Application of lime (CaCO₃) to promote forest recovery from severe acidification increases potential for earthworm invasion

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ABSTRACT

The application of lime (calcium carbonate) may be a cost-effective strategy to promote forest ecosystem recovery from acid impairment, under contemporary low levels of acidic deposition. However, liming acidified soils may create more suitable habitat for invasive earthworms that cause significant damage to forest floor communities and may disrupt ecosystem processes. We investigated the potential effects of liming in acidified soils where earthworms are rare in conjunction with a whole-ecosystem liming experiment in the chronically acidified forests of the western Adirondacks (USA). Using a microcosm experiment that replicated the whole-ecosystem treatment, we evaluated effects of soil liming on *Lumbricus terrestris* survivorship and biomass growth. We found that a moderate lime application (raising

pH from 3.1 to 3.7) dramatically increased survival and biomass of *L. terrestris*, likely via increases in soil pH and associated reductions in inorganic aluminum, a known toxin. Very few *L. terrestris* individuals survived in unlimed soils, whereas earthworms in limed soils survived, grew, and rapidly consumed leaf litter. We supplemented this experiment with field surveys of extant earthworm communities along a gradient of soil pH in Adirondack hardwood forests, ranging from severely acidified (pH < 3) to well-buffered (pH > 5). In the field, no earthworms were observed where soil pH < 3.6. In addition both abundance and species richness of earthworms was greatest in areas where soil pH > 4.4 and human dispersal vectors, including proximity to roads and public fishing access, were most prevalent. Overall our results suggest that moderate lime additions can be sufficient to increase earthworm invasion risk where dispersal vectors are present.

INTRODUCTION

Acidic deposition has resulted in the acidification and depletion of base cation nutrients from poorly-buffered forest soils across much of northeastern North America (Driscoll et al. 2001). Although sulfur and nitrogen oxide emissions, and the resulting deposition of strong acids, have sharply decreased since the passage of the Clean Air Act Amendments of 1990 the recovery of forest ecosystems from acidification has been slow (Lawrence et al. 2012). Impacts of acidic deposition have been particularly pronounced in the Adirondack Mountains of New York State (USA), a region of northern hardwood and mixed conifer forests with naturally acidic soils due to base-poor surficial geology (Driscoll et al. 1991, Driscoll et al. 2001). Application of crushed limestone, which is primarily calcium carbonate (CaCO_3 ; lime), has been used to hasten recovery of the acid neutralizing capacity (ANC) of surface waters. ANC is strongly associated

with important aquatic species such as *Salvelinus fontinalis*, brook trout (Schofield and Keleher 1996, Driscoll et al. 1996). With lower acidic deposition loads and increases in rainwater pH, liming has become an increasingly feasible approach for restoration of acid-impaired forests (Lawrence et al. 2011, Lawrence et al. 2012). Lime additions have been used to promote the productivity and health of *Acer saccharum*, sugar maple. (Long et al. 2011, Moore et al. 2012, Moore et al. 2015). Sugar maple is a valuable tree that experiences decreased crown vigor, recruitment, radial growth and foliar nutrition in chronically acid-impaired forest soils where biological Ca availability is low or negligible (Sullivan et al. 2013).

Although forest liming may support valuable species such as sugar maple, and more broadly foster the recovery of acid-impaired ecosystems (Battles et al. 2014), liming can also have unintended consequences that include deleterious impacts on beneficial invertebrate fauna (Fisk et al. 2006, Pabian et al. 2012, McCay et al. 2013,), as well as facilitation of non-native and invasive earthworms. Earthworms as a functional group have higher abundance, survival, biomass and fecundity in forest soils treated with lime, but responses differ among species with varying pH tolerance and nutritional demands (Springett et al. 1984, Chan and Mead 2003, Raty 2004, Pothoff et al. 2008, Bernard et al. 2009, Moore et al. 2013, Moore et al. 2015).

Among the acid-intolerant earthworms that might be most facilitated by forest liming, *Lumbricus terrestris*, known commonly as the ‘night-crawler’, is noteworthy for both its ecological impact and likelihood of introduction. This species feeds almost exclusively on leaf litter from the soil surface (Edwards and Lofty 1972) and in high densities will reduce litter volume on the forest floor (Hale et al. 2005, Hale et al. 2008). In experimental studies, the application of lime and addition of *L. terrestris* caused reductions in soil nitrogen, leaf litter volume and enchytraeid abundance (Raty 2004, Moore et al. 2013). Moreover, *L. terrestris* is

commonly used for fishing bait and may be found in commercial sources of potting soil, compost and mulch, resulting in a high likelihood of dispersal (Reynolds 1977, Hale 2008). If acidic soils prevent invasions of *L. terrestris*, then large-scale applications of lime (CaCO_3) could improve habitat suitability for these potentially destructive invaders of northern hardwood forests.

