esa ECOSPHERE

Can the eastern red-backed salamander (*Plethodon cinereus*) persist in an acidified landscape?

Cheryl A. Bondi,[1] Colin M. Beier,[1,2,†] Peter K. Ducey,[3] Gregory B. Lawrence,[4] and Scott Bailey[5]

[1]*Graduate Program in Environmental Science, College of Environmental Science and Forestry, State University of New York, Syracuse, New York 13210 USA*
[2]*Department of Forest and Natural Resources Management, College of Environmental Science and Forestry, State University of New York, Syracuse, New York 13210 USA*
[3]*Biological Sciences Department, State University of New York, Cortland, New York 13045 USA*
[4]*United States Geological Survey, New York Water Science Center, Troy, New York 12180 USA*
[5]*United States Department of Agriculture Forest Service, Northern Research Station, North Woodstock, New Hampshire 03262 USA*

Citation: Bondi, C. A., C. M. Beier, P. K. Ducey, G. B. Lawrence, and S. Bailey. 2016. Can the eastern red-backed salamander (*Plethodon cinereus*) persist in an acidified landscape? Ecosphere 7(4):e01318. 10.1002/ecs2.1318

Abstract. Hardwood forests of eastern North America have experienced decades of acidic deposition, leading to soil acidification where base cation supply was insufficient to neutralize acid inputs. Negative impacts of soil acidity on amphibians include disrupted embryonic development, lower growth rates, and habitat loss. However, some amphibians exhibit intraspecific variation in acid tolerance, suggesting the potential for local adaptation in areas where soils are naturally acidic. The eastern red-backed salamander (*Plethodon cinereus*) is a highly abundant top predator of the northern hardwood forest floor. Early research found that *P. cinereus* was sensitive to acidic soils, avoiding substrates with pH < 3.8 and experiencing decreased growth rates in acidic habitats. However, recent studies have documented *P. cinereus* populations in lower pH conditions than previously observed, suggesting some populations may persist in acidic conditions. Here, we evaluated relationships between organic horizon soil pH and *P. cinereus* abundance, adult health (body size and condition), and microhabitat selection, based on surveys of 34 hardwood forests in northeastern United States that encompass a regional soil pH gradient. We found no associations between soil pH and *P. cinereus* abundance or health, and observed that this salamander used substrates with pH similar to that available, suggesting that pH does not mediate their fine-scale distributions. The strongest negative predictor of *P. cinereus* abundance was the presence of dusky salamanders (*Desmognathus* spp.), which were most abundant in the western Adirondacks. Our results indicate that *P. cinereus* occupies a wider range of soil pH than has been previously thought, which has implications for their functional role in forest food webs and nutrient cycles in acid-impaired ecosystems. Tolerance of *P. cinereus* for more acidic habitats, including anthropogenically acidified forests, may be due to local adaptation in reproductively isolated populations and/or generalist life history traits that allow them to exploit a wider resource niche.

Key words: acidic deposition; generalist; local adaptation; northern hardwood forests; *Plethodon cinereus*; soil acidity; woodland salamanders.

Received 10 April 2015; revised 30 September 2015; accepted 5 December 2015. Corresponding Editor: G. Middendorf.

Copyright: © 2016 Bondi et al. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† **E-mail:** cbeier@esf.edu

Introduction

Environmental changes caused by human activities create new abiotic and biotic conditions that may fall outside the tolerance limits for which some species evolved (Vitousek et al. 1997, Tilman and Lehman 2001). Rapid change to environments can lead to declines and local extirpations of populations unable to persist in novel conditions, interrupting their roles in ecosystem processes. Forests of northeastern North America have undergone changes due to acidic deposition, nitrogen inputs, and forest compositional shifts—all of which alter biogeochemical cycles and terrestrial ecosystems (Likens et al. 1970, Federer et al. 1989, DeHayes et al. 1999, Driscoll et al. 2001, Lovett et al. 2009). Deposition of sulfuric and nitric acids accelerates the loss of essential nutrients (Ca, Mg, K) from forest soils, and in areas where base cation supply is insufficient to neutralize acid inputs, soil acidification can occur (Johnson et al. 1994, Warby et al. 2009). Decreases in soil pH, alongside depletion of essential nutrients, introduce novel and potentially stressful conditions to local flora and fauna to which some species may not be adapted. On the other hand, soil habitats that are naturally acidic due to local interactions between bedrock, climate, and vegetation may harbor native populations that are tolerant to increases in acidification and maintain a diverse and functional ecosystem. In addition, generalist species that have greater plasticity in their physiology and life history may be more tolerant of a wide range of environmental conditions and persist in altered habitats, providing some degree of resilience to environmental changes (Richmond et al. 2005).

Many amphibian species are sensitive to soil and water acidity, although species and populations adapted to naturally occurring acidic conditions may be more resilient to decreases in pH. Acidic conditions in aquatic habitats disrupt development, delay and reduce hatching success, and increase sodium loss from amphibian embryos (Gosner and Black 1957, Pough 1976, Freda and Dunson 1985a,b). In terrestrial environments, soil acidity negatively impacts amphibian density and species richness (Wyman 1988, Wyman and Jancola 1992), growth rates, and ion regulation (Wyman and Hawksley-Lescault 1987, Frisbie and Wyman 1992). While some species are relatively sensitive to acidity, others exhibit considerable tolerance, such as those that breed in acidic bogs (e.g., *Lithobates (Rana) virgatipes* and *Hyla andersoni)* and acidic woodland pools (e.g., *Lithobates (Rana) sylvaticus* and *Hyla femoralis*) (Gosner and Black 1957, Pierce 1985, Freda and Dunson 1986).

In addition to interspecific differences in tolerance to acidity, some species display considerable intraspecific variation in tolerance, which suggests local adaptation and geographic variation in physiological responses to environmental acidity (Pierce 1985). Intraspecific variation has been reported for survival and development of amphibian embryos to acidic waters including *Ambystoma maculatum* and *L. sylvaticus* (Cook 1983, and reviewed in Pierce 1985); these studies provide evidence that environmental acidity may act as a selective pressure in local species evolution. Natural soil acidity varies widely across the northeastern United States due to local geological conditions and topography (Bailey 2000), which may set the stage for geographic variation in the acid tolerance of generalist amphibian species.

Terrestrial salamanders are abundant predators in forest ecosystems and play a significant ecological role in forest food webs and nutrient cycling (Davic and Welsh 2004, Semlitsch et al. 2014). Reductions in salamander populations and local extirpations may lead to trophic cascades and have ecosystem level consequences (Burton and Likens 1975, Best and Welsh 2014). The eastern red-backed salamander (*Plethodon cinereus*) is the most abundant salamander—and perhaps the most abundant vertebrate (Burton and Likens 1975)—in the hardwood forests of northeastern North America and southeastern Canada. *Plethodon cinereus* is a top predator in the soil detritus food web, and its density and distribution regulate invertebrate assemblages and their roles in decomposition and nutrient cycling (Wyman 1998, Rooney et al. 2000, Walton et al. 2006, Walton 2013). Previous research has shown that *P. cinereus* is sensitive to acidic soils and avoid substrates with a pH below 3.8 (Wyman and Hawksley-Lescault 1987, Wyman 1988, Wyman and Jancola 1992, Sugalski and Claussen 1997) and are found in greater abundances in forests with higher soil pH and base

cation availability (Beier et al. 2012). Laboratory experiments have shown that *P. cinereus* exposed to acid substrates between pH 3–4 have reduced growth rates, while substrate pH < 3 caused increased sodium efflux rates and acute mortality (Wyman and Hawksley-Lescault 1987). Overall these studies indicate that very acidic soils can compromise the habitat quality and health of *P. cinereus*, resulting in lower abundance or local extirpation, especially in acid-impaired forests with lower pH than occurs naturally in the region.

