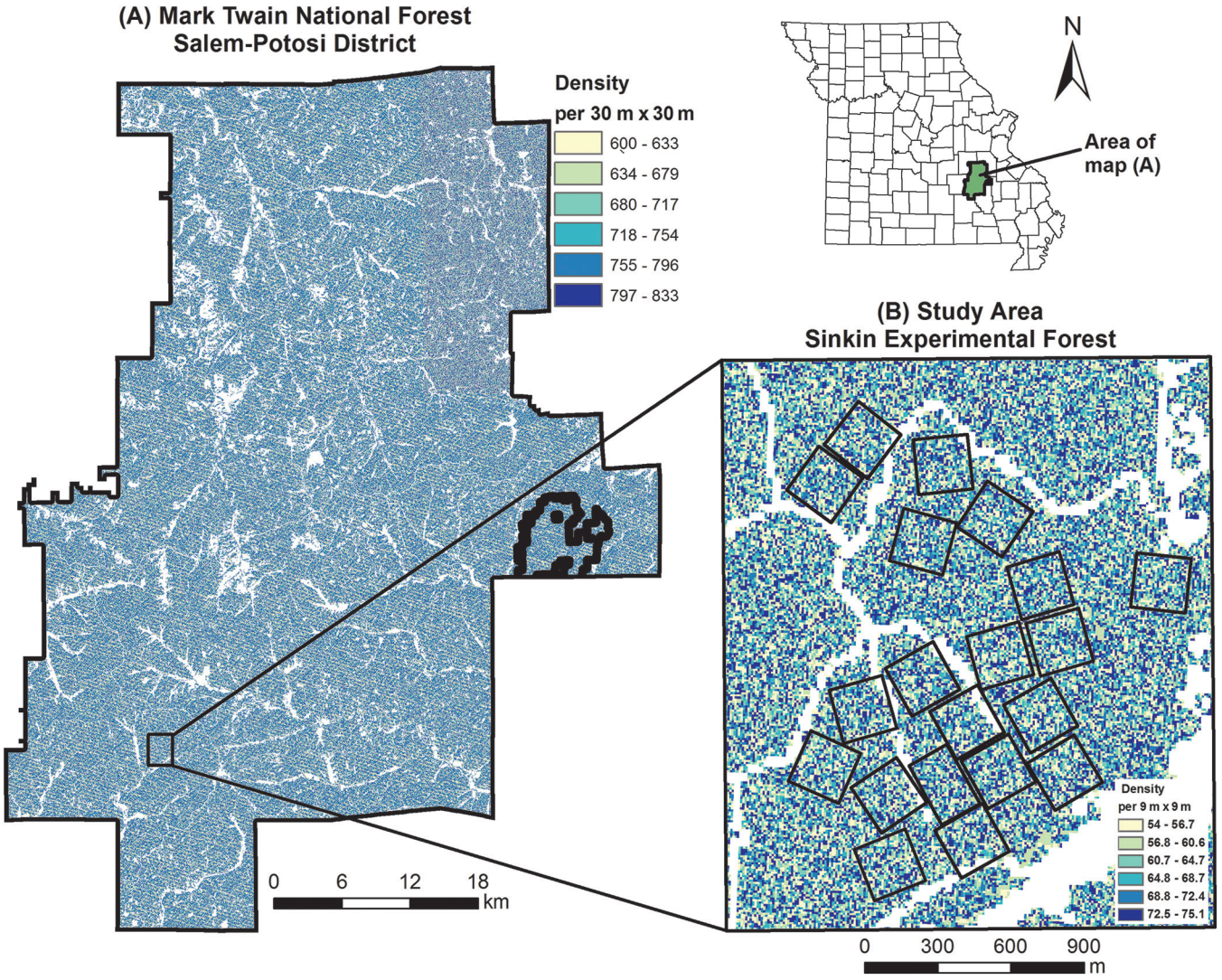
*Protein was determined by multiplying dry mass nitrogen content of salamanders by the standard conversion 6.25 (after Boyd and Goodyear 1971).