We present experimental and observational evidence of the effects of forest liming on earthworms – with a focus on *Lumbricus terrestris* – in the Adirondack Mountains, New York (USA). An experimental microcosm study was used to determine potential effects of a current ecosystem-scale liming treatment on the survivorship and biomass growth of *L. terrestris* in acidified soils ($\text{pH} < 3.5$; base cation saturation $< 12\%$) where this species has currently not been observed. We also conducted earthworm surveys, using soil extraction and timed search methods, in upland hardwood forests across the Adirondacks to evaluate earthworm abundance and species composition across a wide gradient in soil pH and base cation availability. We then evaluated the potential consequences of liming in Adirondack hardwood forests with respect to earthworm invasion risk.

METHODS and MATERIALS

Liming experiment – We conducted a microcosm experiment to evaluate the potential effects of a whole-ecosystem liming treatment on *L. terrestris* survivorship and growth, but without introducing these potentially invasive earthworms *in situ*. The whole-ecosystem experiment is being conducted in two small first-order catchments on the northwestern end of Honnedaga Lake, located in the southwestern Adirondacks, in Herkimer County, NY. Soils are spodosols with very poor buffering capacity that were formed in thin glacial till (Josephson et al. 2014) and due to their location have received among the highest chronic N and S deposition

inputs in North America (Driscoll et al. 2001). As a result, the soils at our study sites are some of the most acidic that can be found in upland hardwood forests in the region (Sullivan et al. 2006, Sullivan et al. 2013). In October 2013, 136 metric tons (150 U.S. tons) of pelletized Ca limestone was applied by helicopter, equivalent to a dosage of $1.4 \text{ Mg Ca ha}^{-1}$, to the 30 ha treatment watershed within the drainage of Honnedaga Lake. The high Ca pelletized lime originated from Shelburne, Vermont and was comprised of 36.5% Ca, 0.5 % Mg, and 91.25% CaCO_3 , with the pellet material being a highly soluble sodium salt lignin. The goal of the watershed treatment was to increase Ca availability in the soils and stream of this watershed to accelerate recovery from effects of acidic deposition. A nearby catchment of similar size, with similar biogeochemical and vegetation characteristics, was used as a reference.

We used a 3x3 factorial design with three levels of soil lime additions: 4.85 g, 9.7 g and 0 g (control), which were approximately equivalent to the *in situ* dosages of $1.4 \text{ Mg Ca ha}^{-1}$, $4.8 \text{ Mg Ca ha}^{-1}$, and 0 Mg Ca ha^{-1} , respectively. The second experimental factor was exposure duration, i.e., the amount of time earthworms in microcosms were left in the growth chamber before destructive harvesting. The levels of this factor were 14, 28 and 42 days. We established 54 microcosms with 6 replications per treatment. Microcosms were plastic greenhouse containers (24 x 10 cm) filled with soil and covered with leaf litter. Soil from the lower O, A, and upper B horizons was removed from the reference watershed at Honnedaga Lake in August 2014. Soil samples were mixed together, dried, sieved and added to microcosms to a height of 20 cm. Pelletized limestone from the same batch used in the Honnedaga Lake study was dissolved in deionized water and added as a slurry to the soil surface. Leaf litter (10 g) collected from the Honnedaga Lake reference watershed was added to each microcosm following lime slurry application and was replaced every two weeks (old leaf litter was removed prior to adding new

leaf litter). Two individuals of *L. terrestris* were weighed and added to each microcosm. Mesh screens and cheesecloth were secured on the top and bottom of the containers. Live earthworms were obtained from Carolina Biological Supply Company. Microcosms were placed in a growth chamber with 14 hours of daylight, a fluctuating temperature regime (21°C during daylight hours and 19°C during night), and were watered 2-3 times per week.

