

Research



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Range-wide salamander densities reveal a key component of terrestrial vertebrate biomass in eastern North American forests

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Characterizing the population density of species is a central interest in ecology. Eastern North America is the global hotspot for biodiversity of plethodontid salamanders, an inconspicuous component of terrestrial vertebrate communities, and among the most widespread is the eastern red-backed salamander, *Plethodon cinereus*. Previous work suggests population densities are high with significant geographic variation, but comparisons among locations are challenged by lack of standardization of methods and failure to accommodate imperfect detection. We present results from a large-scale research network that accounts for detection uncertainty using systematic survey protocols and robust statistical models.

We analysed mark–recapture data from 18 study areas across much of the species range. Estimated salamander densities ranged from 1950 to 34 300 salamanders ha⁻¹, with a median of 9965 salamanders ha⁻¹. We compared these results to previous estimates for *P. cinereus* and other abundant terrestrial vertebrates. We demonstrate that overall the biomass of *P. cinereus*, a secondary consumer, is of similar or greater magnitude to widespread primary consumers such as white-tailed deer (*Odocoileus virginianus*) and *Peromyscus* mice, and two to three orders of magnitude greater than common secondary consumer species. Our results add empirical evidence that *P. cinereus*, and amphibians in general, are an outsized component of terrestrial vertebrate communities in temperate ecosystems.

1. Introduction

Characterizing the scale and variation in population density across a species' range is a central interest of ecology. Changes in species' abundance and distribution have accelerated in recent history due to anthropogenic drivers such as climate change [1] and biological invasions [2]. The pace and scale of environmental changes make characterizing the variation in population density at large geographic scales an important baseline for addressing fundamental and applied questions in ecology [3]. Understanding ecosystem function, the capacity to test hypotheses about the patterns and drivers of range-wide variation in abundance, and the ability to set reasonable conservation goals, all require accurate and precise quantification of population densities across large geographic areas [4,5]. Statistically sound monitoring efforts covering large geographic extents are invaluable for testing ecological theory and forecasting the response of populations to large-scale perturbations, such as understanding the effects of climate change on ecosystems [6–8].

Patterns in species abundance can have multiple generating mechanisms including physiological, genetic, environmental and community interactions [9]. A major theory in ecology predicts that a species shows a pattern of declining density at range edges (the 'abundant centre' [10] and 'abundant core' hypotheses [11]), resulting from a constant relationship between demographic rates and environmental conditions, which become decreasingly suitable towards the range edge. Finding support for drivers of variation in density may also be confounded by local adaptation of populations to environmental conditions which vary across a species range [12]. Revealing underlying mechanisms of range-wide patterns requires unbiased estimates of species abundances.

For many species, estimating population densities is constrained by our ability to accurately observe populations. This difficulty is especially true for terrestrial salamanders that spend much of their life underground and unavailable for detection [13–15]. Though terrestrial vertebrates are estimated to be a relatively small proportion of the Earth's total biomass [16], many vertebrate taxa have disproportionate influences on ecosystem function through their trophic position, ability to engineer ecosystems and the human value assigned to them [17–20]. Much of the research on the role of high-biomass species, however, has been focused on large mammals and highly visible taxa. Examples from North America include the roles of white-tailed deer (*Odocoileus virginianus*) in shaping forest ecosystems [21–24], of wolves (*Canis lupus*) in the function of western systems [25,26], of beavers (*Castor canadensis*) as ecosystem engineers [20,27], or of the now extinct passenger pigeon (*Ectopistes migratorius*) in eastern forests [28].

There is evidence that terrestrial plethodontid salamanders in general, and the red-backed salamander (*Plethodon cinereus*) specifically, occur at high densities in eastern North American forests [29]. However, our knowledge of true salamander population densities (table 1) is imperfect as most estimates are derived from count surveys [32,41–43] or single-field season mark–recapture studies [38,44–46]. The difficulty in generating accurate estimates of density is typical of salamanders using subterranean habitats and reflects the challenges of measuring species with cryptic behaviours more generally [47].

