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Literature Review on the Effects of Chronic Soil Calcium Decline and Soil Acidification on Terrestrial Forest Crustaceans and Molluscs

Prepared for: Friends of the Muskoka Watershed
Job #: J230021

February 22, 2023

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February 22, 2023

HESL Job #: J230021

Dr. Norman Yan
Friends of the Muskoka Watershed
Via email: normandyan@gmail.com

Dear Dr. Yan:

Re: Final Report - Literature Review on the Effects of Chronic Soil Calcium Decline and Soil Acidification on Terrestrial Forest Crustaceans and Molluscs

I am pleased to submit the following final report summarizing the literature review on the effects of chronic soil calcium decline and soil acidification on terrestrial crustaceans and molluscs.

I thank you for the opportunity to undertake this interesting assignment and hope that the findings of the literature review are helpful to the Friends of the Muskoka Watershed.

Sincerely,
Per. Hutchinson Environmental Sciences Ltd.

Andrea Smith, Ph. D.
Senior Scientist

Signatures

Report Prepared by:

Andrea Smith, Ph. D.
Senior Scientist

Executive Summary

Long-term atmospheric deposition of strong acids ('acid rain') has caused widespread changes to forests in eastern North America and Europe. The effects of acid rain on forest trees have been relatively well studied. In contrast, relatively little is known about the impacts on other terrestrial forest biota. Calcium is an essential nutrient for plants and animals, and its deficiency in forest soils could have cascading effects throughout forest food webs. Forest organisms with high calcium demand, such as land snails and isopods, may be especially threatened by soil acidification and subsequent calcium leaching. These terrestrial invertebrates play a critical role in forest ecology, decomposing forest litter, recycling nutrients, building soils, and acting as food and sources of calcium for other forest taxa, including other invertebrates, amphibians, reptiles, birds, and mammals. Negative impacts of soil acidification and calcium decline on terrestrial crustacean and mollusc species could potentially have significant implications for forest decomposition, nutrient dynamics, and trophic interactions in forest ecosystems.

The Friends of the Muskoka Watershed is interested in documenting current science on the effects of chronic soil acidification and soil calcium decline on terrestrial crustaceans and molluscs. The following report summarizes results from a literature review that was conducted to synthesize the state of knowledge on the topic.

Relatively little research has focused on the effects of soil acidification and calcium decline on terrestrial crustaceans and molluscs, and most of the existing literature has focused on land snails. Of the 31 papers reviewed in this study, 17 examined effects on land snails and/or isopods, and six examined effects on snails, isopods, and birds, for a total of 23 papers focused on this topic over the last 50 years (1969-2019). Prior to 2002, all studies reviewed were conducted in Europe, however, since that time an equal number have come from eastern North America (although none from Canada).

The literature review indicated that snails and isopods respond negatively to acidification and calcium leaching, and positively to enriched calcium availability (either through natural calcium-rich soil conditions or experimental liming). Numerous studies documented changes in snail abundance, species richness, and density in relation to calcium availability in soil or litter. The few studies available for isopods showed that calcium availability affected their distribution, and growth and mortality rates. Calcium depletion and its impacts on these invertebrate taxa may affect higher trophic levels, such as birds, both directly (e.g., through effects on eggshell formation) and indirectly (e.g., through increased exposure to toxic metals). Studies in North America suggest that calcium limitation may be widespread for the avian community, but relatively undetected because of its subtle effects.

The impacts of soil acidification and calcium decline on forest biota remain largely unknown. While calcium availability appears to be a strong driver of forest communities at multiple trophic levels, other factors, including soil and litter moisture, availability of other elements, and forest type and age, likely interact with, and influence the importance of, calcium levels. More research is needed to better understand the effects of soil acidification and calcium decline on terrestrial forest biota, particularly in forests of eastern Canada.

Table of Contents

List of Tables

1. Introduction

Long-term atmospheric deposition of strong acids ('acid rain') has caused widespread changes to forests in eastern North America and Europe (Graveland and van der Wal 1996, Huntington 2000, Lovett et al. 2009). Sulphate and nitrate in precipitation leach important cation nutrients, such as calcium and magnesium, from foliage, leaf litter, and soil, leading to the acidification of soils (Lovett et al. 2009). In regions where soils are naturally low in base cations, soil acidification can have profound effects on forest tree species with high calcium or magnesium requirements (e.g., Sugar Maple, *Acer saccharum*; Basswood, *Tilia americana*; Lovett et al. 2009). Loss of soil calcium has been linked, for example, to reduced health of Sugar Maple, adversely affecting tree growth and overall condition, seedling survival and regeneration, and foliar nutrition (Azan et al. 2019). Calcium depletion of forest soil can be further exacerbated by timber harvesting, which removes high quantities of calcium stored in tree wood and leaves from forest ecosystems (Schaberg et al. 2001). Soil acidification can also mobilize aluminum in forest soil, which is toxic to tree roots in high concentrations (Lovett et al. 2009).