Burton and Likens 1975*a*, 1975*b*). Our estimates in Missouri (7 300 – 12 900 salamanders·ha⁻¹) are 2–4 times greater than they report. Furthermore, we show that density estimates of other small plethodontid species reported in the literature are nearly an order of magnitude greater (grand mean of 23 215 salamanders·ha⁻¹) than reported by Burton and Likens (1975*a*, 1975*b*). This greater number of salamanders translates into much greater biomass, nutrients, and energy in forest ecosystems than previously reported. We believe this also supports the argument that previous results have underestimated the importance of salamanders in exerting top-down predatory effects and trophic processes in forest ecosystems, although we acknowledge that geographic variation may account for some differences. Furthermore, we suggest that the impact of salamanders has likely been underappreciated because of the underestimation of salamander abundances based on traditional surface counts that have not taken into account low detection probabilities and variation in habitat quality that is now possible using hierarchical models (Halstead et al. 2012; Kéry and Schaub 2012; K.M. O'Donnell et al., submitted and being revised[1]).

Earlier work has established that terrestrial salamanders likely play a significant role in forest ecosystems based on their efficient conversion of assimilated energy into new tissue that is available for consumption (Burton and Likens 1975*a*). If we assume the production to assimilation ratio of 60.7% reported by Burton and Likens (1975*b*) is appropriate for *P. serratus* in our system, then values of biomass production of *P. serratus* available to other trophic levels is vastly higher. Our study shows that *P. serratus* provides 5 769 – 10 195 g·ha⁻¹ of wet biomass, 5 287 – 9 343 g·ha⁻¹ of protein to forest consumers, and a better source of energy (higher protein and N content) for predators than birds, mice, or shrews (Burton and Likens 1975*a*). Our study also indicates that salamanders may be a significant source of other nutrients for higher trophic levels (e.g., Ca, P). The higher standing-crop estimates at Sinkin Experimental Forest that we documented are based on greater density estimates of salamanders but also on larger mean body size of *P. serratus* (0.79 g body mass) compared with *P. cinereus* at the Hubbard Brook Forest (0.63 g body mass) (Burton and Likens 1975*a*, 1975*b*). Although few systematic studies of salamander predation have been conducted, a review of the literature revealed that many more predators consume small plethodontid salamanders than has been reported in previous studies (Hamilton 1930, 1951; Hurlbert 1970; Table 5). Many of these predators can then become agents of energy and nutrient transfer to other ecosystems, while terrestrial salamanders are nonmigratory and typically remain in small home ranges.

Earlier work also indicates that salamanders likely play a role in regulating invertebrate populations that are responsible for the breakdown of forest leaf litter (Wyman 1998). If we assume that terrestrial salamanders play a role in forest ecosystems (e.g., Wyman 1998; Walton 2005, 2013; Walton and Steckler 2005; Best and Welsh 2014), our study reinforces these past findings, and because of the added biomass revealed through abundance modeling that accounts for detection probability, we suggest it could

Fig. 1. Map of projected Southern Redback Salamander (*Plethodon serratus*) density estimates within (A) the Salem-Potosi District of the Mark Twain National Forest in southeastern Missouri, USA. (B) Study area within the Sinkin Experimental Forest.