At the end of each exposure duration period (14, 28 and 42 days), we measured survivorship and live biomass of *L. terrestris* in a group of randomly selected microcosms. Microcosms were destructively harvested and were not repeatedly measured. Survivorship at the microcosm level was recorded if both earthworms were alive and present at the sampling date. Mortality was recorded if one or both earthworms were dead or, in the case of the lime treatments only, escaped from the microcosm. To estimate the biomass change per microcosm, we subtracted the average initial live mass from the average final live mass (at the removal date) for each microcosm. We only used live earthworms to estimate biomass changes.

After the experiment concluded, we analyzed soil from microcosms to estimate the effects of the liming treatment. Soils were air dried at room temperature, subsampled and measured for Ca and Al using inductively coupled plasma optical emission spectrometry after extraction with 1 M NH₄Cl and 1 M KCl, respectively. Percent organic matter was estimated using the loss on ignition method, and pH was measured in 0.01 M CaCl₂. All soil analyses were conducted at the USGS Water Science Center in Troy, NY. Further details on soil analysis can be found by referencing the methods utilized in Lawrence et al. (2012).

We used the nonparametric Fisher's Exact Test (Fisher 1922) to identify effects of lime and exposure duration on earthworm survivorship, and two-way ANOVA to measure treatment effects on biomass change. The effects of our soil liming treatments on pH, percentage of

organic matter and exchangeable [Ca] and [Al] were assessed using a one-way ANOVA. The Tukey method was used for all pairwise means comparison (Tukey 1953). We used residual analysis to examine assumptions of normality and Levene's test for homogeneity of variance. All tests were conducted with an $\alpha = 0.05$.

Field survey – We conducted sampling for earthworms at 14 upland hardwood forests that had been previously studied (Beier et al. 2012). Together these sites represented a regional gradient in soil pH (2.80 – 5.04) and exchangeable [Ca] (Oa horizon 3.7 – 53.89 cmol_c kg⁻¹; B horizon 0.35 – 7.73 cmol_c kg⁻¹ for upland hardwood forests in the Adirondack Mountains, NY). Soil variation was due largely to differences in parent material lithology as well as acidic deposition inputs (Sullivan et al. 2013). Soil chemistry data, including pH and exchangeable [Ca] in the Oa and B horizons, were compiled by Beier et al. (2012). All sites were located in upland northern hardwood or mixed hardwood forests (with no greater than 25% conifer basal area in the overstory), between 400 and 700 m elevation, at least 100 m from open water, and had not been logged since 1950.

Earthworm sampling was conducted using both mustard extraction and timed-search methods at two intervals: from 11 June to 4 July 2014, and from 29 September to 11 October 2014. At each site, a 10x10 m plot was established around the locations of existing quantitative soil pits from which the site-level data were compiled (see Beier et al. 2012). Within this plot, 0.125 m² plots in each corner were sampled using mustard extraction. A mustard solution of 10g/L (Lawrence and Bowers 2002) was poured inside the 0.125 m² plot frame and earthworms were sampled for a 10 minute period. Afterward, a timed search was conducted beneath all cover objects within the 10 x 10m plot by two observers for 20 minutes each. All earthworms collected were stored in 10% buffered formalin and identified to species using the dichotomous keys in

Reynolds (1977) and Schwert (1990). Earthworm counts based on the two collection methods and two survey periods were summed to estimate total earthworm abundance and species composition at the site level.

RESULTS

Soil liming treatments significantly increased soil pH and exchangeable [Ca], decreased exchangeable [Al], and had no effect on soil percent organic matter (Table 1). Addition of lime increased soil pH from 3.18 in the control microcosms to 3.67 and 4.25, for the 1.4 Mg Ca ha⁻¹ and 4.8 Mg Ca ha⁻¹ liming treatments, respectively (Table 1).

We observed a large positive effect of soil liming on *L. terrestris* survivorship ($p < 0.0001$) in microcosms. No earthworm mortality was observed in 78% (14/18) of microcosms with mean pH 3.66, and in 83% (15/18) of the microcosms with mean pH 4.25. Survivorship was lowest in the unlimed treatment with mean pH 3.18, with 83% of the microcosms experiencing partial or complete mortality (Figure 1). Nearly all mortality in the unlimed treatment occurred within the first two weeks of introduction. Survivorship decreased with longer exposure duration, but this effect was not considered significant ($p = 0.07$).

Soil liming had a positive effect on *Lumbricus terrestris* biomass change ($p < 0.0001$). We observed that earthworms in limed microcosm soils were able to grow and consume nearly all of the provided leaf litter. By contrast, mean biomass declined sharply for the few worms that survived in the unlimed microcosms (Figure 1). Neither the effects of exposure duration, nor the interaction between liming and duration, were significant (both $p = 0.18$).

