

Changes in faunal and vegetation communities along a soil calcium gradient in northern hardwood forests

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Abstract: Depletion of Ca from forest soils due to acidic deposition has had potentially pervasive effects on forest communities, but these impacts remain largely unknown. Because snails, salamanders, and plants play essential roles in the Ca cycle of northern hardwood forests, we hypothesized that their community diversity, abundance, and structure would vary with differences in biotic Ca availability. To test this hypothesis, we sampled 12 upland hardwood forests representing a soil Ca gradient in the Adirondack Mountains, New York (USA), where chronic deposition has resulted in acidified soils but where areas of well-buffered soils remain Ca rich due to parent materials. Along the gradient of increasing soil $[Ca^{2+}]$, we observed increasing trends in snail community richness and abundance, live biomass of redback salamanders (*Plethodon cinereus* (Green, 1818)), and canopy tree basal area. Salamander communities were dominated by mountain dusky salamanders (*Desmognathus ochrophaeus* Cope, 1859) at Ca-poor sites and changed continuously along the Ca gradient to become dominated by redback salamanders at the Ca-rich sites. Several known calciphilic species of snails and plants were found only at the highest-Ca sites. Our results indicated that Ca availability, which is shaped by geology and acidic deposition inputs, influences northern hardwood forest ecosystems at multiple trophic levels, although the underlying mechanisms require further study.

Résumé : L'épuisement du Ca dans les sols forestiers à cause des dépôts acides a eu des répercussions potentiellement généralisées sur les communautés forestières mais ces impacts demeurent largement inconnus. Étant donné que les escargots, les salamandres et les plantes jouent un rôle essentiel dans le cycle du Ca des forêts feuillues nordiques, nous avons émis l'hypothèse que la diversité, l'abondance et la structure de leurs communautés varieraient en fonction de la disponibilité du Ca. Pour tester cette hypothèse, nous avons échantillonné 12 forêts feuillues en milieu sec dans les monts Adirondacks, dans l'État de New York aux États-Unis d'Amérique, où des dépôts chroniques ont acidifié les sols mais où il y a encore des endroits où les sols ont un pouvoir tampon élevé et demeurent riches en Ca à cause du matériau originel. À mesure que la concentration de Ca^{2+} augmentait le long du gradient, nous avons observé des tendances à la hausse de l'abondance et de la richesse des communautés d'escargots, de la biomasse vivante de salamandres rayées (*Plethodon cinereus* (Green, 1818)) et de la surface terrière des arbres qui forment la canopée. Les communautés de salamandres étaient dominées par la salamandre sombre des montagnes (*Desmognathus ochrophaeus* Cope, 1859) dans les stations pauvres en Ca et changeaient progressivement le long du gradient de Ca pour devenir dominées par la salamandre rayée dans les stations riches en Ca. Plusieurs espèces calcicoles connues d'escargots et de plantes ont été observées seulement dans les stations les plus riches en Ca. Nos résultats indiquent que la disponibilité du Ca, qui est déterminée par les conditions géologiques et les apports de dépôts acides, influence les écosystèmes de feuillus nordiques à de multiples niveaux trophiques bien que les mécanismes sous-jacents nécessitent plus de recherche.

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Introduction

Research on forest ecosystem processes has suggested that Ca availability plays a critical role in shaping ecosystem structure, function, and responses to change (McLaughlin and Wimmer 1999). In the industrialized regions of Europe and northeastern North America, Ca depletion from soils has been attributed to atmospheric deposition of NO_3 and SO_4 , commonly known as “acid rain” (Likens et al. 1972; Driscoll et al. 2001). Soil acidification, with concomitant generation of mobile anions such as Al^{3+} , drives Ca leaching from forest soils (Lawrence et al. 1995), resulting in Ca deficits that may have pervasive impacts at multiple scales from organisms to ecosystems (Likens et al. 1998; DeHayes et al. 1999; Hamburg et al. 2003). Because Ca availability is primarily shaped by geological (parent material) and biological factors (vegetation composition and age), the impacts of acidic deposition on base cation saturation (including Ca^{2+}) and the acid-neutralizing capacity of soils typically vary across a landscape, resulting in spatial variability in acidification (Sullivan et al. 2006) and its biotic impacts, which can be pervasive (Graveland and Drent 1997; Driscoll et al. 2001; Lovett et al. 2009).

In eastern North America, research has focused on the mechanisms and consequences of Ca depletion from forest soils and vegetation, which are the primary sinks and sources in the Ca cycle (Lawrence et al. 1995; Likens et al. 1998; Yanai et al. 2005). The effects of forest Ca depletion at higher trophic levels are poorly understood. The sensitivity of terrestrial gastropods and songbirds to Ca deficits have been observed in Europe (Wäreborn 1992; Graveland et al. 1994) and eastern North America (Hames et al. 2002; Pabian and Brittingham 2007). Terrestrial salamanders may also be sensitive to Ca availability. These amphibians are abundant and widely dispersed and play a critical role in the metabolism and movement of Ca in the forest trophic web (Burton and Likens 1975a; Burton 1976). Negative impacts of acidic deposition and soil acidification on salamander growth and reproduction (Wyman and Hawksley-Lescault 1987; Wyman and Jancola 1992) have been observed and may be explained by changes in the forest floor prey assemblages important for salamander diets (Ormerod and Rundle 1998). However, the impacts of Ca depletion on faunal communities have been difficult to generalize because of interspecific variation in Ca demand and differential sensitivity to closely related factors like soil pH (Fisk et al. 2006).

Our objective in this study was to describe differences in gastropod, salamander, and vegetation communities among northern hardwood forest sites that represented the known range of variability in soil Ca in the Adirondack Mountains, New York (Sullivan et al. 2006). Using this gradient, we quantified variation at the species and community levels that may be attributed to biotic Ca availability based on the exchangeable $[\text{Ca}^{2+}]$ of the Oa and B soil horizons. To better understand how Ca availability shapes biodiversity in northern hardwood forests, we sampled taxa that fill essential roles in the ecosystem Ca cycle, represent different trophic levels (producers, detritivores, and consumers), and are often used as bioindicators of environmental change. We addressed three hypotheses.

(1) Species richness of snails, salamanders, and vascular plants is positively correlated with soil Ca. At Ca-rich sites,

we expected that species with high Ca requirements would not be excluded, despite chronic acid rain inputs, and their presence will contribute to greater richness. Species without high Ca requirements should still be present at Ca-rich sites, unless some other factor, such as competition or lack of suitable habitat, excludes them from the community (Horsák 2006).