To address this challenge, we estimated local densities of the red-backed salamander using robust and consistent mark–recapture methods for 18 forested study areas across much of the species range (figure 1). These data have been collected by a collaborative and coordinated research network, which we call the Salamander Population and Adaptation Research Collaboration network (SPARCnet). We then use these data for two purposes. First, we examine patterns in seasonal and latitudinal variation in population density. We expected seasonal differences in population density related to temporal differences in population dynamics, and that densities would be related to position in the geographic range (where latitudinal gradients exist in climate and land use across the species range). Second, we use these data to estimate local salamander biomass, correcting for imperfect detection, and compare these to estimates of biomass for other vertebrate species in North America known to influence ecosystem processes. We demonstrate that the red-backed salamander has substantial biomass among terrestrial vertebrate species in these ecosystems. The expected ecological impact of their high density is further amplified by their position as predators in the forest floor food chain, contributing to their outsized role in these systems.

2. Methods

At 18 locations throughout the red-backed salamander range (figure 1), SPARCnet researchers installed 3–9 study plots, each consisting of a regularly spaced array of coverboards, which facilitate capture by mimicking natural cover habitat [14,15,48]. All sites were located in the temperate forest ecoregion, except the Hubbard Brook plots which are in the northern forest type (electronic supplementary material, table S1). All arrays consisted of 50 pine or fir 30 × 30 × 2.5 cm coverboards in a 5 × 10 m grid with 1 m spacing between boards. Coverboards were first sampled after at least 10 weeks to allow time for salamander discovery and colonization. Though sites were not selected completely randomly, they were chosen without prior

Table 1. Red-backed salamander (*P. cinereus*) densities across populations as reported in the literature. For the method, capture mark–recapture is abbreviated as CMR and spatial capture–recapture is abbreviated as SCR. SPARCnet is the Salamander Population and Adaptation Research Collaboration network.

state	density (salamanders per ha)	reference	method
Michigan	476	[30]	count
Michigan	4900	[31]	count
New Hampshire	2632	[32]	count
New York	5000	[33]	count
Massachusetts	1189	[34]	count
Ohio	1850	[35]	count
Virginia	22 000	[36]	count
Virginia	28 200	[37]	count
Pennsylvania	2118	[38]	CMR
New Hampshire	15 300	[39]	CMR
Virginia	32 800	[40]	CMR
18 locations across much of the species range	11 580	SPARCnet Average (this study)	SCR
Virginia	34 300	SPARCnet (this study)	SCR

knowledge of salamander densities (i.e. we did not intentionally select sites with particularly high salamander densities). Sampling with the use of coverboards is limited to seasonal windows as surface activity is constrained by conditions such as temperature and moisture. Timing of tolerable surface conditions varies latitudinally but generally occurs within spring (March–May) and autumn (September–November), and this is true of all SPARCnet sites apart from the southernmost site (Richmond, VA) where salamanders are typically surface-active from October to May. Arrays were sampled on an average of 4.4 occasions (range 0–8 sampling occasions) within an individual sampling season, and plots were sampled between 2013 and 2019 (electronic supplementary material, tables S1 and S2). Individual salamanders were given unique marks using visible implant elastomer (Northwest Technology Inc.), a fluorescent polymer with high retention rates that does not affect growth, survival or reproduction in amphibians [49–51].

The true density of red-backed salamanders was estimated using spatial capture–recapture methods [14,15,52], which describe the number and distribution of individuals within a pre-determined area, known as the state space (S). In this analysis, S was defined as an area including the array plus a 3.6-m buffer around the array, which encompasses the home ranges of all individuals exposed to capture [53]. A 0.25-m resolution state space was used in our analysis (in which cells, s , describe the location of coverboards and the locations between and surrounding coverboards considered as potential activity centres). The encounter model defines detection data as y_{ijk} (where $y = 1$ if captured, 0 if not) for each individual (i), at each coverboard (j) and on each occasion (k), and our encounter model assumes that detection under a coverboard is a multinomial process (a ‘multicatch’ model that allows individuals to be captured only under a single coverboard per sampling event [14]), where we allow for heterogeneity in detection probability based on the proximity of coverboards to individuals’ activity centres. The detection probability (p_{ijk}) of an individual at a coverboard is assumed to decrease with the distance between the coverboard (at location \mathbf{x}_j) and the individual’s activity centre (\mathbf{s}_i); a capture at the activity centre has a probability p_{0ijk} . The parameter σ describes how rapidly capture probability declines with distance and is informative of space use [52] in the half-normal model:

$$p_{ijk} = p_{0ijk} \times \exp(-\text{dist}(\mathbf{x}_j, \mathbf{s}_i)^2 / 2\sigma^2).$$