However, recent research suggests that some local populations of *P. cinereus* are more tolerant to acidic soils than previously thought. Moore and Wyman (2010) described a population of *P. cinereus* in the Lake Clair Watershed of eastern Canada where the pH of the forest floor was 3.0–3.2 and the pH of the upper mineral soil was 3.8–4.1 (Houle et al. 1997). This population suggests that at least some *P. cinereus* individuals can live in very low pH habitats, but to draw broader conclusions about acid tolerance beyond this single site and population, further study is needed. Because of their significant ecological role in forest ecosystems it is important to understand how these abundant vertebrates respond to variation in soil acidity, and whether they persist in acidic forests or are absent from these areas.

We investigated whether *P. cinereus* is sensitive to acidic soils in northern hardwood forests by evaluating the hypothesis that this species' abundance, body condition, and adult body size would decrease as soil pH decreased (i.e., as acidity increases). A gradient design incorporating 34 upland hardwood forests was used to represent the breadth of regional variation in soil acidity of northern hardwood forests, which ranges from base-rich to naturally acidic and anthropogenically acidified soils (Bailey 2000, Driscoll et al. 2001). We evaluated relationships between organic soil horizon pH and salamander population metrics across the 34 upland forests, and tested whether substrate pH influenced microhabitat selection of the forest floor at a subset of sites. We predicted that if acidic soils are unfavorable to *P. cinereus,* we would observe lower abundance, smaller body size, and poorer body condition at sites with low soil pH, and at the microhabitat scale this salamander would select substrates with higher soil pH.

Materials and Methods

Study region and site-level soils and vegetation data

We conducted this study at 34 northern hardwood forests located within the White, Green, and Adirondack Mountains of the northeastern United States (Fig. 1). The study region is part of the New England physiographic province within the Appalachian Highland division. Lithology varies considerably across the region; near-surface bedrock and parent material includes granite, quartzite, dolomite, marble, schist, amphibolite, and biotite gneiss in the Green and White Mountains, whereas anorthosite underlies large areas in the central Adirondacks (Bailey 2000). Soils of the region are dominated by Spodosols and surficial deposits are glacial till. Variability in soil texture, lithology, and topographic position contributes to spatial heterogeneity in soil acidity, which represents both natural conditions and those exacerbated by acidic deposition (Sullivan et al. 2013). These sites are characterized as mature hardwood forests with sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), and yellow birch (*Betula alleghaniensis*) dominant in the overstory, with red spruce (*Picea rubens*) and balsam fir (*Abies balsamea*) present at higher elevations. The sites have varying topography with an elevation range 250–885 m, and slopes between 0% and 68% (Table 1).

Previous research measured soil chemistry at our study sites, allowing us to sample a gradient of soil acidity in northern hardwood forests (Table 1). At 32 of the sites (excluding Bartlett-C82 and Bartlett-C85) soil pH was measured using 0.01 mol/L $CaCl_2$ extraction. Soil data at 16 sites in the White and Green Mountains (excluding Bartlett-C82 and Bartlett-C85) are a composite of three soil pits from the Oa/A horizon (see methods in Horsley et al. 2008). In the Adirondack Mountains, soils data are averages of either four (T-24-2, T-24-5, T-16-2, T-16-4; G. Lawrence unpublished data) or three (all other Adirondack sites) soil pits from the Oa horizon (see methods in Lawrence et al. 2008, Page and Mitchell 2008). Soil samples from Bartlett Experimental Forest (Bartlett-C82 and Bartlett-C85) in the White Mountains were collected from the Oa horizon and pH was measured in water (2:1 volume: mass) with constant stirring (Multiple Element

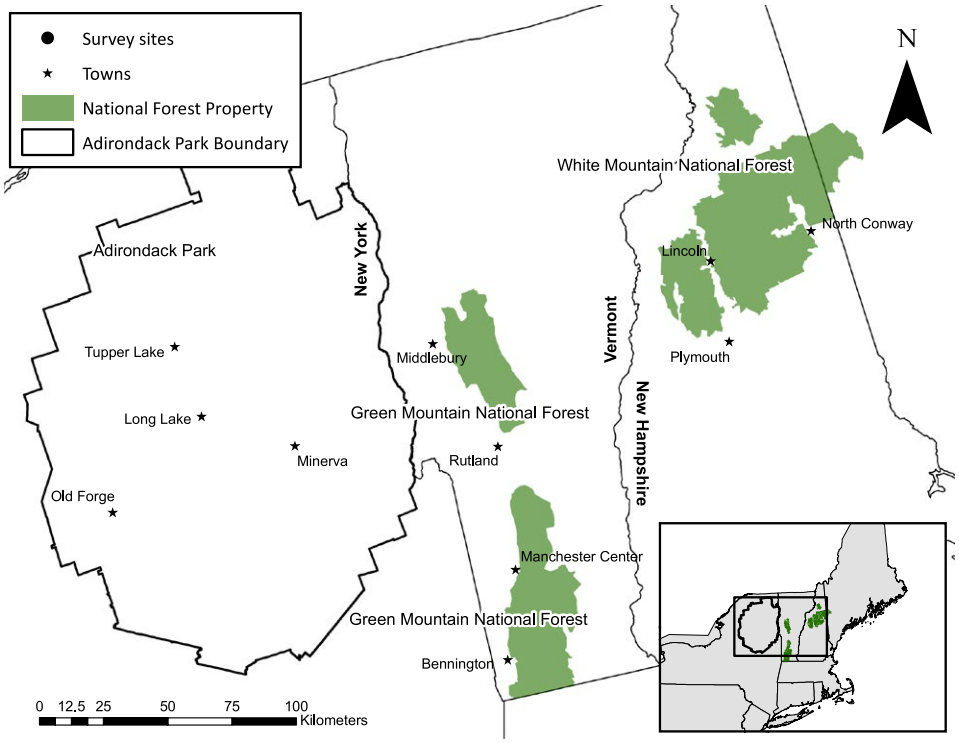

Fig. 1. Map of the study region and survey sites in New York, Vermont and New Hampshire (USA).

Limitation in Northern Hardwood Ecosystems project, http://www.esf.edu/melnhe/, unpublished data). This method yields a higher pH value compared with $CaCl_2$ extraction, so these sites may fall higher on the soil pH gradient than if they were measured using salt extraction (Ross et al. 2015). The mean soil pH across all sites is 3.62 (Table 1), site VTBC01 has the lowest pH (2.73) and VTEQ04 has the highest (5.54).

Salamander abundance and microhabitat selection

We performed time-constrained active cover searches for terrestrial salamanders in the summers of 2011 (White and Green Mountain sites) and 2013 (T-24-2, T-24-5, T-16-2, T-16-4 Adirondack sites) between June and August. At each site, surveys were centered on the location where previous soil sampling had occurred and searches did not exceed more than a 25 m distance from the starting location to avoid entering areas with different soil chemistry. Searches were done by three observers for 30 min and were focused on cover objects of the forest floor and involved searching beneath course woody debris, bark, fern mats, and rocks, and capturing all salamanders encountered (if a salamander escaped then the species was noted). Salamanders were identified to species and measured for total length (TL), snout to vent length at anterior angle (SVL), and maximum head width (HW), using digital calipers to the nearest 0.1 mm, and body mass was measured to the nearest 0.5 g with a handheld spring scale (Pesola, Switzerland[1]). We also incorporated data from previous surveys by Beier et al. (2012) in June 2009 at 12 sites in the Adirondack Mountains which involved the same search effort.

We measured the canopy tree composition at each site using fixed radius plots that were placed within the center survey plot. In these plots we recorded species, abundance, and diameter at breast height (DBH; 1.3 m) of canopy trees (DBH ≥ 5 cm). To measure ground cover we randomly placed 4–1 m^2 quadrats within the center plot and visually estimated the percentage ground cover of herbaceous plants, coarse woody debris, rocks, seedlings, and ferns.

Table 1. Soil chemistry, forest cover type, and field characteristics for study sites in northeastern United States.