The effects of acid rain on forest trees have been relatively well studied (especially for economically important species, such as Sugar Maple; April and Hluchy 2008). In contrast, relatively little is known about the impacts on other terrestrial forest biota (Beier et al. 2012). Calcium is an essential nutrient for plants and animals, and its deficiency in forest soils could have cascading effects throughout forest food webs (Schaberg et al. 2001, Hotopp 2002). Forest organisms with high calcium demand, such as land snails and isopods, may be especially threatened by soil acidification and subsequent calcium leaching (Bondi 2015). These terrestrial invertebrates play a critical role in forest ecology, decomposing forest litter, recycling nutrients, building soils, and acting as food and sources of calcium for other forest taxa, including other invertebrates, amphibians, reptiles, birds, and mammals (Jordan and Black 2012, Tompson et al. 2013). Negative impacts of soil acidification and calcium decline on terrestrial crustacean and mollusc species could potentially have significant implications for forest decomposition, nutrient dynamics, and trophic interactions in forest ecosystems (Ohta et al. 2014, Bondi 2015).

The Friends of the Muskoka Watershed (FOTMW) is interested in documenting current science on the effects of chronic soil acidification and soil calcium decline on terrestrial crustaceans and molluscs. The following report summarizes results from a literature review that was conducted to synthesize the state of knowledge on the topic.

2. Information Sources

Two online research search engines, Google Scholar and Web of Science™, were used to identify and assemble a list of current scientific literature related to soil acidification, soil calcium decline, and terrestrial invertebrates. The focus of the study was on forests typical of the Muskoka region, including mixed hardwood forests of eastern North America and central and northern Europe, and on terrestrial crustaceans and molluscs. Search terms included 'forest soil acidification', 'forest soil calcium decline', 'soil calcium depletion', 'terrestrial crustaceans', 'terrestrial molluscs', and 'terrestrial invertebrates'.

A total of 37 papers were identified through the online search. These publications were screened by scanning abstracts and narrowed down to 31 papers focused on the topic, spanning the period 1969 to 2019. All relevant literature was read in full and is summarized in the following sections of the report.

3. Summary of Literature Review

3.1 Effects on Crustaceans and Molluscs

3.1.1 Gastropods

Most of the existing literature on the effects of soil acidification and calcium decline on crustaceans and molluscs is focused on land snails (Table 1). Snails are useful biological indicators of ecosystem health due to their limited mobility, small home ranges, specific habitat requirements, and sensitivity to environmental conditions (Jordan and Black 2012). Snails have higher calcium requirements than other invertebrates because of their shells and represent the most concentrated form of calcium in the detrital food web (Bondi 2015). They assimilate calcium from bedrock and soil as calcite ($CaCO_3$), and from leaf litter, which contains the more soluble calcium citrate form (Wäreborn 1969, Juřičková et al. 2008). Calcium deficiency can lead to thinner and more fragile shells, making snails vulnerable to desiccation, physical damage, and predation (Johannessen and Solhøy 2001). Most land snails feed on a variety of plant material, including living vegetation, rotting leaves, wood, sap, and fungi (Hotopp 2002). They also ingest soil particles and scrape rocks and snail shells to obtain additional calcium to support shell development, reproduction, and other physiological functions (Graveland and van der Wal 1996, Hotopp 2002).