We model pixel-specific density, D , and σ using a log-linear model. The D and σ parameters are modelled with effects of season, where β_0 are intercepts and β_v are estimated regression coefficients:

$$\text{logit}(p_{ijk}) = \beta_0 + \sum_v \beta_v X_v,$$

$$\log(D(s_i)) = \beta_0 + \sum_v \beta_v X_v.$$

Based on previous studies within the network [14,15,53–55], an effect of season (i.e. autumn and spring) was estimated for D and σ in all models except for that of Richmond, VA, a site that does not have multiple discrete activity seasons across the survey periods (electronic supplementary material, table S1). We combine all years of data for the analysis and generate season-specific average density estimates for each site. Similarly, a behavioural effect (b) is included in the detection model in which individuals were more likely to be captured on consecutive occasions, corresponding to a correlation in surface activity. All analyses were conducted in the open-source statistical computing environment R [56] using the oSCR package for fitting models [57]. We plotted the resulting densities for each location and season to investigate seasonal and patterns of density.

We queried the global animal density database TetraDENSITY [58] and summarized the taxonomic composition for the 100 highest-density North American taxa in the database (measured in animals per square kilometre), as well as median and maximum densities for each of the four terrestrial vertebrate classes (Amphibia, Reptilia, Mammalia and Aves).

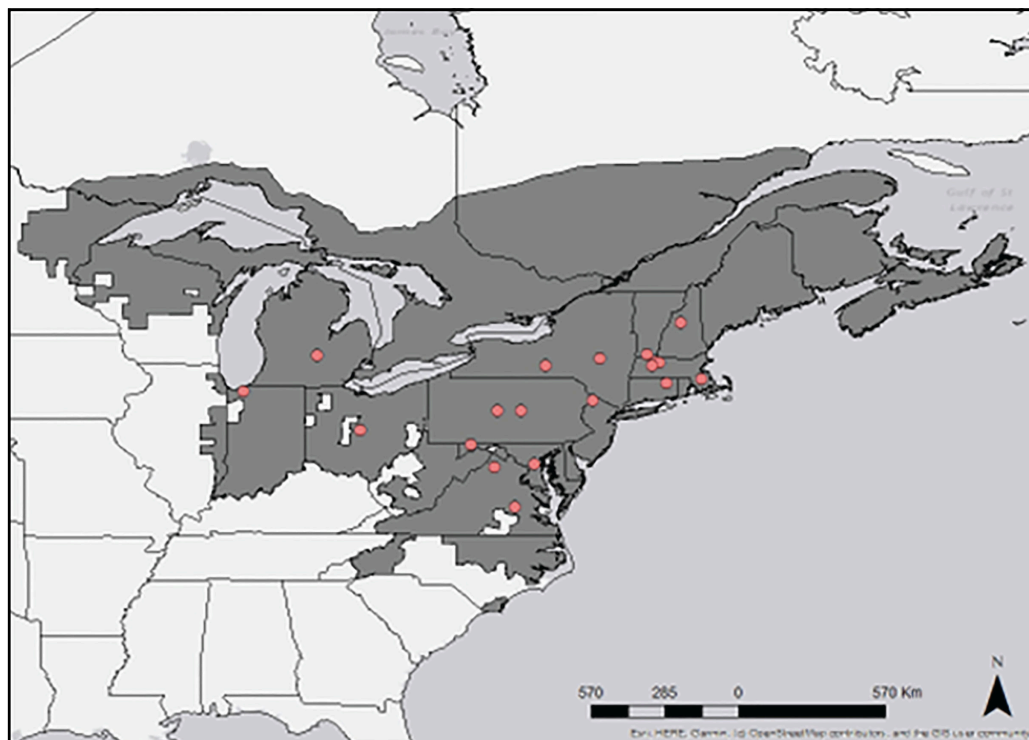


Figure 1. Distribution of study sites (red circles) within the red-backed salamander (*P. cinereus*) range (dark grey) across North America.