(2) Measures of abundance, including population size (snails), live biomass (salamanders), and total basal area (trees), are positively correlated with soil Ca. We expected that higher-Ca sites would have greater snail abundance for two reasons: (i) Ca would not be a limiting factor for reproduction and (ii) higher Ca would support populations of calciphilic species, resulting in higher overall abundance. For salamanders, because the redback salamander (*Plethodon cinereus* (Green, 1818)) (redbacks) is known to be sensitive to soil acidification, we expected its abundance to increase with soil Ca. We expected that increasing biomass of redbacks, which is the most abundant vertebrate species in northern hardwood forests (Burton and Likens 1975b), would drive up total salamander biomass (with increasing soil Ca). Lastly, our hypothesis for tree basal area was based on prior studies that have associated soil Ca with forest productivity and health (see McLaughlin and Wimmer 1999).

(3) Community structure varies significantly along the Ca gradient resulting from interspecific differences in sensitivity to soil acidification and (or) base cation depletion. For gastropods and woody plants, we expected that calciphilic (“Ca-loving”) species would occur in greater abundance as soil $[\text{Ca}^{2+}]$ increased, resulting in community-level changes in species composition and relative abundance. For salamanders, because we expected an increasing abundance of redbacks as soil Ca increased, we hypothesized that larger redback populations would negatively influence other woodland salamander species because they are known to be highly territorial (Petranka 1998).

A secondary objective of our study was to provide insight on whether “patches” of highly buffered Ca-rich soils could serve as “neoreugia” (sensu Nekola 1999) for calciphilic species within the matrix of a chronically acidified forest landscape. Such refugia could have significant conservation value in both understanding and mitigating the impacts of acid rain on biodiversity and ecosystem health in the eastern United States (Lovett et al. 2009).

Methods

Study sites and sampling design

We conducted sampling at 12 upland northern hardwood forest sites in the Adirondack Mountains (Table 1) where recent studies have described soil chemistry, including base cation concentrations of organic and mineral horizons (Lawrence et al. 2008, Page et al. 2008). In addition to soil $[\text{Ca}^{2+}]$ and pH of the Oa and B horizons, we compiled a group of site variables including mean elevation, aspect, model-derived estimates of NO_3 and SO_4 wet deposition (Ito et al. 2002), percent ground cover (e.g., herbaceous plants, ferns, bryophytes, tree seedlings, shrubs, rock, tree bole, and open water), and plot distance to the nearest stream. These site characteristics were included because they are either known or hypothesized to be related to Ca availability. The

Table 1. Summary of characteristics of 12 upland northern hardwood forest sites in the Adirondack Mountains, New York, representing a gradient in soil Ca in the Adirondack region.

Site name	Elevation (m)	Aspect	Soil [Ca ²⁺] (cmol·kg ⁻¹)			Estimated wet deposition (kg·ha ⁻¹ ·year ⁻¹)			Location	
			Oa (SD)	B (SD)	SO ₄	NO ₃	Latitude (°N)	Longitude (°W)		
HWF14	624	SW	53.89 (3.99)	7.73 (1.37)	21.7	15.85	44.004	-74.245		
NWoods	487	W	39.17 (2.50)	2.74 (0.85)	17.93	15.31	43.809	-74.050		
Mason	582	E	24.95 (3.24)	2.25 (0.57)	23.28	18.08	43.593	-74.429		
330T	520	N	21.96 (3.74)	2.99 (1.05)	17.44	14.57	44.241	-74.349		
NSpec	609	SE	18.71 (5.49)	2.00 (1.95)	25.42	18.58	43.531	-74.387		
HWF15	627	S	16.22 (2.99)	1.00 (0.32)	20.92	15.72	44.004	-74.248		
24001	561	NE	12.05 (7.09)	1.13 (1.38)	24.23	18.43	43.762	-74.687		
28011	655	N	11.46 (7.38)	1.34 (1.61)	26.83	19.23	43.650	-74.676		
28030	567	S	10.19 (5.38)	0.81 (0.39)	25.21	18.74	43.750	-74.738		
BasicBuck	646	N	7.43 (6.62)	0.42 (0.40)	26.62	18.96	43.715	-74.741		
27026	619	E	5.65 (5.25)	0.37 (0.18)	27.03	19.3	43.699	-74.750		
28014	668	N	1.83 (1.00)	0.28 (0.09)	29.09	19.7	43.639	-74.684		

Note: Soil chemistry data are based on Page et al. (2008) and Lawrence et al. (2008). Deposition estimates were derived from the spatial model outputs of Ito et al. (2002) for 1990–1999 deposition inputs based on the site coordinates using ArcGIS.

distance-to-stream variable was used as a proxy for possible effects of habitat traits on salamander communities, as some Plethodontidae species are more likely to be found near streams (Jaeger 1971).

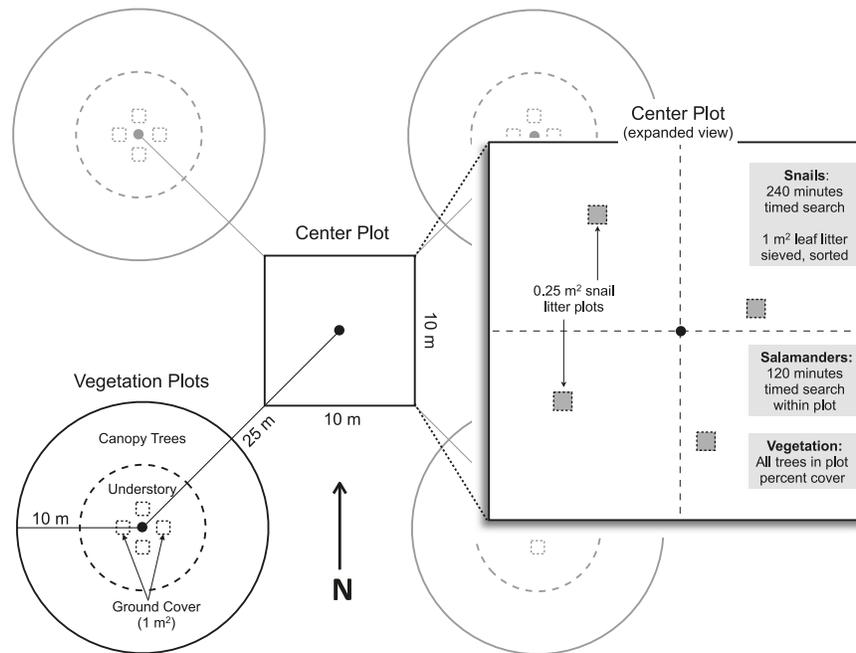
At each site, we established plots for sampling land snails, salamanders, vegetation, and ground cover (Fig. 1) based on the GPS locations of prior soil sampling. All [Ca²⁺] data in the study were based on exchangeable cation concentrations, which represents the amount available for biotic uptake. Soil chemistry data from Page et al. (2008) were collected in three soils pits per site located 30 m from a center point at 120°, 240°, and 360° azimuths. We averaged these three samples to represent soil Ca at the site level. We relocated and used the previous center points for establishing plots at the following sites: HWF14, NWoods, Mason, 330T, NSpec, and HWF15 (Table 1). Soils data from Lawrence et al. (2008) included Oa and B horizon [Ca²⁺] that were averaged from three soil pits within a 0.1 ha plot. These plot locations were used to establish our sampling plots at the following sites: 24001, 28011, 28030, BasicBuck, 27026, and 28014 (Table 1). Air temperature and relative humidity at ground level were measured in the center plot using a handheld digital hygrometer prior to all snail and salamander sampling periods.