Land snails tend to be more abundant and diverse in areas characterized by calcium-rich soils compared with calcium-deficient areas (Juřičková et al. 2008, Bondi et al. 2019). Chemical characteristics of upper soil horizons and leaf litter, such as calcium content, pH, and base saturation, may reflect nutrient availability and habitat suitability for snails, and numerous studies have found that forest snail communities are influenced by these parameters. For example, studies from mixed and deciduous forests in Sweden found that snail abundance and species richness were positively correlated with the calcium content of forest litter (Wäreborn 1969), while snail density was positively correlated with calcium content, pH, base saturation, and base cation concentration of forest litter (Gärdenfors et al. 1995). Similar findings were documented in the Netherlands, where snail density was positively correlated with calcium concentration, and to a lesser extent, pH, of leaf litter (Graveland and van der Wal 1996). Snail abundance was also positively correlated with calcium levels, pH and base saturation of soils in oak forests in Norway (Johannessen and Solhøy 2001). In the central Appalachian Mountains of Maryland, snail density and species richness showed positive correlations with extractable calcium, water soluble calcium, and pH in upper soil horizons (Hotopp 2002). Snail abundance was positively correlated with calcium leaf litter concentrations at Hubbard Brook Experimental Forest, in New Hampshire (Skeldon et al. 2007), while snail abundance and species richness were positively associated with soil calcium levels in hardwood forests in the Adirondack Mountains, in New York (Beier et al. 2012).

There is not always a clear relationship between snail assemblage patterns and soil and litter conditions. Juřičková et al. (2008) studied snails at two sites in the Czech Republic with strong gradients in soil calcium. They found that soil pH was a good predictor of soil calcium levels when the gradient was long and included highly calcareous rock (i.e., high pH indicated high soil calcium, which influenced snail species richness, composition, and total abundance). However, in this case litter calcium levels did not reflect soil calcium conditions and did not correlate highly with snail distribution patterns. In contrast, when the soil calcium gradient was shorter, and included calcium-deficient habitat, soil pH was no longer a good predictor of soil calcium availability, and litter calcium levels were more strongly correlated with snail species richness. Juřičková et al. (2008) concluded that different measures of calcium availability cannot necessarily serve as reliable surrogates for each other. Soil calcium levels were the best predictor of snail species composition, likely because they are less sensitive to seasonal fluctuations, and thus more stable, than litter levels (Juřičková et al. 2008).

Snail distribution patterns may also be influenced by other environmental variables, such as soil moisture and temperature, availability of dead wood, slope, microtopography, and predator abundance (Wäreborn 1969, Skeldon et al. 2007). However, in calcium-poor forests, calcium availability appears to be the main mechanism limiting snail populations (Gärdenfors et al. 1995, Hamburg et al. 2003, Skeldon et al. 2007). Stand age may also play a role in forest calcium cycling and how readily calcium is mobilized from the soil. Hamburg et al. (2003) found that snails were three times more abundant in young hardwood forest stands (<30 years old) compared with old forest stands (>30 years old) at previously harvested sites in New Hampshire, and that snail abundance was related to calcium content in the forest litter. Early successional tree species regenerating clearcuts often include species such as Pin Cherry (*Prunus pensylvanica*), which has high foliar calcium concentrations (Skeldon et al. 2007). As forests age, dominance shifts to tree species with lower calcium levels, such as American Beech (*Fagus americana*). Hamburg et al. (2003) documented corresponding declines in calcium mobilization with stand age (3.3-4.7 g Ca/m2/yr from soils in young stands vs. <1 g/m2/yr from soils in old stands) and suggested that younger forests were better able to transfer soil calcium to other components of the ecosystem, and to create stores of calcium in the forest floor and in living biomass. As a result, older forests were potentially more susceptible to calcium depletion than younger stands (Hamburg et al. 2003).

Numerous studies have found that snail populations in acidified forests respond favourably to liming, probably because the process improves calcium availability. Snail density increased by 10 to 90 times after experimental liming (2 tons of limestone/ha or 0.18 kg/m^2 of limestone) occurred in beech forests in Sweden, although the positive effects were more evident at sites where litter calcium concentrations were below 12%, suggesting a threshold effect of treatment (Gärdenfors et al. 1995). Liming of soil (0.3 kg/m^2 of dolomitic lime) in forests in the Netherlands resulted in increases in the extractable calcium content of soil and a corresponding increase in snail numbers (Graveland and van der Wal 1996). Four years after treatment, limed plots in both young (12 year old) and old (40 year old) oak forest stands had significantly more snails than unlimed plots. Limed plots in young forest had 20 times more snails than limed plots in old forest, and snail density in these plots was comparable to that measured in calcium-rich forests (Graveland and van der Wal 1996). Shell sand (1.6 kg/m^2) applied to oak forest in Norway led to a significant increase in both the abundance and species richness of snails compared with reference plots (Johannessen and Solhøy 2001). The observed increases were thought to be due to snails migrating into the area from surrounding calcium-poor habitat, since the liming duration (5 weeks) was likely too short for changes to be documented in reproductive rate (Johannessen and Solhøy 2001).