Region and Site	Soil pH	Latitude	Longitude	Elevation†	Slope†	Aspect‡	Deciduous overstory	Conifer over-story	Total tree basal area
Adirondack Mountains									
T-24-05	2.88	43.53468	−74.86005	708	19	SW	0.82	0.18	27.02
T-16-02	2.95	43.53347	−74.85342	716	26	S	0.96	0.04	29.97
BasicBuck§	3.03	43.74012	−74.71065	646	15	N	0.94	0.06	25.05
T-24-02	3.11	43.53563	−74.86092	713	23	S	0.88	0.12	34.22
T-16-04	3.29	43.53361	−74.84910	716	12	NW	0.85	0.15	30.18
28011§	3.52	43.64996	−74.67657	655	30	N	1.00	<0.01	27.89
HWF15§	3.62	44.00433	−74.24788	627	5	S	0.79	0.21	47.37
NSpec§	3.63	43.53142	−74.38695	609	25	SE	1.00	<0.01	29.70
27026§	3.80	43.69843	−74.74988	619	30	E	0.94	0.06	24.22
Mason§	3.86	43.59337	−74.42912	582	20	E	1.00	0.00	44.01
28030§	3.87	43.75045	−74.73892	567	15	S	0.99	0.01	27.61
24001§	4.03	43.76776	−74.71442	561	20	NE	0.84	0.16	34.28
330T§	4.09	44.24080	−74.34871	520	0	N	0.99	0.01	24.29
28014§	4.10	43.63881	−74.68411	668	20	N	0.96	0.04	28.93
NWoods§	4.12	43.80930	−74.05002	487	35	W	1.00	0.00	44.96
HWF14§	5.04	44.00382	−74.24552	624	25	SW	0.90	0.10	51.29
Green Mountains									
VTBC01¶	2.73	44.09015	−73.05123	589	15	SW	0.98	0.02	34.55
VTWD01¶	2.81	43.36733	−72.9128	654	13	SE	1.00	<0.01	34.51
VTTV01¶	3.40	43.38507	−72.84328	672	33	N	1.00	<0.01	49.32
VTOJ01¶	3.44	43.36156	−72.93236	515	15	SW	1.00	<0.01	35.44
VTEQ02¶	3.68	43.16293	−73.09455	481	15	E	1.00	0.00	28.00
VTEQ01	5.03	43.15896	−73.10113	641	68	E	1.00	0.00	45.66
VTEQ04	5.54	43.16018	−73.09677	499	55	E	1.00	0.00	37.29
White Mountains									
NHCP06	2.98	43.90879	−71.60963	606	45	S	0.86	0.14	30.12
NHJB02	3.05	44.03342	−71.88412	843	28	SW	1.00	0.00	38.78
NHBO06	3.18	43.92865	−71.39465	885	60	E	0.91	0.09	39.89
NHJB01¶	3.22	44.03436	−71.89082	720	26	SW	1.00	0.00	23.47
NHCP05¶	3.30	43.90723	−71.61177	578	23	SE	1.00	0.00	30.58
NHBO01	3.44	43.92779	−71.38683	624	7	E	1.00	0.00	29.65
NHBO09	3.55	43.91608	−71.38078	475	27	E	1.00	0.00	37.80
NHWH01¶	3.84	43.98785	−71.90552	444	28	NE	1.00	0.00	62.91
NHSC01¶	3.89	43.97367	−71.18802	250	7	S	1.00	0.00	44.92
Bartlett-C82	4.04	44.054121	−71.29917	351	19	NE	0.99	0.10	35.57
Bartlett-C85	4.16	44.053793	−71.29767	333	11	NE	1.00	0.00	30.22

† Estimated from USGS 10-m digital elevation model (United States Geological Survey, National Elevation Dataset) for sites in the Adirondacks, Bartlett-C82, and Bartlett-C85. At other sites elevation and slope were measured in the field.

‡ Estimated from USGS 10-m digital elevation model.

§ Data compiled from surveys done in the Adirondacks in summer of 2009 by Beier et al. (2012).

¶ Sites where surface soil cores were collected in 2012 at salamander use and random locations.

We used generalized linear models to analyze *P. cinereus* abundance in relation to soil acidity, vegetation characteristics, abundance of other salamander species, and survey field conditions. Models used a Poisson distribution with log-link function and were compared using Akaike's Information Criterion corrected for small sample sizes (AICc), using maximum likelihood estimation of parameters. The independent variables were: organic soil horizon pH, presence of *Desmognathus* spp. (*D. fuscus* and *D. ochrophaeus*), slope, aspect, elevation, proportion of total basal area of deciduous overstory trees, ground cover, and moisture conditions. We included percentage of coarse woody debris and ferns (ground cover variables) to account for differences in habitat

structure of the forest floor that can influence the abundance of *P. cinereus* at a site (Grover 1998). Cumulative precipitation 24 h prior to a survey was included as a proxy for forest floor moisture because salamanders come out from cover objects following rain events to forage, increasing their abundance in the leaf litter (Taub 1961, Heatwole 1962, Jaeger 1972, 1980, Grover 1998).

We used resource selection analysis to determine whether salamanders select substrates with higher pH. We compared the acidity of locations where salamanders were collected to random locations at a subset of sites (n = 9) in the White and Green Mountains in summer 2012 (Table 1). At each salamander collection point (location) we collected the top 10 cm of the Oa/A horizon using a soil corer, and then replicated this core sample in a location selected using a random direction and distance within 10 m of the salamander's location. A total of 190 matched pairs were collected from the forest floor using this method. Soil samples were air-dried, sieved to remove wood pieces and rocks, homogenized (10 g) with distilled deionized water to make a paste, and measured using a bench pH meter (Mettler Toledo, Ohio, USA).

A generalized linear mixed effects model was used to test whether salamanders select microhabitats of the forest floor with higher pH. We tested the main effects of site (nine levels), soil core (salamander used vs. random location), and the interaction of site*soil core on soil pH. We added a random effect to account for the known correlation between salamander and random locations due to site-level differences in soil pH. Pairwise differences in soil pH at salamander and random locations by site were assessed following Tukey–Kramer adjustment. The soil pH used by juveniles was compared to that used by adults using a t-test.

Body condition and adult body sizes

Body condition indices are used to quantify the mass of an individual associated with energy reserves after the mass associated with components of the body has been accounted for (Schulte-Hostedde et al. 2005). We used the residuals from an ordinary least squares regression of log transformed body mass on a linear measure of body size (log of TL) to represent the mass associated with body reserves (Schulte-Hostedde et al. 2005, Welsh et al. 2008).

$$\log(\text{body mass}) = \beta_0 + \beta_1 \times \log(\text{total body length}) + \delta$$

A salamander with a positive residual has higher body mass than would be predicted based on its total length and is considered to be in better condition than an individual with a negative residual value. Because body condition changes with age and there is considerable variation in juvenile body sizes, we calculated residual indices for adults only to represent health of the reproducing individuals of the population. To compare adult body sizes and condition we used individuals greater than 35 mm SVL (N = 236) because that is the minimum size when adults are mature in northern latitudes (Leclair et al. 2006). We used Spearman rank-order correlation to measure the strength of the association between adult body condition and sizes (SVL and mass), and site-level organic soil pH. Statistical analyses were done using version 11.0 JMP statistical software (SAS Institute Inc., Cary, North Carolina, USA) and the significance of association was tested at α = 0.05.

Results

Salamander abundance and soil acidity

We observed a total of 366 *P. cinereus* from surveys in 2011 (Green and White Mountains) and 2013 (Adirondack Mountains; sites T-24-2, T-24-5, T-16-2, T-16-4). To these data we added observations from 96 additional *P. cinereus* in the Adirondack Mountains based on 2009 surveys by Beier et al. (2012). The lowest *P. cinereus* abundance was one individual at site 28014 in the Adirondacks and the maximum was 33 individuals at VTEQ02 in the Green Mountains (Fig. 2).