In field surveys, we only observed earthworms in upland hardwood forests with organic horizon (Oa) soil pH > 3.63 , and nearly all earthworms (97%) were observed in forests with Oa

pH ≥ 4.42 . The upper pH threshold corresponds approximately to Oa horizon [Ca] $\geq 26 \text{ cmol}_c \text{ kg}^{-1}$ (Figure 2) or B horizon [Ca] $\geq 2.5 \text{ cmol}_c \text{ kg}^{-1}$ (not shown). A total of 7 species were observed in 6 genera; minor differences in earthworm abundance and species diversity were observed between the two sampling intervals and sampling methods (Appendix 1).

We also noted a strong qualitative contrast between two closely adjacent study sites HWF14 and HWF15, which are located only 250 m apart, but due to fine-scale differences in parent materials, the pH at HWF14 (5.04) is much higher than HWF15 (3.62), and organic soil [Ca] at HWF14 ($53.89 \text{ cmol}_c \text{ kg}^{-1}$) is nearly three times that at HWF15 ($16.22 \text{ cmol}_c \text{ kg}^{-1}$) (Appendix 2; also see Beier et al. 2012). Six earthworms were collected at HWF14, but none were observed at HWF15. Both sites have similar land use history and relatively low invasion pressure due to their location far from lakes or roads on the Huntington Wildlife Forest (a SUNY ESF research property closed to public access).

DISCUSSION

Our study confirms that liming of forest soils can create more suitable habitat for acid-intolerant earthworms, such as *Lumbricus terrestris*, and provides further evidence of the importance of soil pH as a limiting factor for earthworm establishment in northern hardwood forests. Forest liming in Canada led to an increase in *L. terrestris* survivorship, mass, and reproductive output (Moore et al. 2013); and in New York, liming was associated with increased survivorship of *Amyntas agrestis* and growth rate of *Eisenia foetida* (Bernard et al. 2009). Relative to these studies, however, our microcosm experiment – and the whole-ecosystem liming study on which it was based – involved soils that were much more acid-impaired to begin with, and applied lesser dosages of lime, resulting in much smaller increases in soil pH. We raised pH

in the microcosms from 3.1 to 3.7, whereas the above studies raised soil pH from 3.5 – 4.5 to 5 – 7.

Our data support the notion that acidified hardwood forest soils in the Adirondacks – a regional ‘hot-spot’ for acid deposition in eastern North America – may constrain earthworm invasion. In microcosms that contained acidified Adirondack forest soils of pH 3.1, less than 15% of *L. terrestris* survived a six-week period, and those that survived did not gain biomass. By raising the pH to 3.7, a value at the low end of the pH range for *L. terrestris*, (Laverack 1961, Vimmerstedt 1983, Judas et al. 1997), over 75% of *L. terrestris* survived, rapidly consumed leaf litter, and gained biomass over a six-week period. Doubling the lime dosage, which raised pH > 4.0, caused little additional positive effect on *L. terrestris* survivorship and growth over the short duration of the experiment.

The rapid mortality of *L. terrestris* observed in unlimed microcosms indicated that pH was likely the proximate factor, beyond any additional or synergistic negative effects that might be expected from nutritional deficiencies caused by low calcium availability (which is concomitant with low pH). Low survivorship in very acid soils may be attributed in part to disruptions in physiological processes in earthworms, such as electrolyte and mucus production, (Rusak and Marshall 2000) caused by the exposure to inorganic Al which is mobilized in acidified soils (Lawrence et al. 1995). Earthworms detect and avoid substrates that are too acidic and contain high concentrations of Al (Laverack 1961, Edwards and Lofty 1972, Auclerc et al. 2011, Zhang et al. 2013).

In addition, the nutritional quality of leaf litter also shapes earthworm communities (Hendriksen 1990, Reich et al. 2005, Hobbie et al. 2006; Holdsworth et al. 2008, Holdsworth et al. 2012); however, these interactions may be less important in forests with very acid soils

(Bernard et al. 2009). Recent studies indicate that earthworm distributions in conifer and hardwood plantations in New York are more closely associated with soil pH than tree species composition (Stoscheck et al. 2012); while in Germany, the effects of deciduous tree composition on earthworm abundance were only detectable in soils with relatively high pH (Ammer et al. 2006).