Land snail abundance was studied over 10 years in response to liming in two watersheds at the Hubbard Brook Experimental Forest. Snail abundance was 73% higher in the watershed that received liming (as wollastonite, $CaSiO_3$, 0.16 kg/m^2) than in the reference watershed three to seven years following application (Skeldon et al. 2007). The two watersheds showed no differences in snail abundance in the three years prior to treatment, and no differences were found in slug abundance between the two sites in any year. Isotopic tracer analysis determined that an average of 76% of calcium in snail shells five years after liming was attributable to the application (Skeldon et al. 2007). In Pennsylvania, liming (0.45 kg/m^2) resulted in an initial 23-fold increase in snail abundance three years post-application, and an 11-fold increase five years after treatment, compared to no significant change at reference sites (Pabian et al. 2012). Similarly, snails increased in abundance in experimentally limed (1 kg/m^2) forests in New York, corresponding with higher rates of litter decay than in unlimed plots (McCay et al. 2013).

Calcareous road dust also appears to influence forest snail populations. Land snails were studied along 50 m transects perpendicular to roads surfaced with limestone gravel in mixed forests in the Appalachian Mountains of Kentucky (Kalisz and Powell 2003). Extractable calcium and pH in soil were significantly higher along roads than 25 or 50 m away, both declining with distance from the roads. While snail abundance and species diversity did not differ along the transects, dry mass of snails was significantly higher at the roadsides compared with 25 or 50 m away and was positively correlated with both extractable calcium and pH. The increased dry mass of snails close to roads was driven by a taxonomic shift of the snail community, with roadside habitat dominated by a large snail species (*Triodopsis albolabris*) which was absent 50 m from the road (Kalisz and Powell 2003).

3.1.2 Isopods

Few studies were found in the literature review that focused on terrestrial crustaceans, and these only examined terrestrial isopods (Ormerod and Rundle 1998, Tompson et al. 2013, Ohta et al. 2014; Table 1). The limited research available on the effects of soil acidification and calcium decline on these organisms suggests that, like land snails, isopods are highly sensitive to calcium availability. Terrestrial isopods have high calcium demands to support the development and frequent molting of their mineralized cuticle (Tompson et al. 2013). Calcium also regulates their gut pH, allowing them to digest plant polysaccharides (Tompson et al. 2013).

The number of isopods remained low at all sites on calcium-poor soils in Norway and Wales, regardless of experimental acidification or liming (comprising less than 0.1-0.7% of total invertebrates; Ormerod and Rundle 1998). Interestingly, no molluscs were collected at any of the study sites, including reference locations. Ormerod and Rundle (1998) concluded that calcium-rich invertebrates, such as crustaceans and molluscs, may already be naturally rare in base-poor locations, independent of acid deposition. The isopod *Porcellio scaber* (a European wood louse which has been introduced throughout the world) responded positively to liming in a laboratory microcosm experiment. Animals had lower growth rates when exposed to strongly acidic (pH 3) compared with weakly acidic (pH 5) simulated precipitation. Individuals in limed microcosms (0.8 kg/m^2) exhibited higher growth rates and lower risk of mortality than those in unlimed conditions. When exposed to strongly acidic simulated precipitation, isopods in limed conditions had higher whole-body calcium concentrations than those in unlimed microcosms (Tompson et al. 2013). The distribution of the isopod *Ligidium japonicum* (a Japanese wood louse) was influenced by both soil extractable calcium concentration and leaf litter calcium content in Japanese forests (Ohta et al.

2014). Cedar plantations, where the species was found, had significantly higher concentrations of both soil extractable and litter calcium content (three to four times higher), than evergreen broad-leaved forests, where the species was absent (Ohta et al. 2014).

3.2 Effects on Higher Trophic Levels

3.2.1 Birds

Changes in invertebrate prey caused by soil acidification and calcium decline can have repercussions on higher trophic levels in forest ecosystems. During the breeding season, female birds require significant amounts of calcium for egg-laying, on the order of 10 to 15 times more than similarly sized mammals (Hames et al. 2002). Small forest birds may use more calcium to produce a single clutch of eggs than is found in their entire skeletons (Pabian and Brittingham 2011). Unable to store much calcium in their skeleton, female birds must thus depend on calcium-rich food to support eggshell production (Graveland et al. 1994) and snail shells are a primary source of calcium for many breeding forest songbirds (Graveland and van der Wal 1996). Insufficient supply of calcium during reproduction can lead to thin brittle eggs that break easily, are prone to desiccation, and which fail to develop properly (Hames et al. 2002). Chicks also have high calcium requirements for skeletal development (Schlender et al. 2007). Toxic compounds such as aluminum, cadmium, and lead are increasingly mobilized under conditions of soil acidification and calcium depletion, which may also lead to a toxic food supply for passerines (Hames et al. 2002).