To compare among species with large differences in body size, we calculated the wet biomass (kg km^{-2}) for red-backed salamanders in our study areas and for a comparison set of other vertebrate species that co-occur in eastern North American forest ecosystems, had large geographic ranges and for which reliable density estimates were available. Our goal was not to be exhaustive but instead to allow for a general comparison to other high-biomass terrestrial vertebrate species in other taxa and at different levels of the food chain. Estimates of biomass for red-backed salamanders were based on our density estimates and the mean mass of salamanders across our study areas [59]. The species we chose for comparison included three primary consumers: historic estimates of passenger pigeons (*Ectopistes migratorius*) in nesting colonies; white-tailed deer based on low, medium and high-density estimates for eastern North America; and study-specific estimates for *Peromyscus maniculatus* and *P. leucopus* (deer mouse and white-footed mouse). We also included a common mammalian and avian omnivore, American black bear (*Ursus americanus*) and wild turkey (*Meleagris gallopavo*). Finally, we included two secondary consumers, coyote (*Canis latrans*) and red-tailed hawk (*Buteo jamaicensis*). For each species, we calculated biomass in kilograms per square kilometre using estimates of density and mean mass from primary literature sources (summarized in §3).

3. Results

Across the sampled portion of the red-backed salamander range, our mean estimated density was 11 580 salamanders ha^{-1} (1 157 9700 salamanders km^{-2}). There was a large variation in site-specific densities, where mean densities for each of our study areas ranged from 1950 to 34 300 salamanders ha^{-1} (figure 2). USGS-collected data can be found in Grant [60]. Overall mean densities in the autumn (11 500 salamanders $\text{ha}^{-1} \pm 8300$ s.d.) were similar to spring densities (11 600 ± 8600 s.d.). We found that some areas had seasonal differences in density, but without a clear pattern; eight sites had higher mean densities in autumn than spring and six sites had higher spring densities (figure 2). A quadratic fit to the spring and autumn data shows a minimum density around 41.5° latitude, with increasing density towards the southern and northern study areas (figure 3).

Among the 2617 records in the TetraDENSITY database for the most common North American terrestrial vertebrate species (i.e. records for continental US, Canada and Mexico [58]), only 131 records were for species from class Amphibia. Despite this, 90 of 100 records with the highest densities across all 2617 vertebrate records were for Amphibia (all with more than 45 000 individuals km^{-2} (450 individuals ha^{-1})); the remaining 10 records were for lizard species in class Reptilia. Among the 90 records in class Amphibia, 82 were from the order Urodela in the family Plethodontidae, and 55 of the records were for the genus *Plethodon*. Our estimated median density of the red-backed salamander was 996 500 salamanders km^{-2} (9965 salamanders ha^{-1}). The maximum density for any amphibian was 9 140 000 individuals km^{-2} (91 400 individuals ha^{-1}) for the invasive *Eleutherodactylus coqui* in Hawaii; the median density for all of the Amphibia records was 1 430 000 individuals km^{-2} (1430 individuals ha^{-1}). This median density was greater than the maximum observed density for any Reptilia records and more than 10 times the maximum density observed for records for any mammal or bird species. The median density for Reptilia, Mammalia and Aves, was 895.5 individuals km^{-2} (8.955 individuals ha^{-1}), 136.9 individuals km^{-2} (1.369 individuals ha^{-1}), and 22.5