There was no association of *P. cinereus* abundance with soil pH along the gradient represented among sites (Fig. 2). Based on AICc scores, the soil pH model of *P. cinereus* abundance had less support than a null model (Table 2). The model including presence of *Desmognathus* spp. and aspect had the most support in explaining *P. cinereus* counts per unit of search effort. There were fewer *P. cinereus* where *Desmognathus* spp. were present ($\beta = -0.70$, $P < 0.001$) and on north facing slopes ($\beta = -1.03$, $P < 0.001$). The amount of rainfall the day before the survey and percent cover

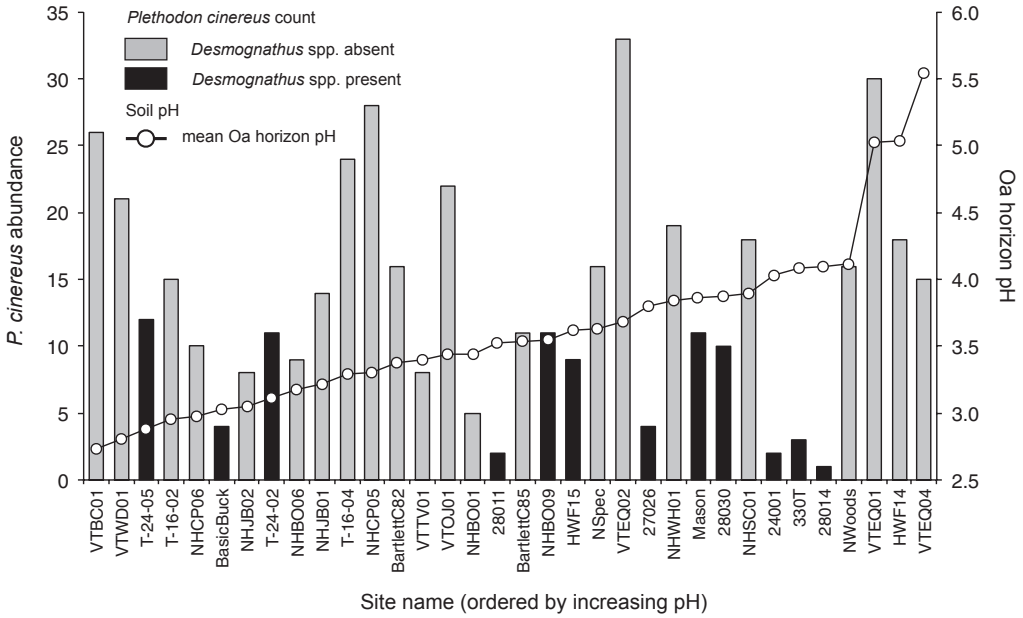

Fig. 2. Counts of *Plethodon cinereus* observed per search effort (left *y*-axis) at 34 upland hardwood forests in the northeastern United States. Site order represents a gradient of soil pH (Oa horizon) of northern hardwood forests across the region (right *y*-axis). Bars shaded in black indicate where dusky salamanders (*Desmognathus* spp.) were also present.

Table 2. Generalized linear models of *Plethodon cinereus* abundance in upland hardwood forests (n = 32) as a function of environmental factors and presence/absence of dusky (Desmognathus spp.) salamanders, using Poisson distribution with log-link function.

Model	Parameters	Estimate	P value	AICc	Δ AICc
Desmognathus spp. + Aspect	9	–	–	240.3	–
Desmognathus spp.	1	−0.68	<0.001	–	–
North slope	1	−1.11	<0.001	–	–
Desmognathus spp.	2	−0.96	<0.001	252.0	11.7
Aspect	8	–	–	265.3	25.0
North slope	1	−1.41	0.000	–	–
Percent deciduous cover	2	2.38	0.004	316.7	76.4
Elevation	2	−0.00	0.005	317.8	77.5
Null	1	–	–	323.2	82.8
Slope	2	0.00	0.14	323.3	83.0
24 h rain (cm)	2	0.04	0.487	325.0	84.6
Percent woody debris	2	0.00	0.820	325.4	85.1
Soil pH	2	0.05	0.485	325.0	84.7

of coarse woody debris did not have support in the model comparison (Table 2). Because *Desmognathus* spp. were primarily observed at sites in the Adirondacks, we reevaluated the models excluding sites where *Desmognathus* spp. were present ($n = 12$). For these sites, the soil pH model had less support than the null model (ΔAICc > 2) and was not a significant predictor of *P. cinereus* abundance ($P = 0.39$).

Body condition and adult body sizes

We collected morphometric data on a total of 440 *P. cinereus* (Table 3). Of these, 54% observed were classified as adults (mean SVL

Table 3. Summary of morphometric measurements of Plethodon cinereus populations in 34 northern hardwood forests in the Adirondack, Green, and White Mountains (USA).

		Snout to vent length (mm)		Mass (g)	
	N	Mean (SD)	Range	Mean	Range
Adirondack Mountains					
Adult	96	39.0 ± 3.1	35.0–49.0	0.90 ± 0.2	0.5–1.6
Juvenile	60	26.8 ± 5.8	14.5–34.6	0.44 ± 0.3	0.1–1.2
Green Mountains					
Adult	49	38.8 ± 2.6	35.0–46.4	0.93 ± 0.2	0.6–1.5
Juvenile	93	27.7 ± 5.7	15.6–34.8	0.47 ± 0.3	0.05–1.2
White Mountains					
Adult	91	40.1 ± 3.0	35.0–49.7	0.88 ± 0.2	0.4–1.6
Juvenile	51	28.3 ± 4.3	16.5–34.9	0.37 ± 0.2	0.1–0.8
All sites	440				
Adult	236	39.4 ± 3.0	35.0–49.7	0.89 ± 0.2	0.4–1.6
Juvenile	204	27.6 ± 5.4	14.5–34.9	0.43 ± 0.2	0.05–1.2

= 39.4 mm; mean body mass = 0.89 g) and 46% were juveniles (mean SVL = 27.6 mm; mean body mass = 0.43 g).

Body size and condition of adult *P. cinereus* did not vary with soil acidity (Fig. 3). Adults had similar body sizes across the soil pH gradient, and there were no correlations between soil pH and SVL (Fig. 3a; $\rho = 0.07$; $P = 0.34$) or mass (Fig. 3c; $\rho = -0.01$, $P = 0.90$). The body condition of adults did not vary with soil pH (Fig 3b; $\rho = -0.02$, $P = 0.72$).

Acidity of microhabitats

Across a subset of sites ($n = 9$), the mean pH at locations occupied by *P. cinereus* (4.47) closely approximated the mean pH at random locations (4.46; Fig. 4). The most frequently used substrates had a pH range between 3.8 and 4.4 (42% of observations), and 12% of *P. cinereus* were found at locations with pH < 3.8. The lowest soil pH used by an individual *P. cinereus* was 3.49 at two sites (NHCP05 and VTBC01). Juveniles (SVL < 35 mm) were found on substrates less than 3.8 pH approximately 13% of the time. Juveniles were observed in microhabitats with pH similar to that of adults ($T = 1.12$, $P = 0.23$).

Plethodon cinereus did not select locations of the forest floor with a significantly different pH than locations randomly available in the immediate vicinity (Fig. 5). There was no significant effect of soil core location (salamander use vs. random) on forest floor pH ($P = 0.60$; $F = 0.26$). Salamanders occupied substrates with significantly different pH values among the 9 sites ($P < 0.0001$; $F = 59.7$), with the lowest mean pH of 3.77 (±0.18) at VTBC01 and highest of 5.24 (±0.58) at VTEQ02.

However, the actual pH range of microhabitats where *P. cinereus* were observed may be more likely between pH 2.7–4.3. We note that pH values reported above in the habitat selection analysis, based on soil cores, may be overestimated by 0.7–1.0 pH units relative to the site-level pH measures. For example, the site-level pH of 2.73 at VTBC01 is roughly ten times more acidic than the average forest floor pH of 3.77 measured via soil cores. This discrepancy was due to laboratory assay methods of the soil cores (pH in water) vs. site-level ($CaCl_2$ extraction) to measure pH (Ross et al. 2015).