magnify any estimates of top-down trophic effects salamanders exert on reducing or regulating leaf-litter prey populations. We acknowledge that some experimental studies have shown no top-down effects of salamanders in forest systems (e.g., Homyack et al. 2010; Hocking and Babbitt 2014). However, we suggest that in addition to geographic variation in climate affecting rates of leaf-litter breakdown and invertebrate population growth, part of the reason may be the use of experimental densities that are lower than actual field densities of salamanders. It is likely that the added salamander density and biomass we found in the Sinkin Experimental Forest may contribute to stronger effects on invertebrate prey as reported in several experimental studies. For example, Wyman (1998) reported a 11%–17% reduction in leaf-litter loss resulting from salamander predation on invertebrates using salamander densities of 0.6–2.0 m^{-2}. Best and Welsh (2014) reported a 5.6%–13.3% reduction in leaf-litter loss using a single salamander density of 0.67 m^{-2}. Furthermore, Walton (2013) used peak salamander densities of only 0.36 m^{-2}. If higher salamander density treatments (or biomass) were used in these past studies that accounted for low detection (e.g., mean high = 4.51 m^{-2} based on mark–recapture or population modeling; Table 4), we would expect a greater reduction in leaf-litter loss in forests, perhaps double or more of what was reported. If true, this could also extend the estimates of C retention in forest ecosystems from 261 to 476 kg·ha^{-1} reported by Wyman (1998) or 200 kg·ha^{-1} reported by Best and Welsh (2014) to an estimate anywhere from 2 to 4 times greater C retention based on the range of densities that we report for Sinkin Experimental Forest or reported for other species in different locations (Table 4).

Our results also emphasize that salamander abundance and biomass varies as a function of aspect at Sinkin Experimental Forest. These results highlight two points: (1) that salamanders are not evenly distributed across the forest landscape and (2) that their role in ecosystem function is likely more concentrated in certain habitats related to aspect. This would result in northeast-facing slopes being hotspots of biomass, nutrients, and energy transfer, and hence functional processes. If the role of salamanders in forest ecosystems is predictably concentrated on such habitat features, in our case more concentrated on northeast-facing slopes, we suggest that conservation and management efforts should be directed more at protecting these high-quality habitats which may also protect forest processes.

Finally, our study reveals greater biomass, nutrients, and energy derived from salamanders in forests of the Missouri Ozark Highlands than previously reported, and likely extends to most forest ecosystems occupied by small woodland salamanders of the

Table 4. Comparison of published natural densities for eastern small terrestrial plethodontid salamanders (Eastern Redback Salamander (*Plethodon cinereus*); Peaks of Otter Salamander (*Plethodon hubrichti* Thurow, 1957); Webster's Salamander (*Plethodon websteri* Highton, 1979); Southern Redback Salamander (*Plethodon serratus*)).

		Density		
Species	Location	No.·m^{-2}	No.·ha^{-1}	References
P. cinereus	Michigan	0.0496*	496	Test and Bingham 1948
P. cinereus	Pennsylvania	0.212*	2 118	Klein 1960
P. cinereus	Michigan	0.43*	4 300	Heatwole 1962
P. cinereus	New Hampshire	0.295*	2 950	Burton and Likens 1975*b*
P. cinereus	Virginia	2.2*	22 000	Jaeger 1979
P. cinereus	Virginia	2.82*	28 200	Mathis 1991
P. cinereus	New York	0.37*	3 700	Wyman and Jancola 1992
P. cinereus	Massachusetts	0.36*	3 600	Mathewson 2009
P. cinereus	Ohio	0.23*	2 300	Walton 2013
P. hubrichti	Virginia	0.24*	2 400	Kramer et al. 1993
		4.5†	45 000	
P. websteri	South Carolina	0.375*	3 750	Semlitsch and West 1983; R.D. Semlitsch, unpublished data
		5.39†	53 900	
P. cinereus	Virginia	0.528*	5 280	Buderman and Liebgold 2012
		3.282†	32 820	
P. cinereus	Virginia	2.8‡	28 000	Jung et al. 2000
		18.46§	184 600	
P. serratus	Tennessee–North Carolina	1.43‡	14 300	Bailey et al. 2004*c*
		2.76§	27 600	
P. serratus	Missouri	0.73‡	7 300	This study (2014)
		1.29§	12 900	
Grand mean		2.32	23 215	

Note: If a study provided more than one estimate of density among sites or years, values were averaged.
*Data based on surface active counts.
†Data based on mark–recapture population estimates.
‡Data based on minimum population model estimates accounting for detection probability.
§Data based on maximum population model estimates accounting for detection probability.