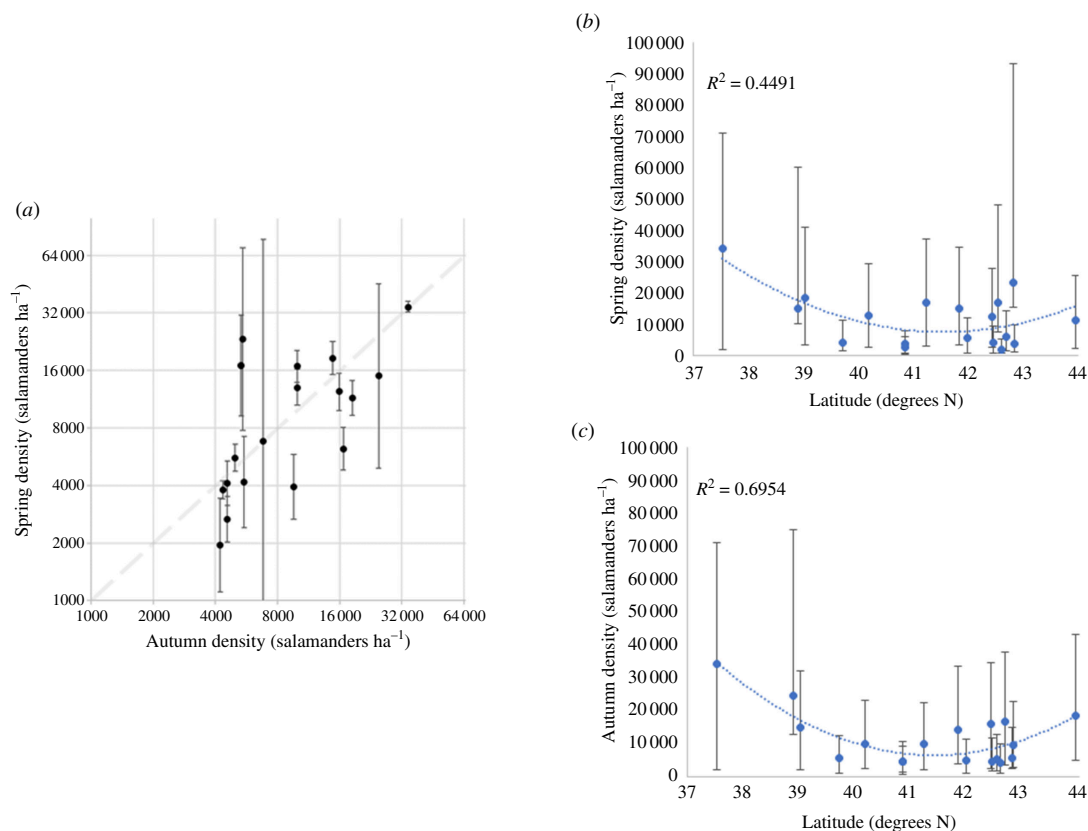


Figure 2. Estimated (a) salamander densities (and 95% confidence intervals) for spring and autumn sampling seasons for each of the 18 SPARCnet study areas in our study. The diagonal grey dashed line denotes equivalent spring and autumn densities. (b,c) Mean estimates (and 95% confidence intervals) of salamander densities for SPARCnet study sites versus latitude for both spring (b) and autumn (c) sampling seasons. The blue dotted line is a quadratic fit to the data, and the R^2 is the coefficient of determination.