Discussion

We found no relationship between soil acidity and the abundance or health of eastern red-backed salamanders in northern hardwood forests, based on the most extensive surveys conducted to date, in terms of geographic variation and across a range of soil acidity. We observed *P. cinereus* populations in five forests with extremely acidic soils (pH < 3.0), which was unexpected given that lethal pH limits for *P. cinereus* have long been thought to be pH 2.5–3.0 (Wyman and Hawksley-Lescault 1987). *Plethodon cinereus* used microhabitats with similar pH to randomly chosen locations in their environment, suggesting that pH does not limit fine-scale distribution on the forest floor at these sites. Overall our results suggest *P. cinereus* can persist across a wide range of habitat acidity, including anthropogenically acidified soils resulting from chronic sulfate and nitrate deposition (Driscoll et al. 2001).

Our findings contrast with foundational studies of *P. cinereus* tolerance of soil chemistry. Earlier studies were conducted in forests of southeastern New York, where soils are influenced by underlying limestone, which is a common bedrock type, and a component of glacial till parent materials (Wyman and Hawksley-Lescault 1987, Wyman 1988, Frisbie and Wyman 1992, Wyman and Jancola 1992). At these sites mean soil pH ranged between 3.9 and 4.0 (Wyman and Hawksley-Lescault 1987, Wyman 1988); whereas we sampled a wider gradient of soils and included both natural acidic and

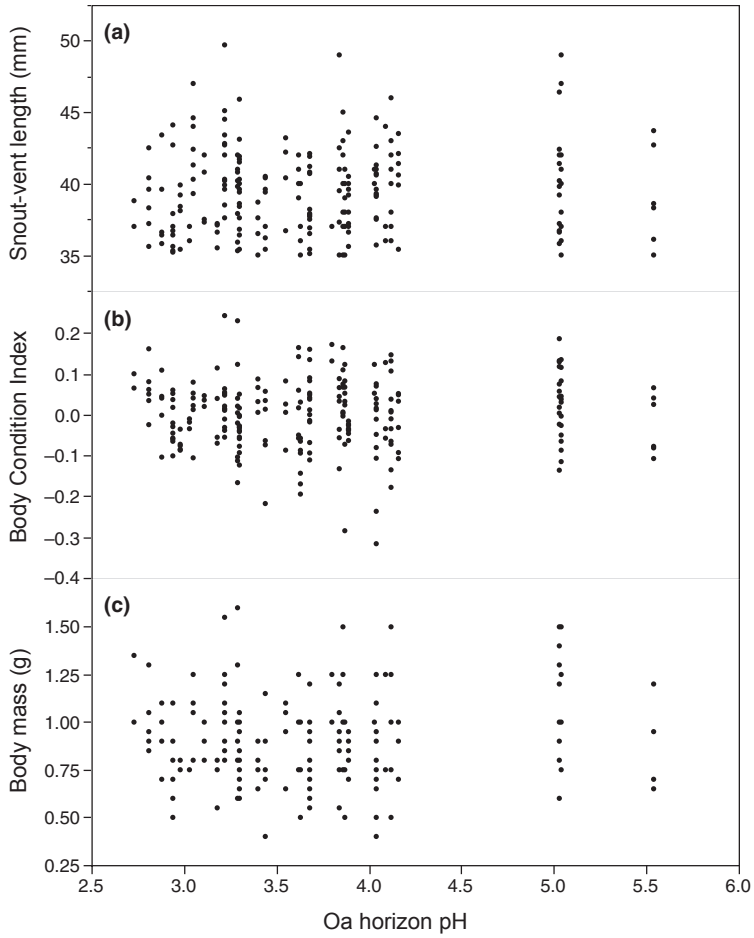

Fig. 3. Variation in adult *Plethodon cinereus* a) snout to vent length, b) body condition index, and c) live biomass as a function of organic (Oa horizon) soil pH, based on surveys of 34 upland hardwood forests in northern New York, Vermont and New Hampshire (USA).

anthropogenically acidified soils with an overall mean pH of 3.65 (±0.64). We also found no evidence that *P. cinereus* select substrates with higher pH than nearby random locations on the forest floor, which also contrasts with prior evidence of selection for less acidic microhabitats (Wyman and Hawksley-Lescault 1987, Sugalski and Claussen 1997).

If there is unfavorable habitat in their environment *P. cinereus* should repeatedly avoid it and select for more preferable conditions, so during any given survey the salamanders should be distributed at more suitable locations with higher frequency. Our habitat selection analysis showed that eastern redbacks were not distributed across the forest floor in microhabitats with higher soil pH. Microhabitat selection by plethodontid salamanders is a combination of biotic (e.g., presence of conspecifics, other salamander species, and prey) and abiotic conditions (e.g., soil moisture, temperature, pH) (Heatwole 1962, Wyman and Hawksley-Lescault 1987, Sugalski and Claussen 1997, Grover 1998, Jaeger 1990, Quinn and Graves 1999). We recognize the limitations of our habitat analysis because we are unable to isolate the importance of substrate pH within the context of other environmental variables. A resource selection analysis that incorporates measures of soil moisture, temperature, presence of prey and other salamanders, would help elucidate whether soil pH limits the amount of suitable habitat for *P. cinereus* on the forest floor. We note that the pH measurements used for habitat selection

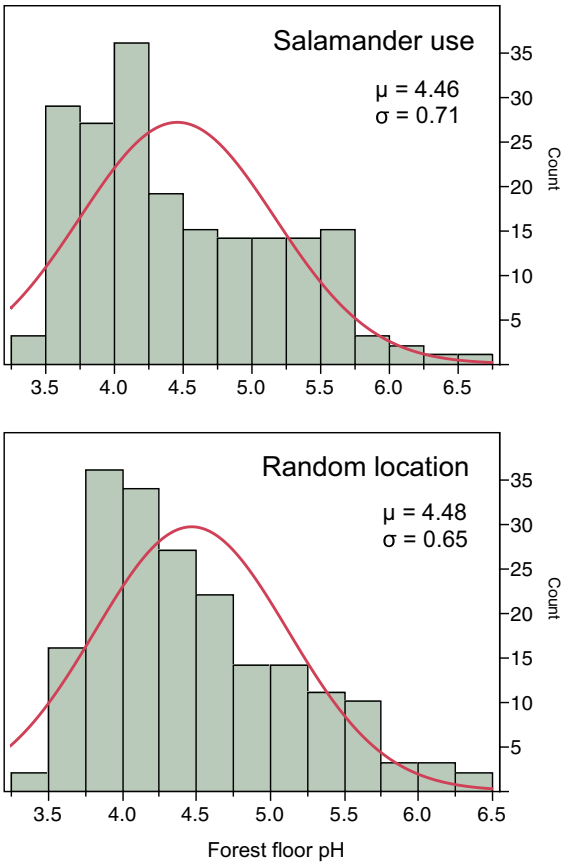

Fig. 4. Distributions of forest floor pH of samples collected at salamander use and random locations in nine upland hardwood forests in Vermont and New Hampshire (USA). Gaussian (normal) probability distributions were fitted to estimate parameters.

analysis (soil cores measured with deionized water extraction) were on average 1.04 pH units higher than the site-level measurements (soil pit samples measured with $CaCl_2$ extraction). In general, pH measurements in deionized water tend to be up to ~0.7 units higher than those reported using salt ($CaCl_2$) extraction (Ross et al. 2015). As a result, we probably underestimated substrate acidity (i.e., overestimated pH) in the habitat selection analysis, however, this error was much smaller than the pH gradient sampled.