Acid rain has been linked to numerous reproductive impairments for forest passerines in Europe due to calcium deficiency, including eggshell defects, clutch desertion, unhatched eggs, incubation of empty nests, and delayed laying (Drent and Wodendorp 1989, Graveland et al. 1994, Graveland and van der Wal 1996, Mänd et al. 2000; Table 1). Feeding experiments, in which breeding birds were supplemented with additional sources of calcium (such as snail shells and chicken eggshells) improved reproductive success of forest passerines in acidified habitats (Graveland et al. 1994, Graveland and van der Wal 1996, Mänd et al. 2000).

The songbird community may be differentially affected by soil acidification. A study in German beech forests found that Song Thrush (*Turdus philomelos*) and Nuthatch (*Sitta europaea*) increased territory density in relation to soil calcium content, and Song Thrush and Blackbird (*Turdus merula*) had higher nesting success (measured as number of fledglings) in forests with the highest calcium content compared with forests with the lowest content (Schlender et al. 2007). Several songbird species, however, showed unexpected increases in territory density with rising soil acidification (Robin, *Erithacus rubecula*; Chaffinch, *Phylloscopus collybita*, and Coal Tit, *Parus ater*). This pattern seemed to be related to the primary diet of these species (arthropods, beechnuts) which were more common in acidified habitats (Schlender et al. 2007). Blackbirds, meanwhile, appeared to offset the negative effects of acidification by nesting close to forest edges, which allowed them to forage in adjacent less acidic agricultural habitats (Schlender et al. 2007).

Studies in North America have not documented eggshell deformities in forest birds resulting from acid deposition, but longer term or more subtle effects may be influencing populations (e.g., decreased winter survival of fledglings or lower return rates of adults; Hames et al. 2002; Table 1). In addition, North

American birds may skip breeding altogether when calcium levels are insufficient (Pabian and Brittingham 2011). Pabian and Brittingham (2011) found that Ovenbird (*Seiurus aurocapilla*) had higher territory density, larger clutch sizes, and more nests in forest sites where liming had occurred compared to unlimed sites in Pennsylvania but no differences were observed in egg characteristics. An additional observational study found that natural soil calcium content was correlated with ovenbird territory density, clutch size, and nest density, but not with egg characteristics (Pabian and Brittingham 2011). The observed changes to ovenbird productivity and density were believed to be due to snails since snail abundance increased with liming and was positively correlated with soil calcium levels (Pabian and Brittingham 2011). Liming resulted in continued increases in songbird abundance, soil pH, and calcium levels five years after application (Pabian et al. 2012). While snail abundances initially increased on limed sites (23-fold three years after liming) they declined five years post-application (but were still more abundant than pre-liming), potentially due to increased bird predation (Pabian et al. 2012).

Table 1. Summary of Literature Review Studies.

Taxa	Location	Effects	Reference
Snails	Sweden	• Snail abundance and species richness were correlated with calcium content of forest litter • Snail abundance was correlated with soil moisture	Wäreborn (1969)
	Sweden	• Snail density declined by 27-80% over 14 to 46 years in calcium-poor soils • Snail density was highly correlated with calcium concentration, pH, base saturation and base cation concentration of leaf litter • Liming increased snail density by 10-90 times	Gärdenfors et al. (1995)
	Norway	• Liming led to increase in snail abundance and species diversity • Snail abundance was correlated with soil calcium, pH and base saturation	Johannessen and Solhøy (2001)
	Maryland (USA)	• Snail density and species richness were correlated with soil extractable calcium, water soluble calcium and pH • Snail density was positively associated with basal area of Sugar Maple (which occurred in soils with highest pH and highest exchangeable calcium levels) and was negatively associated with basal area of Red Maple (*Acer rubrum*; which had lower leaf	Hotopp (2002)