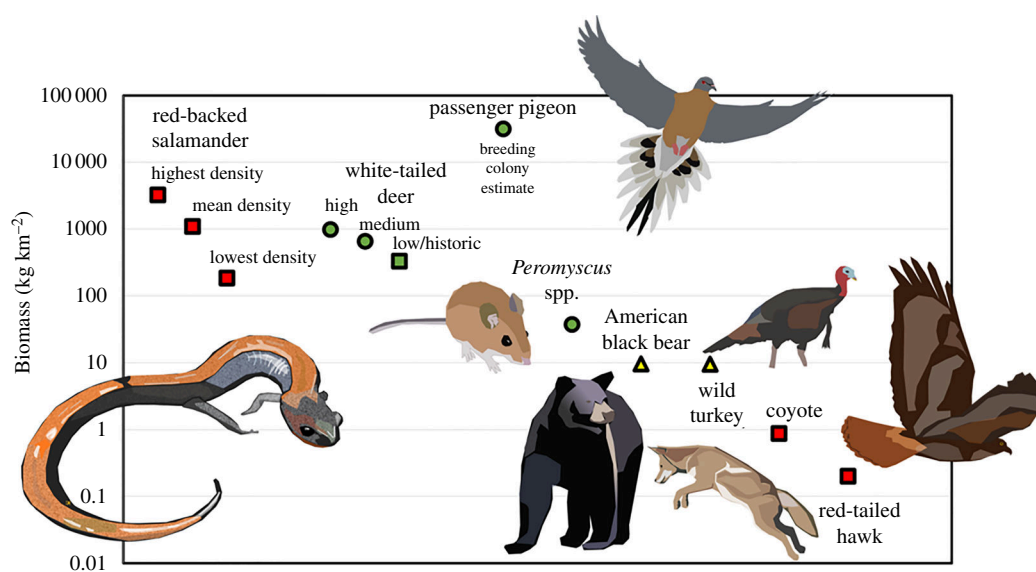


Figure 3. A comparison of red-backed salamander (*P. cinereus*) densities estimated in this study to biomass estimates for common vertebrates in terrestrial North American temperate forest ecosystems.

individuals km⁻² (0.225 individuals ha⁻¹), respectively ($n = 227, 1256$ and 1003). These patterns are consistent with global trends summarized in [61].

Figure 3 shows our calculated biomass values for other species with large geographic ranges that share habitat with the red-backed salamander. The average biomass of salamanders in our study plots was comparable to highly abundant herbivores, similar to estimates for high-density white-tailed deer populations, and more than an order of magnitude greater than *Peromyscus* spp. populations. Our highest-density SPARCnet site (Richmond, VA) had a salamander biomass equivalent to one-sixth of estimates for breeding colonies of passenger pigeon. When compared with omnivore species, average densities of red-backed salamanders were more than two orders of magnitude higher for biomass, and more than three orders of magnitude higher than densities for the other strictly carnivorous species.

4. Discussion

Using mark–recapture data, we demonstrate that the red-backed salamander occurs at consistently high densities. Based on our estimates, we find that red-backed salamanders may account for up to 13 times the biomass reported in the seminal study from one site in New Hampshire, USA [32]. Furthermore, the average salamander biomass we estimated is greater than endothermic primary consumers such as white-tailed deer and deer mice that have well-documented impacts on the function and structure of eastern North America forests [62,63]. When comparing the biomass of the red-backed salamander to other secondary consumers, we find that they are a clear outlier within terrestrial ecosystems in eastern temperate forest ecosystems. Their biomass exceeds that of highly abundant avian and mammalian omnivores and carnivores by two to three orders of magnitude. Given the top position of red-backed salamanders in many forest floor food chains ([64]; but see [65]), they are therefore likely to have a comparatively large role in ecosystem processes among vertebrate species in these systems. Summarizing information in the TetraDENSITY database reveals that there are other amphibian species that occur at high local densities, suggesting that greater attention to the role amphibians play in driving ecosystem processes is deserved.

Importantly, our use of standardized survey protocols and spatial capture–recapture methods allow direct estimation of true population densities while accommodating for observation errors and allowing comparison among locations. We found wide variation among populations across the species range sampled (figures 2 and 3). Forest salamanders have low detection rates, in part because of their cryptic behaviour and subterranean habitat use [13,66]. Despite being a hidden component of forest biodiversity, salamanders' high biomass means that they likely play an important role in forest ecosystem functioning [47,67] while their specific contribution to a forest patch may be expected to vary among sites [65]. Our study is not the first to infer that plethodontid salamanders occur at high densities. Previous estimates of density based on count data (table 1) also suggest among-population variation in densities, though most are likely substantial underestimates of density due to imperfect detection and are difficult to compare because of different survey and estimation methods. Indeed, when capture probabilities are accounted for in density estimates—both in our study and in other studies (table 1)—much higher densities are reported.