Local adaptation may explain observations that *P. cinereus* can tolerate a lower pH than indicated by previous field and laboratory studies. In areas where soils are naturally base-rich, including the early studies noted above done in southeastern New York, local *P. cinereus* populations may never encounter very low pH *in situ*, and therefore may be adapted to the basic conditions of the locality and unable to tolerate very acidic substrates simulated in a laboratory. In contrast, in regions where soils are naturally acidic *P. cinereus* populations may have developed local adaptation(s) for lower pH tolerance (Moore and Wyman 2010). In theory, if selective pressures were sufficiently strong, these populations may have become gradually more acid-tolerant as soil acidification occurred via natural processes and/or anthropogenic inputs (Driscoll et al. 2001). Several studies have found that amphibians exhibit intraspecific variation in response to environmental stressors (e.g., road salts and some pesticides), implying that evolutionary change can occur on an ecological time scale (Carroll et al. 2007, Brady 2012, Cothran et al. 2013, Hopkins et al. 2013). Populations of *Rana arvalis* breeding in acid waters have higher acid tolerance based on embryo survival, hatching success, and time to metamorphosis (Andrén et al. 1989, Rasänen et al. 2003). Pond-breeding salamanders of the northeastern United States have also exhibited geographic variation in acid tolerance; *Notophthalmus viridescens* and *Ambystoma maculatum* from acidic ponds had higher survival when exposed to low pH conditions than those from basic localities (Cook 1983, Sherman and Munster 2012). For eastern red-backed salamanders, genetic differentiation of local populations over short distances (200 m) and limited dispersal (Cabe et al. 2006) suggest that reproductive isolation could facilitate rapid selection for acid tolerance if selective pressures are strong enough. Although we did not assess survivorship, we found no evidence that salamander size or body condition was lower in very acidic habitats. Transplant experiments could be used to evaluate the hypothesis that local *P. cinereus* populations have developed tolerance to acidic habitats.

A second potential explanation for the pH tolerance of *P. cinereus* is the generalist life history of this species, which may allow it to exploit a wider resource niche as conditions change. Numerous studies have demonstrated that *P. cinereus* is a dietary generalist, feeding widely on the extant variety of leaf litter invertebrates in the forest floor (Burton 1976, Fraser 1976, Maerz et al. 2005, Snyder 2011). At acidic sites, the costs

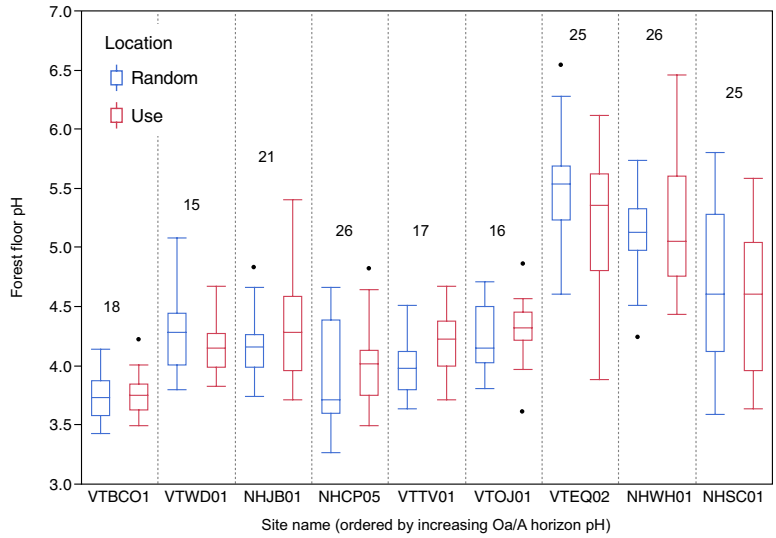

Fig. 5. Forest floor pH at salamander use (solid) and random (hollow) locations at nine upland hardwood forests in Vermont and New Hampshire (USA). Sites are ordered left to right by mean soil pH; values above plots indicate the number of matched pairs of individual *P. cinereus* collected at each site.

of being a generalist associated with the physiological challenges of exploiting a wider resource niche may be outweighed by the benefits of being able to exploit low pH environments (Richmond et al. 2005). *Plethodon cinereus* has the widest geographical range of the genus, and possesses considerable morphological (e.g., plasticity in head shape) and behavioral variation, which may enable it to exploit a wide range of environmental conditions (Maerz et al. 2006, Adams et al. 2007).

Because we sampled salamander communities across an area that included sympatric distributions of other woodland salamanders we were able to observe biotic factors correlated with *P. cinereus* abundance, such as interspecific interactions (Gibbs et al. 2007). In the Adirondacks, Beier et al. (2012) found an inverse relationship between *P. cinereus* and *Desmognathus ochrophaeus* abundance along a gradient of soil calcium and pH, with *D. ochrophaeus* dominant on very acidic sites, *P. cinereus* dominant on base-rich sites, and each in equal abundance at the gradient midpoint. These findings were interpreted as confirmation that *P. cinereus* requires base-rich habitats. However, when these Adirondack surveys were incorporated in our current study—including sites outside of the range limits of *D. ochrophaeus* in eastern North America—the pH of the forest floor habitat was no longer an important factor explaining *P. cinereus* abundance. Based on our surveys, the presence of *Desmognathus* spp. was the best predictor of *P. cinereus* abundance in northern hardwood forests due to the presence of *D. ochrophaeus* at the Adirondack sites with fewer *P. cinereus*. *Desmognathus ochrophaeus* breeds in small seepages and adults are found in the adjacent terrestrial habitat beneath logs and rocks (Gibbs et al. 2007). Where the two species are sympatric, there may be territorial antagonism and competition for resources, because *D. ochrophaeus* will displace *P. cinereus* from cover objects and drive off intruders to maintain their territories (Smith and Pough 1994). It remains unknown whether *D. ochrophaeus* has a lower pH threshold than *P. cinereus* in the Adirondacks and is therefore able to exclude or reduce colonization by *P. cinereus*. Another explanation could be related to different habitat requirements. Because *D. ochrophaeus* requires running water (e.g., seeps) for breeding and larval development, and adults rarely travel more than 100 meters from a water source (Pauley 1995), we most likely observed greater *D. ochrophaeus* abundance in some Adirondack forests due to some aspect of their habitat, such as ephemeral stream channels or spring soil moisture (Moore et al. 2001).

Our estimates of *P. cinereus* abundance were low compared to surface counts from other

northern hardwood forests, as well as population densities based on studies that incorporate detection probabilities (Burton and Likens 1975, b, Wyman and Jancola 1992, Mathewson 2009, Semlitsch et al. 2014). To obtain density estimates of terrestrial amphibians, repeated surveys, and mark-recapture efforts within a defined area are required to calculate detection probabilities. In this study, we were unable to calculate densities of salamanders per unit of search area because we used timed-constrained searches and only searched each site once. Because salamanders are fossorial and spend significant amounts of time below the surface, cover searches only account for 2–32% of the total individuals present (Taub 1961, Petranka and Murray 2001). It remains unknown whether the populations we observed are remnant and persisting under acidic conditions at low abundances; further research at the very acid sites (pH < 3.0) that incorporates detection probabilities and density estimates could help to address these questions.

We compared *P. cinereus* abundance and body metrics with acidity of the Oa/A horizons that serve as their primary habitat. Some surveys (Taub 1961) found *P. cinereus* up to 0.30 m deep, but in floodplain soils. These woodland salamanders have limited ability to burrow and primarily move down through soft organic substrates such as leaf litter or humus (Heatwole 1960). In our collective experience conducting soil and faunal sampling in these forests, we have never encountered *P. cinereus* in the coarse textured mineral soil horizons (B and C). For these reasons, we are confident that our measures of organic soil horizon pH reflect the typical habitat conditions for *P. cinereus* in these northern hardwood forests.