Our results suggest that even a moderate liming treatment (relative to prior studies) could facilitate earthworm invasion in acid-impaired hardwood forests. Our field survey identified a minimum pH threshold of between 3.6 and 5.0 for earthworm presence, which corresponds well to previous work (Shakir and Dindal 1997; Curry 1998; Stoscheck et al 2012). Although we observed a minimum pH threshold (for earthworm presence) of approximately 4.4 in the field survey, compared to 3.6 in the experimental study, it is likely that a liming treatment similar to that conducted at Honnedaga Lake would sufficiently raise pH at all of our survey sites to exceed the minimum pH threshold for *L. terrestris*. Discrepancies in soil pH thresholds between the field and experimental studies are likely attributable to differences in land use history and exposure to dispersal vectors. High densities of earthworms in rural and remote forest landscapes are commonly associated with boat launches, roads and campsites (Holdsworth et al. 2007), where exposure to human dispersal vectors is greatest. Our survey results may have been influenced by such precursors for earthworm introduction, which we did not explicitly control for in our data analysis, but instead sought to minimize by sampling in remote forests far from roads and human settlements.

In addition, the liming dosage used in our microcosm experiment, which emulated the treatment applied to a 30 ha watershed at Honnedaga Lake, is similar to real-world management practices for the purposes of soil nutrient recovery and stand improvement. Although large lime

applications pose logistical challenges and could have undesirable ecological effects, smaller and geographically focused liming treatments targeted at valuable resources can be practical and potentially cost effective. Where creation of suitable habitat for invasive earthworms could be an unintended consequence of liming, this risk could be mitigated simply by relying on the toxicity of unlimed soils surrounding the restoration site. In acidified landscapes such as the western Adirondacks, unlimed areas with very acidic soils could be left to provide a barrier to migration of the invasion front from introduction points (e.g., along roads, old fields, boat launches) to interior forests.

Although remote forests in protected areas like the Adirondacks may be at relatively low risk to earthworm invasion, preventing earthworm introductions by people requires education and outreach programs, as well as regulations on the use and disposal of live bait in recreational fishing areas. It is widely believed by the public that earthworms are beneficial to the environment (Seidl and Klepeis 2011) and most people are unaware that earthworms may be invasive or have negative effects in northern forest ecosystems. Such beliefs can result in improper disposal of earthworms, particularly those used as fishing bait (Killian et al. 2012). To minimize earthworm introduction risk in acid-impaired forests where lime applications have or will occur, invasive species education and mitigation measures may be incorporated in forest management plans that seek to promote recovery from acidification.

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Table 1. Mean soil microcosm pH, exchangeable [Al] and [Ca], and percent organic matter by soil lime treatment. Mean values (SE) within a column that share a letter are not significantly different at $\alpha = 0.05$ based on the Tukey method.

Soil Lime Treatment	pH	Exchangeable Al (cmol _c kg ⁻¹)	Exchangeable Ca (cmol _c kg ⁻¹)/kg	Soil Organic Matter (%)
Control	3.18 (0.05) ^A	13.36 (0.52) ^A	3.34 (0.19) ^A	38.35 (1.05) ^A
1.4 Mg Ca ha ⁻¹	3.67 (0.05) ^B	5.59 (0.33) ^B	12.62 (0.44) ^B	44.04 (3.18) ^A
4.8 Mg Ca ha ⁻¹	4.25 (0.06) ^C	0.84 (0.14) ^C	25.71 (1.50) ^C	44.46 (2.03) ^A

FIGURE CAPTIONS

Figure 1. The response of survivorship to lime treatment (A) and exposure duration (B), and live biomass change to lime treatment (C) and exposure duration (D) of *Lumbricus terrestris* in soil microcosms. Survivorship is reported at the microcosm level (both worms survived) and treatment effects were evaluated using Fisher's Exact Test. Mean changes in biomass (± 1 SE) were measured for only living *L. terrestris*, which resulted in uneven sample sizes. Results for exposure duration effects include all treatment levels of lime. Treatment effects were evaluated using Tukey's method for comparison of means (values that share a letter are not significantly different at $\alpha=0.05$).

Figure 2. Cumulative distributions of earthworm abundance (all species) along gradients in pH and exchangeable [Ca] in the Oa soil horizon in upland hardwood forests of the Adirondack Mountains, New York.

Figure 1

Figure 2