Land snails were sampled in a 10 m × 10 m plot using both litter sieving and timed search techniques. During a 2-week period in June 2009, we collected a total of 1 m² of leaf litter (including the entire Oa horizon) in four equal amounts (0.25 m²) from each of the four 5 m × 5 m quadrants of the center plot. Litter samples were air-dried, sieved into fractions, and searched using magnifying visors. During the same period, we conducted timed searches within the 10 m × 10 m plot for a total of 2 person-hours per site. We repeated this survey at each site during a 2-week period in July 2009, resulting in a total of 4 h of timed search per site. All sampling was done during the hours between 9 a.m. and 5 p.m. and the same technicians conducted timed searches at all sites. All collected specimens were identified to species, counted, and archived.

Salamanders were collected in the 10 m × 10 m center plot (Fig. 1) using a timed search of 2 person-hours per site (during the morning). The search area was extended beyond plot boundaries as needed to target natural cover objects in close vicinity, but searchers always remained within 20 m of plot center. Timed searches were conducted during a 2-week period in July 2009. All specimens collected were identified to species, weighed, measured (snout-to-tail length and snout-to-vent length), and released.

We measured vegetation and ground cover in the center plot and in four adjacent fixed-radius plots located 25 m in the four cardinal directions from the center plot (Fig. 1). In these plots, we recorded species, abundance, condition, and diameter at breast height (DBH) (1.3 m) of canopy trees (DBH ≥ 5 cm), species and count of understory trees (DBH < 5 cm), and percent ground cover (for the entire center plot). The fixed-radius plots had a 10 m radius for canopy trees, a 5 m radius for understory trees, and four randomly located 1 m² quadrats to census tree seedlings and ground cover (Fig. 1). We identified all herbaceous, fern, and woody shrub species in the ground cover plots and these data were compiled with tree species data to estimate overall vascular

Fig. 1. Design and layout of snail, salamander, and vegetation sampling plots installed at 12 upland northern hardwood forests in the Adirondack Mountains, New York.



plant species richness. Vegetation and cover data from all sample plots were aggregated for analysis.

Analysis

We tested the first and second hypotheses (diversity and abundance versus soil Ca) with least-squares regression analysis using JMP 8.0 (SAS Institute Inc., Cary, North Carolina). Soil Ca, site elevation, and wet deposition estimates were used as explanatory variables. Response variables in regression models include measures of species richness and diversity (for snails only), species- and community-level abundance, and plant community characteristics, such as percent ground cover. Land snail diversity was based on Simpson's D and Shannon's H indices (Magurran 1988). Diversity indices were not calculated for salamanders because of the small number of species found or for plants because we did not measure relative abundance of all plant species (only trees). We also used Spearman's rank method to evaluate correlations among the site-level explanatory variables used in regression analysis. Because site was the unit of analysis, all results presented were based on $n = 12$ (and for regressions, $df = 11$). A nonparametric rank correlation (Spearman's ρ) was used to evaluate the relationship between the two overall most abundant salamander species along the Ca gradient; this analysis had $n = 9$ because one of the species was absent from three sites.

Several variables required transformation prior to regression analysis. The soil $[Ca^{2+}]$, snail abundance (count), and salamander abundance (live biomass) data were log transformed for normality. For salamanders, 1.0 g was added to the raw biomass data prior to log transformation to include sites in the analysis where species biomass was zero (e.g., 3 of 12 sites for mountain dusky salamander (*Desmognathus ochrophaeus* Cope, 1859) (mountain duskies)). Other key site-level (explanatory) variables, including SO_4 and NO_3

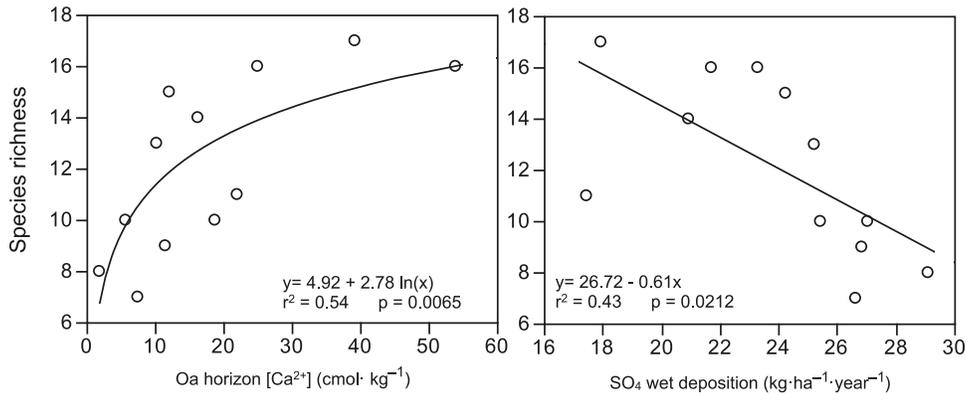
deposition and elevation, fit a normal distribution based on a Shapiro–Wilk test ($p > 0.05$) and were not transformed.

The third hypothesis (community structure versus Ca) was tested with nonmetric multidimensional scaling (NMS) for each community independently and for the snail, salamander, and tree communities combined into one species matrix for ordination using PC ORD (McCune and Grace 2002). Other vascular plants were not included in the NMS analysis because we only determined their presence–absence, not relative abundance. All four NMS ordinations were run with the same “attributes” matrix that included the following group of site characteristics: Oa and B horizon $[Ca^{2+}]$, soil pH, NO_3 , and SO_4 wet deposition estimates, site elevation, aspect, total overstory basal area, mean tree DBH, percent ground cover (by cover type), and plot distance to the nearest stream.

Snail data were compiled from both the litter sieving and timed search collections; we used count data for snails because many of the specimens collected were too small for accurate mass determination. For analysis purposes, only those individuals identified to species were included in overall abundance estimates. We used live biomass data for salamanders because there was no significant within-species or across-site variation in mean body mass among sites. Basal area data were used to estimate the relative abundance of tree species.