The tolerance of the eastern redback salamander to very acidic conditions has broad ecological importance given the species' critical role in structuring food webs as well as nutrient cycling processes in northern hardwood forests (Burton and Likens 1975). Our study did not measure population parameters such as survival, fecundity, or recruitment, and therefore cannot make projections of population size or demographics as a function of habitat chemistry. However, we can confidently report that *P. cinereus* does persist in areas with very acidic organic soils and has not been extirpated from acid-impaired ecosystems. We observed a *P. cinereus* population at the lowest pH yet recorded for the species (2.73) in the Green Mountains of Vermont. Local adaptation, as well as generalist life history traits may enable such tolerance of acidic conditions, which were previously thought lethal. Such mechanisms can be investigated using transplant experiments along natural and anthropogenic gradients in forest soil acidity.

Acknowledgments

This research was supported by a grant from the U.S. Forest Service Northeastern States Research Cooperative (www.nsrc.org). We are grateful to Chelsea Geyer, Jamie Wahls, Amanda Temple, Drew Smith, and Sabrina Green for field and laboratory assistance, and to Blair Page, Steve Horsley, Robert Long, and Richard Hallett for sharing data from their research sites. Plots from Bartlett Experimental Forest (USDA Forest Service Northern Research Station) were established as part of a larger project on Multiple Element Limitation in Northern Hardwood Ecosystems (http://www.esf.edu/melnhe/), funded by the National Science Foundation. We thank the staff of the Green Mountain National Forest, White Mountain National Forest, and the Equinox Preservation Trust, for their cooperation in providing access to their lands. We obtained Scientific Collecting permits from New Hampshire Fish and Game, Vermont Fish and Wildlife, and New York Department of Environmental Conservation to handle salamanders, and followed methods approved by the Institutional Animal Care and Use Committee of the State University of New York, College of Environmental Science and Forestry (IACUC #120403). Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Note

1. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Literature cited

Adams, D. C., M. E. West, and M. L. Collyer. 2007. Location-specific sympatric morphological divergence as a possible response to species interactions in West Virginia plethodon salamander communities. Journal of Animal Ecology 76:289–295.

Andrén, C., M. Mårdén and G. Nilson. 1989. Tolerance to low pH in a population of moor frogs, *Rana*

arvalis, from an acid and a neutral environment: a possible case of rapid evolutionary response to acidification. Oikos 56:215.

Bailey, S. W., 2000. Geologic and edaphic factors influencing susceptibility of forest soils to environmental change. Pages 27–49 *in* R. A. Mickler, R. A. Birdsey, and J. Hom, editors. Responses of Northern U.S. forests to environmental change, ecological studies. Springer, New York, USA.

Beier, C. M., A. M. Woods, K. P. Hotopp, J. P. Gibbs, M. J. Mitchell, M. Dovčiak, D. J. Leopold, G. B. Lawrence, and B. D. Page. 2012. Changes in faunal and vegetation communities along a soil calcium gradient in northern hardwood forests. Canadian Journal of Forest Research 42:1141–1152.

Best, M. L., and H. H. Jr Welsh. 2014. The trophic role of a forest salamander: impacts on invertebrates, leaf litter retention, and the humification process. Ecosphere 5:16.

Brady, S. P. 2012. Road to evolution? Local adaptation to road adjacency in an amphibian (*Ambystoma maculatum*). Scientific Reports 2:235; doi:10.1038/srep00235.

Burton, T. M. 1976. An analysis of the feeding ecology of the salamanders (Amphibia, Urodela) of the Hubbard Brook Experimental Forest, New Hampshire. Journal of Herpetology 10:187–204.

Burton, T. M., and G. E. Likens. 1975. Energy flow and nutrient cycling in salamander populations in the Hubbard Brook Experimental Forest, New Hampshire. Ecology 56:1068–1080.

Cabe, P. R., R. B. Page, T. J. Hanlon, M. E. Aldrich, L. Connors, and D. M. Marsh. 2006. Fine-scale population differentiation and gene flow in a terrestrial salamander (*Plethodon cinereus*) living in continuous habitat. Heredity 98:53–60.

Carroll, S. P., A. P. Hendry, D. N. Reznick, and C. W. Fox. 2007. Evolution on ecological time-scales. Functional Ecology 21:387–393.

Cook, R. P. 1983. Effects of acid precipitation on embryonic mortality of *Ambystoma* salamanders in the Connecticut Valley of Massachusetts. Biological Conservation 27:77–88.

Cothran, R. D., J. M. Brown, and R. A. Relyea. 2013. Proximity to agriculture is correlated with pesticide tolerance: evidence for the evolution of amphibian resistance to modern pesticides. Evolutionary Applications 6:832–841.

Davic, R. D., and H. H. Jr Welsh. 2004. On the ecological role of salamanders. Annual Review of Ecology, Evolution, and Systematics 35:405–434.

DeHayes, D. H., P. G. Schaberg, G. J. Hawley, and G. R. Strimbeck. 1999. Acid rain impacts on calcium nutrition and forest health. BioScience 49:789–800.

Driscoll, C. T., G. B. Lawrence, A. J. Bulger, T. J. Butler, C. S. Cronan, C. Eagar, K. F. Lambert, G. E. Likens, J. L. Stoddard, and K. C. Weathers. 2001. Acidic deposition in the northeastern United States: sources and inputs, ecosystem effects, and management strategies. BioScience 51:180–198.

Federer, C. A., J. W. Hornbeck, L. M. Tritton, C. W. Martin, R. S. Pierce and C. T. Smith. 1989. Long-term depletion of calcium and other nutrients in eastern US forests. Environmental Management 13:593–601.

Fraser, D. F. 1976. Empirical evaluation of the hypothesis of food competition in salamanders of the genus Plethodon. Ecology 57:459–471.

Freda, J., and W. A. Dunson. 1985a. Field and laboratory studies of ion balance and growth rates of ranid tadpoles chronically exposed to low pH. Copeia 195:415–423.

Freda, J., and W. A. Dunson. 1985b. The influence of external cation concentration on the hatching of amphibian embryos in water of low pH. Canadian Journal of Zoology 63:2649–2656.

Freda, J., and W. A. Dunson. 1986. Effects of low pH and other chemical variables on the local distribution of amphibians. Copeia 1986:454–466.

Frisbie, M. P., and R. L. Wyman. 1992. The effect of soil chemistry on sodium balance in the red-backed salamander: a comparison of two forest types. Journal of Herpetology 26:434–442.

Gibbs, J. P., A. R. Breisch, P. K. Ducey, G. Johnson, J. L. Behler and R. C. Bothner. 2007. Amphibians and Reptiles of New York State: Identification, Natural History, and Conservation. Oxford University Press, New York, NY, USA.

Gosner, K. L., and I. H. Black. 1957. The effects of acidity on the development and hatching of New Jersey frogs. Ecology 38:256–262.

Grover, M. C. 1998. Influence of cover and moisture on abundances of the terrestrial salamanders *Plethodon cinereus* and *Plethodon glutinosus*. Journal of Herpetology 32:489–497.

Heatwole, H. 1960. Burrowing ability and behavioral responses to desiccation of the salamander, *Plethodon cinereus*. Ecology 41:661–668.

Heatwole, H. 1962. Environmental factors influencing local distribution and activity of the salamander, *Plethodon cinereus*. Ecology 43:460–472.

Hopkins, G. R., S. S. French, and E. D. Brodie. 2013. Potential for local adaptation in response to an anthropogenic agent of selection: effects of road deicing salts on amphibian embryonic survival and development. Evolutionary Applications 6:384–392.

Horsley, S. B., S. W. Bailey, T. E. Ristau, R. P. Long, and R. A. Hallett. 2008. Linking environmental gradients, species composition, and vegetation indicators of sugar maple health in the northeastern United

States. Canadian Journal of Forest Research 38:1761–1774.

Houle, D., R. Paquin, C. Camiré, R. Ouimet, and L. Duchesne. 1997. Response of the Lake Clair Watershed (Duchesnay, Quebec) to changes in precipitation chemistry (1988-1994). Canadian Journal of Forest Research 27:1813–1821.

Jaeger, R. G. 1972. Food as a limited resource in competition between two species of terrestrial salamanders. Ecology 53:535–546.