Although we found high variation in density among populations, we did not find a simple pattern of density by latitude aligned with an 'abundant centre' expectation [10,11], which may result from multiple mechanisms. While factors such as climate and land use are correlated with latitude, other drivers of population density may be exerting an influence. First, the observed pattern in density may reflect the glacial history of the region. Ice sheets in the Pleistocene spanned most of the red-backed salamander's range but did not reach where we estimated density to be highest (Richmond, VA). Evidence of recolonization north from southern refugia following glaciation has been found in red-backed salamanders [68–70], though northern refugia may have existed [71], complicating an expected latitudinal trend in density. However, we lack data from a large portion of the northern extent of the range (figure 1), so fully characterizing the relationship between salamander density and glacial history cannot be tested without additional data. Alternatively, land-use history and site-level factors (e.g. soil characteristics, leaf litter type) may have stronger effects on populations than environmental gradients, which vary latitudinally. Finally, populations may be locally adapted to their environment [59], resulting in similar densities despite dissimilar conditions. Variation in environmental conditions across the range may be expected to result in lower densities on range edges that represent climactic extremes. However, local variation in environmental gradients, physiological sensitivity to environmental temperature and moisture and the limited dispersal ability of the salamander [72–74] may promote local adaptation among populations, resulting in more similar densities on the range-wide scale than would be expected [59].

Densities of red-backed salamanders are expected to respond to environmental change, which may make them good forest indicator species [67,75]. Increasingly warm summer temperatures slow growth rates in red-backed salamanders, which is ultimately expected to have negative effects on population growth [76]. Furthermore, between two periods in which red-backed salamanders are not surface-active in most of their range (summer and winter), mortality is higher in summer [76] and thus, annual mortality may be expected to increase along with summer temperatures and lengthening of summer seasons. Identifying additional physiological constraints would inform expectations for future response to climate change. If local adaptation underlies the among-site variation in density, warmer and drier conditions resulting from climate change may have population-level consequences for this dispersal-limited species.

Summarizing information from the TetraDENSITY database reveals that there are other amphibian species that also occur at high densities, warranting greater attention to the role amphibians play in structuring ecosystem processes. The cryptic behaviour and life histories of many amphibians make it difficult to precisely quantify population densities at large scales, which we overcome for red-backed salamanders using spatial capture–recapture methods and the SPARCnet coordinated research network. Continuing to improve coverage of sampling will help further characterize the range-wide variation in density and better estimate the importance of these species.

The difficulty in generating accurate estimates of density is shared for other subterranean-dwelling salamanders and is emblematic of challenges for estimating population densities and dynamics of cryptic species in general [47]. This deficiency is important to address considering expectations for shifts in environmental conditions resulting from land use and climate changes [77–80], which may influence local population densities of amphibians. More research conducted at the scale of species' ranges would help to understand factors governing densities of other high-biomass amphibian species and provide information to estimate contributions to ecosystem functioning.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. Data and code related to this manuscript are available on Dryad [81].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. E.H.C.G.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, supervision, validation, visualization, writing—original draft, writing—review and editing; J.F.: conceptualization, data curation, formal analysis, investigation, methodology, project administration, resources, validation, visualization, writing—original draft, writing—review and editing; E.B.: data curation, writing—review and editing; A.B.B.: data curation, writing—review and editing; J.L.B.: data curation, writing—review and editing; C.D.: data curation, writing—review and editing; K.E.: data curation, writing—review and editing; M.E.: data curation, writing—review and editing; M.C.F.-R.: data curation, writing—review and editing; B.G.: data curation, writing—review and editing; K.L.G.: data curation, writing—review and editing; N.T.H.: data curation, writing—review and editing; R.H.-P.: data curation, writing—review and editing; D.J.H.: data curation, writing—review and editing; A.H.: data curation, writing—review and editing; M.L.: data curation, writing—review and editing; M.G.M.: data curation, writing—review and editing; T.J.H.M.: data curation, writing—review and editing; L.M.: data curation, writing—review and editing; D.M.: conceptualization, data curation, writing—review and editing; W.P.: data curation, writing—review and editing; V.P.: data curation, writing—review and editing; C.S.: data curation, writing—review and editing; S.C.S.: data curation, writing—review and editing; C.S.: data curation, writing—review and editing; L.M.T.: data curation, writing—review and editing; A.R.W.: data curation, writing—review and editing; A.D.W.: data curation, writing—review and editing; K.Y.: data curation, writing—review and editing; D.A.W.M.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, supervision, validation, visualization, writing—original draft, writing—review and editing.

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