We noted significant correlations among the soil $[Ca^{2+}]$ and other site-level abiotic variables and these relationships are presented here to aid in the interpretation of results. Soil $[Ca^{2+}]$ was strongly positively correlated between the Oa and B horizons ($\rho = 0.93$, $p < 0.0001$); for this reason, and because the faunal communities that we studied dwelled primarily in the leaf litter, we present most results below based on the Oa data. The Oa horizon $[Ca^{2+}]$ was not significantly correlated with Oa horizon pH ($\rho = 0.42$, $p = 0.1740$) but was negatively correlated with the estimated wet deposition of SO_4 ($\rho = -0.83$, $p = 0.0010$) and NO_3 ($\rho = -0.85$, $p =$

Fig. 2. Changes in species richness of land snails with soil Ca (Oa horizon $[Ca^{2+}]$) and estimated acidic deposition inputs (wet SO_4 deposition derived from Ito et al. 2002). Snails were collected using both litter sieving and timed search techniques in 12 upland northern hardwood forests in the Adirondack Mountains, New York.



0.0004) derived from the Ito et al. (2002) model. Site elevation was positively correlated with model-derived estimates of SO_4 ($\rho = 0.67$, $p = 0.0168$) and NO_3 ($\rho = 0.65$, $p = 0.0202$) deposition and was negatively correlated with Oa $[Ca^{2+}]$ ($\rho = -0.53$, $p = 0.0754$).

Results

Species composition and diversity

As hypothesized, species richness of land snails was positively related to Oa $[Ca^{2+}]$ ($r^2 = 0.54$, $p = 0.0065$) and negatively related to SO_4 deposition ($r^2 = 0.43$, $p = 0.0212$) and site elevation ($r^2 = 0.37$, $p = 0.0347$) (Fig. 2). There were no significant effects of Oa $[Ca^{2+}]$ on snail community diversity based on Shannon's H ($r^2 = 0.08$, $p = 0.3616$) or Simpson's D ($r^2 = 0.08$, $p = 0.3527$). However, we noted that several species were found primarily (or only) at the highest Ca sites, including *Paravitrea multidentata* (A. Binney, 1840), *Gastrocopta pentodon* (Say, 1822), and *Euconolus polygyratus* (Pilsbry, 1899) (Table 2).

Species richness of the salamander community was not related to Oa $[Ca^{2+}]$ ($r^2 = 0.02$, $p = 0.6678$). Redbacks and mountain duskies were the most common and were found at 12 of 12 and 9 of 12 sites, respectively. Red-spotted newts (*Notophthalmus viridescens* (Rafinesque, 1820)), two-lined salamanders (*Eurycea bislineata* (Green, 1818)), and northern dusky salamanders (*Desmognathus fuscus* (Rafinesque, 1820)) were also found infrequently (at fewer than six sites).

Vascular plant species richness, including trees, shrubs, herbs, and ferns, was not significantly related to Oa $[Ca^{2+}]$ ($r^2 = 0.15$, $p = 0.2056$), although the general trend was positive. Tree species richness was highest (nine species) at the site with the highest Ca (HWF14), which was consistent with our hypothesis. Sugar maple (*Acer saccharum* Marsh.) and American beech (*Fagus grandifolia* Ehrh.) were present at all sites, and yellow birch (*Betula alleghaniensis* Britton) was present at every site except one (Table 3). Among the less common species known to be calciphilic, we found American basswood (*Tilia americana* L.) and eastern hop-hornbeam (*Ostrya virginiana* (Mill.) K. Koch) only at the two highest-Ca sites (HWF14 and NWoods) and white ash (*Fraxinus americana* L.) only at sites in the upper half of the gradient. Among cover types, fern ground cover was strongly

negatively related to Oa $[Ca^{2+}]$ ($r^2 = 0.55$, $p = 0.0059$) and coarse woody debris ground cover was weakly positively related to Oa $[Ca^{2+}]$ ($r^2 = 0.33$, $p = 0.0508$).

Abundance

As hypothesized, we observed differences in snail abundance along the soil Ca gradient. Total abundance was positively related to Oa $[Ca^{2+}]$ ($r^2 = 0.41$, $p = 0.0240$) and was negatively related to site elevation ($r^2 = 0.65$, $p = 0.014$), SO_4 deposition estimates ($r^2 = 0.46$, $p = 0.0147$), and NO_3 deposition estimates ($r^2 = 0.31$, $p = 0.0585$). The most commonly found snail species, *Punctum minutissimum* (Lea 1841), increased in abundance with increasing Oa (Table 2).

For salamanders (Fig. 3), the redback was the most abundant species and their live biomass was strongly positively related to Oa $[Ca^{2+}]$ ($r^2 = 0.60$, $p = 0.0033$), as we hypothesized. The mountain dusky was the second most abundant species and their live biomass was negatively related to Oa $[Ca^{2+}]$ ($r^2 = 0.54$, $p = 0.0068$). The site-by-site relationship between redbacks and mountain duskies (Fig. 4) is described further below. We did not observe any effects of Ca, elevation, or deposition on the total live biomass of the salamander community among sites. Other morphometrics, including mean individual biomass, mean snout-to-vent length, and mean snout-to-tail length, did not vary significantly among sites or continuously across the Ca gradient.

Total live basal area of overstory trees (square metres per hectare) was positively related to $[Ca^{2+}]$ in the Oa horizon ($r^2 = 0.43$, $p = 0.0213$) and B horizon ($r^2 = 0.36$, $p = 0.0388$). The proportion of basal area attributed to standing dead trees (snags) decreased significantly with Oa $[Ca^{2+}]$ ($r^2 = 0.38$; $p = 0.0338$). For the three most abundant tree species (based on relative basal area averaged across sites; Table 3), we found different relationships between relative abundance and the soil Ca gradient: sugar maple was weakly positively related to both Oa $[Ca^{2+}]$ ($r^2 = 0.32$, $p = 0.0567$) and B $[Ca^{2+}]$ ($r^2 = 0.30$, $p = 0.0636$), American beech had a negative but nonsignificant trend ($p > 0.10$) along the Ca gradient, and yellow birch decreased significantly with both Oa $[Ca^{2+}]$ ($r^2 = 0.40$, $p = 0.0267$) and B $[Ca^{2+}]$ ($r^2 = 0.34$, $p = 0.0449$). We did not analyze these relationships for the remaining species because each was absent from three or more sites.

Table 2. Land snail collections at 12 upland hardwood forest sites sampled in 2009 in the Adirondack Mountains, New York.