Jaeger, R. G. 1980. Microhabitats of a terrestrial forest salamander. Copeia 1980:265–268.

Jaeger, R. 1990. Territorial salamanders evaluate size and chitonous content of arthropod prey. Behavioral Mechanisms of Food Selection 20:111–126.

Johnson, A. H., S. B. Andersen, and T. G. Siccama. 1994. Acid rain and soils of the Adirondacks. I. Changes in pH and available calcium, 1930–1984. Canadian Journal of Forest Research 24:39–45.

Lawrence, G. B., B. P. Baldigo, K. M. Roy, H. A. Simonin, R. W. Bode, S. I. Passy and S. B. Capone. 2008. Results from the 2003-2005 Western Adirondacks Stream Survey (WASS), NYSERDA. Report 08-22. New York State Energy Research and Technology Authority, Albany, New York, USA.

Leclair, M. H., M. Levasseur, and R. Leclair. 2006. Life-history traits of *Plethodon Cinereus* in the northern parts of its range: variations in population structure, age, and growth. Herpetologica 62:265–282.

Likens, G. E., F. H. Bormann, N. M. Johnson, D. W. Fisher, and R. S. Pierce. 1970. Effects of forest cutting and herbicide treatment on nutrient budgets in the Hubbard Brook watershed-ecosystem. Ecological Monographs 40:23–47.

Lovett, G. M., T. H. Tear, D. C. Evers, S. E. G. Findlay, B. J. Cosby, J. K. Dunscomb, C. T. Driscoll, and K. C. Weathers. 2009. Effects of air pollution on ecosystems and biological diversity in the Eastern United States. Annals of the New York Academy of Sciences 1162:99–135.

Maerz, J. C., J. M. Karuzas, D. M. Madison, and B. Blossey. 2005. Introduced invertebrates are important prey for a generalist predator. Diversity and Distributions 11:83–90.

Maerz, J. C., E. M. Myers, and D. C. Adams. 2006. Trophic polymorphism in a terrestrial salamander. Evolutionary Ecology Research 8:23–35.

Mathewson, B. 2009. The relative abundance of eastern red-backed salamanders in eastern hemlock-dominated and mixed deciduous forests at Harvard Forest. Northeastern Naturalist 16:1–12.

Moore, J. D., and R. L. Wyman. 2010. Eastern red-backed salamanders (*Plethodon cinereus*) in a highly acid forest soil. The American Midland Naturalist 163:95–105.

Moore, A. L., C. E. Williams, T. H. Martin, and W. J. Moriarity. 2001. Influence of season, geomorphic surface and cover item on capture, size and weight of *Desmognathus ochrophaeus* and *Plethodon cinereus* in Allegheny Plateau riparian forests. The American Midland Naturalist 145:39–45.

Page, B. D., and M. J. Mitchell. 2008. Influences of a calcium gradient on soil inorganic nitrogen in the Adirondack Mountains, New York. Ecological Applications 18:1604–1614.

Pauley, T. K. 1995. Terrestrial salamanders. Pp. 42–52. *In* R. C. Reardon editor. (Handbook Coord.), Effects of Diflubenzuron on Non-Target Organisms in Broadleaf Forested Watersheds in the Northeast U.S.D.A. Forest Service, Report FHM-NC-05095. National Center of Forest Health Management, Morgantown, West Virginia.

Petranka, J. W., and S. S. Murray. 2001. Effectiveness of removal sampling for determining salamander density and biomass: A case study in an Appalachian streamside community. Journal of Herpetology 35:36–44.

Pierce, B. A. 1985. Acid Tolerance in Amphibians. BioScience 35:239–243.

Pough, F. H. 1976. Acid precipitation and embryonic mortality of spotted salamanders, *Ambystoma maculatum*. Science 192:68–70.

Quinn, V. S., and B. M. Graves. 1999. Space use in response to conspecifics by the red-backed salamander (*Plethodon cinereus*, Plethodontidae, Caudata). Ethology 105:993–1002.

Rasänen, K. R., A. Laurila, and J. Merilä. 2003. Geographic variation in acid stress tolerance of the moor frog. Rana arvalis. I. Local adaptation. Evolution 57:352–362.

Richmond, C. E., D. L. Breitburg, and K. A. Rose. 2005. The role of environmental generalist species in ecosystem function. Ecological Modelling 188:279–295.

Rooney, T. P., C. Antolik, and M. D. Moran. 2000. The impact of salamander predation on collembola abundance. Proceedings of the Entomological Society of Washington 102:308–312.

Ross, D. S., et al. 2015. Inter-laboratory variation in the chemical analysis of acidic forest soil reference samples from eastern North America. Ecosphere 6:73.

Schulte-Hostedde, A. I., B. Zinner, J. S. Millar, and G. J. Hickling. 2005. Restitution of mass-size residuals: validating body condition indices. Ecology 86:155–163.

Semlitsch, R. D., K. M. O'Donnell, and F. R. Thompson. 2014. Abundance, biomass production, nutrient content, and the possible role of terrestrial salamanders in Missouri Ozark forest ecosystems. Canadian Journal of Zoology 92:997–1004.

Sherman, E., and K. V. Munster. 2012. Pond pH, acid tolerance, and water preference in newts of Vermont. Northeastern Naturalist 19:111–122.

Smith, E. M., and F. H. Pough. 1994. Intergeneric aggression among salamanders. Journal of Herpetology 28:41–45.

Snyder, C. M.. 2011. Terrestrial salamanders and invertebrates in the Adirondack Mountains: feeding ecology and implications of calcium. Master's Thesis. College of Environmental Science and Forestry, State University of New York USA, Syracuse, New York

Sugalski, M. T., and D. L. Claussen. 1997. Preference for soil moisture, soil pH, and light intensity by the salamander, *Plethodon cinereus*. Journal of Herpetology 31:245–250.

Sullivan, T. J., G. B. Lawrence, S. W. Bailey, T. C. McDonnell, C. M. Beier, K. C. Weathers, G. T. McPherson, and D. A. Bishop. 2013. Effects of acidic deposition and soil acidification on sugar maple trees in the Adirondack Mountains, New York. Environmental Science & Technology 47:12687–12694.

Taub, F. B. 1961. The distribution of the red-backed Salamander, *Plethodon Cinereus*, within the Soil. Ecology 42:681–698.

Tilman, D., and C. Lehman. 2001. Human-caused environmental change: impacts on plant diversity and evolution. Proceedings of the National Academy of Sciences 98:5433–5440.

Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human domination of Earth's ecosystems. Science 277:494–499.

Walton, B. M. 2013. Top-down regulation of litter invertebrates by a terrestrial salamander. Herpetologica 69:127–146.

Walton, B. M., D. Tsatiris, and M. Rivera-Sostre. 2006. Salamanders in forest-floor food webs: Invertebrate species composition influences top–down effects. Pedobiologia 50:313–321.

Warby, R. A., C. E. Johnson, and C. T. Driscoll. 2009. Continuing acidification of organic soils across the Northeastern USA: 1984–2001. Soil Science Society of America Journal 73:274–284.

Welsh, H. H. Jr, K. Pope, and C. Wheeler. 2008. Using multiple metrics to assess the effects of forest succession on population status: A comparative study of two terrestrial salamanders in the US Pacific Northwest. Biological Conservation 141:1149–1160.

Wyman, R. L. 1988. Soil acidity and moisture and the distribution of amphibians in five forests of southcentral New York. Copeia 1988:394–399.

Wyman, R. L. 1998. Experimental assessment of salamanders as predators of detrital food webs: effects on invertebrates, decomposition and the carbon cycle. Biodiversity & Conservation 7:641–650.

Wyman, R. L. and D. S. Hawksley-Lescault. 1987. Soil acidity affects distribution, behavior, and physiology of the salamader *Plethodon Cinereus*. Ecology 68:1819–1827.

Wyman, R. L., and J. Jancola. 1992. Degree and scale of terrestrial acidification and amphibian community structure. Journal of Herpetology 26:392–401.