Table 5. Predators of small terrestrial plethodontid salamanders such as the Eastern Redback Salamander (*Plethodon cinereus*).

Predators	References
Spider	Lotter 1978
Centipede	Meshaka and Trauth 1995
Amphibians	
American Bullfrog, *Lithobates catesbeianus* (Shaw, 1802)	Cochran 1911; Hurlbert 1970
Spring Salamander, genus *Gyrinophilus* Cope, 1869	Wright and Haber 1922
Northern Dusky Salamander, *Desmognathus fuscus* (Rafinesque, 1820)	Del Balso 1995; Jaeger et al. 1998
Large salamanders	Ducey and Dulkiewicz 1994
Reptiles	
Snapping Turtle, *Chelydra serpentina* (L., 1758); Painted Turtle, *Chrysemys picta* (Schneider, 1783)	Hurlbert 1970
Garter Snake, *Thamnophis sirtalis* (L., 1758)	Surface 1906; Hamilton 1951; Hurlbert 1970; Burton 1973
Eastern Ribbon Snake, *Thamnophis sauritus* (L., 1766)	Surface 1906
Ringneck Snake, *Diadophis punctatus* (L., 1766)	Jaeger 1971; Lancaster and Wise 1996
Mammals	
Shrew, genus *Sorex* L., 1758	Cochran 1911
Mole shrew, *Blarina brevicauda* (Say, 1823); smokey shrew, *Sorex fumeus* G.M. Miller, 1895	Hamilton 1930
Mole shrew, *Blarina brevicauda*	Jaeger 1971; Burton 1973
Shrew-mole	Dumas 1956
Raccoon, *Procyon lotor* (L., 1758) (adult)	Hurlbert 1970
Birds	
Purple Grackle, *Quiscalus quiscula* (L., 1758)	Cochran 1911
Hermit Thrush, *Catharus guttatus* (Pallas, 1811); Sharp-Shinned Hawk, *Accipiter striatus* Vieillot, 1808	Coker 1931
Screech Owl, genus *Megascops* Kaup, 1848	Stupka 1953
Steller's Jay, *Cyanocitta stelleri* (Gmelin, 1788)	Dumas 1956
Dipper, genus *Cinclus* Borkhausen, 1797	
Sparrow Hawk, *Accipiter francesiae pusillus* (Gurney, 1875); Red-tailed Hawk, *Buteo jamaicensis* (Gmelin, 1788)	Hurlbert 1970
Other birds	Bent 1948, 1949, 1958, cited in Lannoo 2005

family Plethodontidae. Based on the wide-spread distribution of woodland salamander species in most forested landscapes, the functional role of salamanders may extend to large forested areas of the eastern and western US (Davic and Welsh 2004). Our study has revealed that these salamanders can reach high densities, and by accounting for detectability, we confirm the notion that populations are very large because the majority of individuals are below ground and unavailable for sampling. Furthermore, by combining modeling with fine-scale abundance sampling and GIS analyses of ecologically important habitat features related to abundance in forest systems, it is possible to project our estimates to wider landscapes. For example, if the values we report here are representative of the wider Ozark forest system that encompasses the Salem-Potosi District of the Mark Twain National Forest, based on the same abundance model we developed for the Sinkin Experimental Forest (Fig. 1A; accounting for 14.6% nonforested habitat and varying aspect), then we estimate 1.88–2.65 billion salamanders representing 1485.2–2093.5 metric tons of wet biomass are distributed across a region of 2755.8 km^2. We suggest that salamanders play an even greater role in trophic transfer of energy and nutrients, as well as C retention, in forest ecosystems than previous reported and their decline or extinction is likely to have cascading trophic effects that are currently underappreciated (but see Best and Welsh 2014).

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