Species	HWF14	NWoods	Mason	330T	Nspec	HWF15	24001	28011	28030	BasicBuck	27026	28014	Total
<i>Punctum minutissimum</i>	174	195	67	25	4	38	104		25			4	636
<i>Striatura exigua</i>	17	78	49	91	49	27	105	18	52	22	6	13	527
<i>Zonitoides arboreus</i>	6	26	39	49	63	12	30	97	44	15	27	63	471
<i>Striatura milium</i>		101	29	11	24	5	70	1	22			7	270
<i>Gastrocopta pentodon</i>		110		1			6						117
<i>Striatura ferrea</i>	2	1	7	36	11	15	4	5	5	8	1	4	99
<i>Helicodiscus shimeki</i>	1	6	2	14	18	7	5	4	1		3	6	67
<i>Discus catskillensis</i>	5	4	19	1	5	6	5		4	1	9	6	65
<i>Paravitrea multidentata</i>	32	14	17										63
<i>Neohelix albolabris</i>	5	4	7		2	1	1		12				32
<i>Euchemotrema fraternum</i>				2	1	4	1	2	2	5	3		20
<i>Euconulus polygyratus</i>	8	8	1				1						18
<i>Cochlicopa morseana</i>	3	13					1						16
<i>Triodopsis tridentata</i>	3		4			3	2			1	2	1	16
<i>Anguispira alternata</i>	1					3		3	4	2	1		14
<i>Columella simplex</i>	2	4		6									12
<i>Glyphyalinia rhoadsi</i>	2	5	3			1							11
<i>Haplotrema concavum</i>			9		1			1					11
<i>Neohelix dentifera</i>	1	1		1		1	2		1				7
<i>Appalachina sayana</i>	1						2		2		1		6
<i>Helicodiscus parallelus</i>		1	5										6
<i>Euconulus fulvus</i>			2										2
<i>Mesomphix inornatus</i>											2		2
<i>Vertigo gouldi</i>		1						1					2
<i>Mesodon thyroidus</i>						1							1
<i>Novisuccinea ovalis</i>									1				1
<i>Vitridens ligera</i>			1										1
Unknown	12	27	25	5	14	5	39	30	24	12	5	11	209
Total all species	275	599	286	242	192	129	378	162	199	66	60	115	2703
Shannon's <i>H</i>	1.35	1.88	2.18	1.73	1.69	2.06	1.67	0.99	1.90	1.49	1.66	1.37	
Simpson's <i>D</i>	2.18	4.84	6.72	4.33	4.26	5.72	4.14	1.78	5.14	3.63	3.46	2.52	

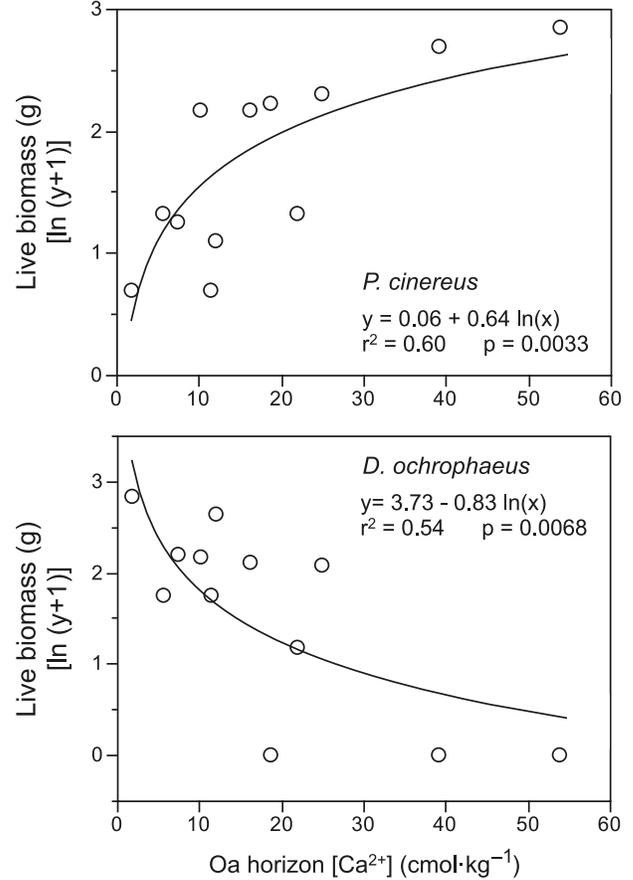
Note: Snails were collected using both litter sieving and timed search techniques. Sites represent a gradient in soil Oa horizon [Ca²⁺] listed in descending order from high Ca (left) to low Ca (right). Most unknown specimens were due to broken or partial shells. Shannon's *H* and Simpson's *D* diversity indices (Magurran 1988) are provided for each site.

Table 3. Forest overstory composition and relative abundance (based on basal area) for 12 upland northern hardwood sites in the Adirondack Mountains, New York.

	Proportion of total basal area (m ² ·ha ⁻¹)												Total basal area (m ² ·ha ⁻¹)
	HWF14	NWoods	Mason	330T	Nspec	HWF15	24001	28011	28030	BasicBuck	27026	28014	
<i>Acer saccharum</i>	0.37	0.36	0.76	0.32	0.41	0.22	0.24	0.31	0.40	0.15	0.28	0.19	
<i>Fagus grandifolia</i>	0.09	0.06	0.21	0.26	0.28	0.22	0.15	0.50	0.54	0.48	0.23	0.39	
<i>Betula alleghaniensis</i>	0.04	0.05	0.04	0.08	0.13	0.02	0.28	0.07	0.04	0.28	0.19	0.27	
<i>Fraxinus americana</i>	0.15	0.49	0.04	0.23	0.17	0.23	0.15	0.01			0.21	0.04	
<i>Acer rubrum</i>	0.04	<0.01		0.05		0.08							
<i>Pinus strobus</i>	0.07					0.21							
<i>Tilia americana</i>	0.18	0.03											
<i>Picea rubra</i>	0.03				<0.01	<0.01	<0.01	<0.01		0.05	0.06	0.04	
<i>Tsuga caroliniana</i>						0.16		0.12	0.02				
<i>Populus tremuloides</i>								<0.01	<0.01	0.01		0.02	
<i>Acer pensylvanicum</i>								<0.01	<0.01	0.02		0.03	
<i>Prunus serotina</i>													
<i>Ostrya virginiana</i>						0.03							
<i>Betula papyrifera</i>	0.02	<0.01											
<i>Prunus pensylvanica</i>													
<i>Abies balsamea</i>													
Total basal area (m ² ·ha ⁻¹)	51.29	44.96	44.01	24.29	29.70	47.37	34.28	27.89	27.61	25.05	24.22	28.93	

Note: Sites represent a gradient in soil [Ca²⁺] and are ordered from highest Ca (left) to lowest Ca (right). Species are arranged in order of mean relative abundance from top (highest) to bottom (lowest).

Fig. 3. Relationships between soil Ca (Oa horizon [Ca²⁺]) and live biomass of redback salamander (*Plethodon cinereus*) and mountain dusky salamander (*Desmognathus ochrophaeus*) at 12 upland northern hardwood forests sampled in 2009 in the Adirondack Mountains, New York. Biomass data were adjusted (+1.0 g) prior to natural log transformation to include sites where species biomass was zero ($n = 3$ for *D. ochrophaeus*) in regression models.



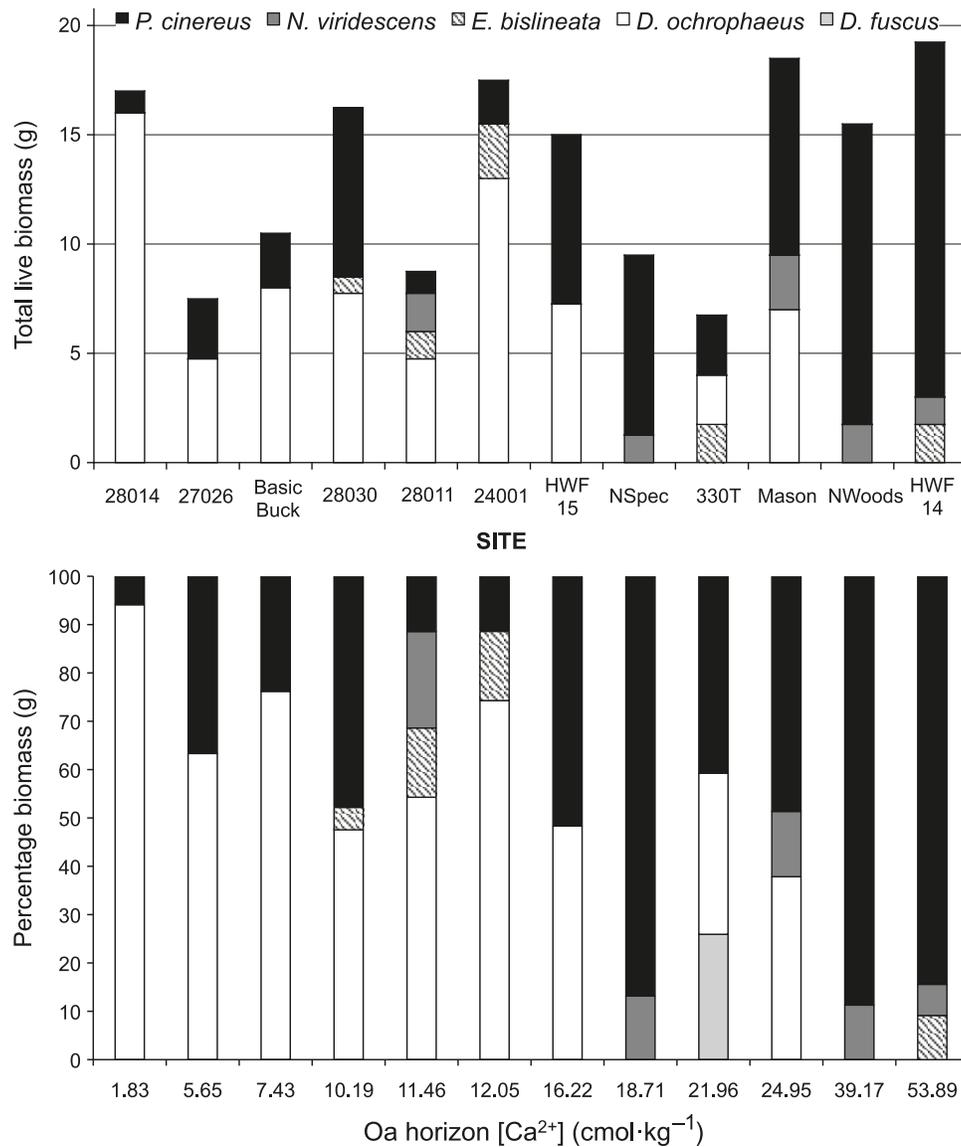
Community structure

As predicted by hypothesis 3, snail community structure varied significantly along the Oa [Ca²⁺] gradient based on a two-dimensional NMS ordination of 12 sites and 27 species (Fig. 5). Wet SO₄ deposition estimates and site elevation were also strongly correlated with the NMS axes and were negatively related to Ca (r^2 cutoff = 0.60).

Salamander community composition varied along the Ca gradient, with redbacks gradually replacing mountain duskies as the dominant species as soil [Ca²⁺] increased; in other words, redbacks were dominant at high-Ca sites, while mountain duskies dominated at low-Ca sites (Fig. 4). As a result, mountain dusky biomass was negatively correlated with redback biomass at the sites where both species were found ($\rho = -0.67, p < 0.05, n = 9$).

Using the same attribute matrix as for snails, the NMS procedure could not find a useful ordination for the salamander community. Several one-dimensional (rank) ordinations were generated and each had a single NMS axis that was strongly correlated with Oa [Ca²⁺], but these results did not provide any new information (in addition to Fig. 3).

Fig. 4. Salamander community structure (based on species relative abundance) along a soil Ca gradient (Oa horizon $[Ca^{2+}]$) consisting of 12 upland northern hardwood forests sites sampled in 2009 in the Adirondack Mountains, New York. Sites are ordered from lowest Ca (left) to highest Ca (right). Note that the HWF14 and HWF15 sites are located 225 m apart (Christopher et al. 2006).



The NMS procedure with tree species data (15 species), using basal area as a measure of relative abundance, also could not consistently find a stable solution. Several normalization and transformation techniques were used to modify tree species abundance data in attempt to find a stable NMS ordination, but none were successful.

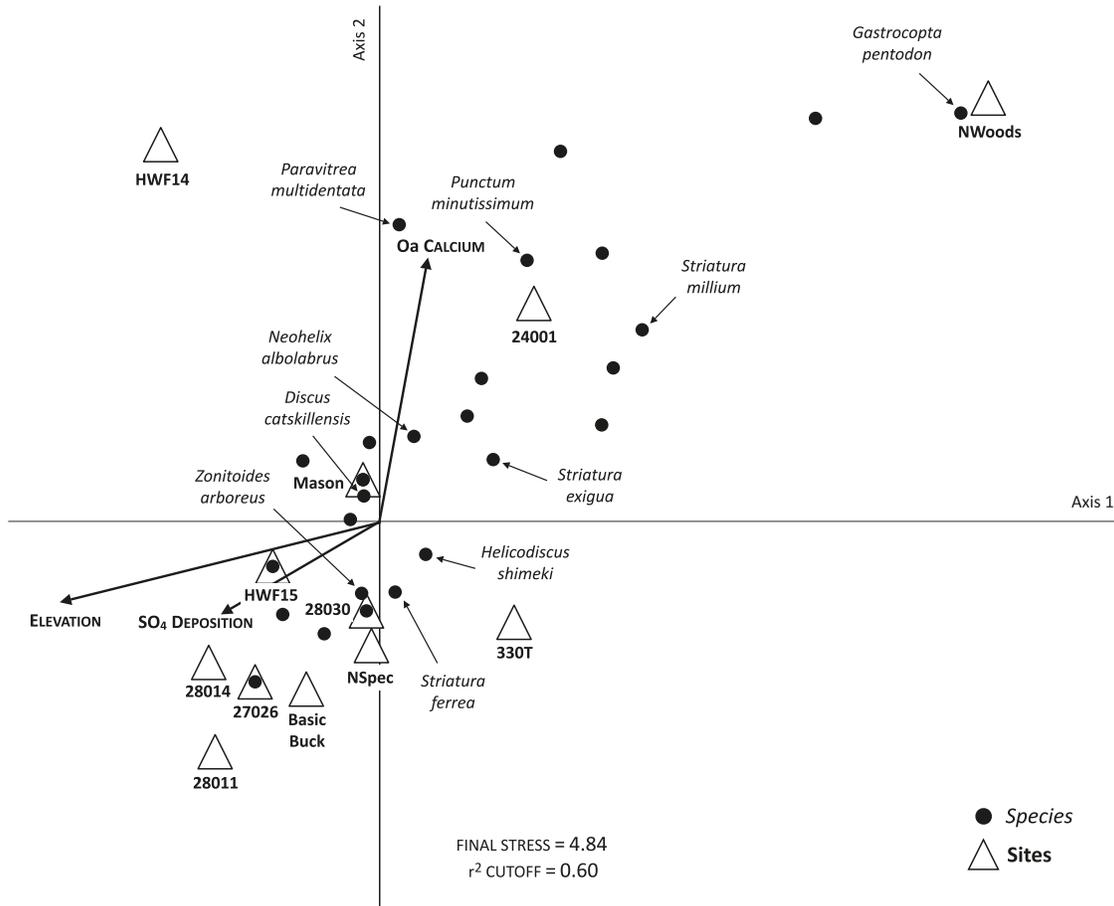
However, with all three communities (snails, salamanders, and trees) combined into one species matrix, the NMS procedure yielded a highly stable two-dimensional ordination of 12 sites and 47 species (Fig. 6). Similar to the snail community NMS results, Oa $[Ca^{2+}]$, elevation, and SO_4 deposition were most strongly correlated with the NMS axes (r^2 cutoff = 0.65).

Discussion

Our results point to several potential relationships between Ca availability and gastropod, amphibian, and plant commu-

unities in northern hardwood forests. Overall, we found support for our hypotheses that these communities, in terms of their species composition, abundance, and community structure, would be significantly shaped by biotic Ca availability (using the proxy of soil exchangeable Ca). We also observed that factors known to influence Ca availability in soils, such as acidic deposition, explained some of the observed variability in snail and salamander communities; however, there were very strong negative correlations ($\rho < -0.80$) between the Ca and deposition variables in our analysis. To complicate the picture further, our observation of decreasing snail abundance with increasing elevation was confounded by a strong positive correlation between elevation and acidic deposition estimates (due to the modeling technique used by Ito et al. 2002). Although all of these correlations make sense in biophysical terms, especially in the Adirondack Mountains where acidic precipitation has strongly influenced soil Ca (Sullivan et al. 2006; Johnson et al. 2008), our study was

Fig. 5. Land snail community ordination results (27 species, 12 sites) from nonmetric multidimensional scaling analysis (PC-ORD; McCune and Grace 2002). The 10 most abundant snail species found (among all sites) are labeled. Biplot vectors are depicted at an r^2 cutoff = 0.60; final stress = 4.84 for the two-dimensional ordination.



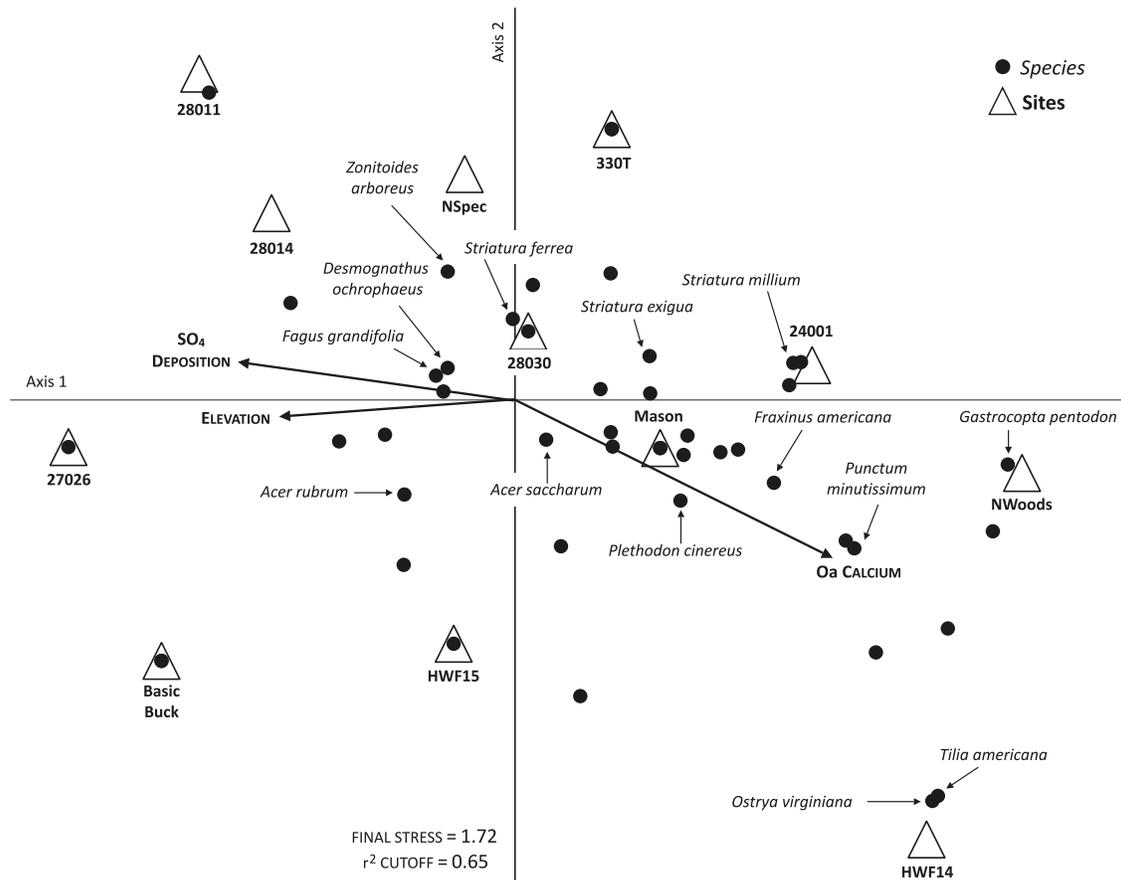
not designed to tease apart these effects on forest communities. Experimental studies are likely needed to investigate how these interacting factors of elevation (microclimate), deposition, and soil chemistry shape the availability and flows of Ca in forest ecosystems across multiple trophic levels.

Our observations of increasing species richness of land snails with increasing soil Ca are consistent with prior studies that found sensitivity to soil acidification (Hotopp 2002; Hamburg et al. 2003) and Ca availability (Johannessen and Solhøy 2001). However, we also observed that total snail abundance decreased along a relatively small gradient in elevation of 181 m (487–668 m). Decreasing snail abundance was mostly due to declining *Striatura* abundance with increasing elevation, as this genus comprised nearly one third of all snails collected. Although it is possible that we inadvertently sampled near an elevational limit for *Striatura* in the Adirondacks, such a range limit has not yet been described. Prior studies have shown that land snail communities are often characterized by differential species responses to a variety of biotic and abiotic factors (Tattersfield et al. 2001; Nekola 2003; Martin and Sommer 2004), which may include the microclimatic variability associated with elevational gradients in mountainous terrain.

The positive effect of soil Ca on redback salamander abundance is an important, although not unexpected, finding that

warrants further study. Redback salamanders are the most abundant vertebrates in the northern hardwood forests of eastern North America (Burton and Likens 1975b; Gibbs et al. 2007) and are considered “keystone” species that strongly influence forest floor trophic webs and the ecosystem-level metabolism of nutrients including Ca (Burton and Likens 1975a; Pechmann and Wilbur 1994). Although our observation of increasing redback biomass with higher soil Ca had not been yet documented in northern hardwood forests, it is consistent with evidence of the pH sensitivity of redbacks during reproduction as well as Al toxicity, which can occur when Al becomes mobilized in acidified soils (Frisbie and Wyman 1992; Wyman and Jancola 1992; Lawrence et al. 1995). It is also consistent with studies of redback salamander diets in the eastern deciduous forests, which have typically found Ca-rich prey such as gastropods and oribatid mites in stomach contents (Burton 1976), including the miniscule (<1 mm) Punctidae snails (Snyder 2011) that our current study found were highly calciphilic (Ca loving). Meanwhile, decreasing abundance of mountain dusky salamanders with increasing soil Ca is probably not due to any negative effect of Ca availability but possibly increased competitions with redbacks, since their abundance increases with Ca. Both plethodontid species are considered highly territorial (Petranka 1998).

Fig. 6. Multiple community (snails, salamanders, and trees) ordination results (47 species, 12 sites) from nonmetric multidimensional scaling analysis (PC-ORD; McCune and Grace 2002). Selected species are labeled based on relative abundance and (or) notable relationships with environmental gradients among sites. Biplot vectors are depicted at an r^2 cutoff = 0.65; final stress = 1.72 for the two-dimensional ordination.



We considered that the observed shift in salamander community composition along the Ca gradient might be alternatively explained by differences in habitat characteristics among sites, such as moisture (Jaeger 1971). Although mountain dusky are typically found more commonly in association with stream habitats (Wyman and Jancola 1992), we found no correlation between mountain dusky abundance and plot distance to the nearest stream. At this stage, our best insights on this question can be drawn from an ad hoc comparison of habitat features at our two closely adjacent (225 m apart) sample sites: HWF14 and HWF15 (see Christopher et al. (2006) for a detailed description of Ca biogeochemistry at these sites). The HWF15 salamander community, located in the middle of the Ca gradient, consisted of redbacks and mountain dusky in nearly equal abundance, while the high-end member HWF14 site consisted almost entirely of redbacks, and mountain dusky were absent (see Fig. 4). A re-sampling of these sites 1 year later (in 2010) found very similar results (Snyder 2011). This led us to conduct an ad hoc comparison of these sites, including measures of litter depth and volume, ground cover objects, proximity to streams, and microclimate. The results indicated no significant differences in these habitat characteristics between HWF14 and HWF15 (C.M. Beier, unpublished data), but a more in-depth investigation is needed to rule out habitat and (or) microclimatic conditions as an explanation for commu-

ity variability. Our current results more directly point to some effect of Ca availability, albeit through an unknown mechanism(s). The current working hypothesis for this mechanism involves differences in diet, particularly those Ca-rich prey including snails and mites (Jaeger 1972; Burton 1976; Fisk et al. 2006). Snyder (2011) recently assayed salamander diets and prey availability at the same Ca gradient sites to evaluate this hypothesis.

Lastly, we observed a general trend in forest composition and structure along the Ca gradient, with lower-volume, American beech – yellow birch forests at Ca-poor sites and higher-volume sugar maple – white ash forests at Ca-rich sites. Although these observations are consistent with known soil–vegetation relationships in the Adirondacks (Page et al. 2008), these results could be attributed partially or wholly to other factors, including historical forest management practices (including logging) and impacts of beech-bark disease, both of which have shaped Adirondack forests (Forrester et al. 2003).

Conclusions

In summary, our findings strongly support the hypothesis that Ca availability plays an important role in shaping northern hardwood forest communities at multiple trophic levels. Like the Adirondacks, much of the northern forest landscape has been affected by chronic acidic deposition leading to bio-

logically significant Ca losses from most (but not all) forest soils (Driscoll et al. 2001; Johnson et al. 2008). Some forest soils retain ample Ca because of base-rich parent materials (Lawrence et al. 1995; Johnson et al. 2008). In these forests, high Ca availability for biota may be maintained despite chronic deposition inputs and other disturbances that deplete nutrient stocks, such as forest harvest (Lawrence et al. 1995; Yanai et al. 2005). Our study of Adirondack forests included several of these Ca-rich sites and indicated that these forests could serve as neoreugia (sensu Nekola 1999) for calciphilic species in the surrounding matrix of acidified forests. In addition to their scientific value, persistent populations of calciphilic species at Ca-rich sites could serve as “rescue” populations for natural or human-aided dispersal to existing or restored sites with adequate soil conditions. Protecting these refugia may therefore be valuable for conserving biodiversity in forest landscapes exposed to acid rain. In addition, with the growing regularity of “bio-blitz” inventories occurring in the northern forest, the identification of Ca-rich forest patches as refugia could be based on utilizing calciphilic species as bioindicators in lieu of extensive soil sampling. Before such practical steps can be taken, several knowledge gaps must be addressed, including those mechanistic questions noted above as well the spatial and temporal dimensions of extant refugia at the species and community levels, the habitat characteristics of refugia, and the capacity of refugia soils to maintain Ca availability despite ongoing deposition and other stressors. Efforts to address these questions will have significant value for landscape conservation strategies that seek to mitigate the impacts of acid rain on biodiversity and ecosystem function.

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