Taxa	Location	Effects	Reference
		litter calcium content)	
	New Hampshire (USA)	- Snail density, litter calcium content, and litter calcium concentration increased in young hardwood stands (<30 years old) but decreased in old hardwood stands (>30 years old) - Young stands had higher hydrologic export of calcium than old stands	Hamburg et al. (2003)
	Kentucky (USA)	- Soil pH and extractable calcium declined with increasing distance from roads surfaced with limestone gravel (which produced calcareous road dust) - Dry mass of snails was 10 times higher at roadsides than 50 m away and was correlated with both pH and extractable calcium - Roadside snail assemblages were dominated by larger snail species which was absent 50 m away	Kalisz and Powell (2003)
	New Hampshire (USA)	- Snail abundance increased 3 to 7 years after liming - Snail abundance was positively correlated with litter calcium concentration and negatively correlated with American Beech (which had low litter calcium concentration)	Skeldon et al. (2007)
	Czech Republic	- Snail abundance, species richness, and species composition were strongly correlated with soil calcium content along a long calcium gradient on highly calcareous bedrock - Snail species composition was influenced by soil calcium along a shorter gradient on calcium-poor soils	Juřičková et al. (2008)
	New York (USA)	- Snail abundance and species richness increased with increasing soil calcium concentration - Some snail species were only found at sites	Beier et al. (2012)

Taxa	Location	Effects	Reference
		with the highest calcium levels	
	New York (USA)	• Snail abundance increased in limed plots	McCay et al. (2013)
Isopods and Snails	Norway and Wales	• Isopods were scarce at all base-poor sites and were unaffected by treatment (experimental acidification and liming) • Molluscs were absent from all base-poor sites	Ormerod and Rundle (1998)
Isopods	Laboratory	• Strongly acidic precipitation caused a lower growth rate vs. weakly acidic precipitation • Individuals in limed microcosms had higher growth rates and lower mortality risk vs. unlimed microcosms • Whole-body calcium concentration was higher in limed vs. unlimed microcosms receiving strongly acidic precipitation	Tompson et al. (2013)
	Japan	• Found in forests with high calcium litter concentrations but not in those with low litter concentrations	Ohta et al. (2014)
Great Tits	Netherlands	• Proportion of breeding pairs with eggshell deformities (no shell or poor-quality shells) increased from 40-57% from 1983 to 1988	Drent and Woldendrop (1989)
	Netherlands	• Snail abundance and species richness declined in calcium-poor soils from 1970 to 1992 • Proportion of birds laying eggs with shell defects increased from 10% in 1983-1984 to 40% in 1987-1988 • Female birds deserted 48% of clutches with eggshell defects vs. 14% of clutches without defects • Supplemental feeding of snail shells and chicken eggshells led to a decline in eggshell defects and increased reproductive success	Graveland et al. (1994)
	Netherlands	• Lower snail density in calcium-poor forests, where birds had defective eggshells vs.	Graveland and van der Wal

Taxa	Location	Effects	Reference
		calcium-rich forests, where birds had normal eggshells • Liming of calcium-poor forests increased extractable calcium content of soils and resulted in snail densities similar to calcium-rich forests 4 years after treatment	(1996)
Great Tits, Pied Flycatchers (*Ficedula hypoleuca*)	Estonia	• Supplemental feeding of snail shells and chicken eggshells led to increased egg volume and eggshell thickness, larger chicks (tarsus length and body weight), and earlier start of breeding	Mänd et al. (2000)
Wood Thrush (*Hylocichla mustelina*)	United States	• Predicted probability of breeding was highly negatively correlated with acid deposition, particularly at high elevation sites with low pH soils	Hames et al. 2002
Songbird community	Germany	• Soil acidification (measured as soil calcium content) influenced songbird species assemblage • Territory densities of Song Thrush and Nuthatch were positively correlated with calcium content • Territory densities of Robin, Chaffinch, and Coal Tit were negatively correlated with calcium content • Nesting success of Song Thrush and Blackbird was higher in calcium-rich forest • Densities of calcium-rich invertebrates (gastropods, isoplds, diplopods) declined with acidification	Schlender et al. (2007)
Ovenbirds	Pennsylvania (USA)	• Liming led to increased snail abundance, increased territory density, larger clutch sizes, and more nests (also observed at reference sites with high natural soil calcium levels)	Pabian and Brittingham (2011)
Songbird community	Pennsylvania (USA)	• Liming increased soil calcium, magnesium, and pH • Snail abundance peaked 3 years after liming but was still greater than pre-liming 5 years	Pabian et al. (2012)

Taxa	Location	Effects	Reference
		after application - Overall bird abundance increased after liming, associated with increases in species that forage on the ground and understory (but not canopy)	

4. Conclusions

Soil acidification and calcium decline can have profound consequences on the forest floor community and trophic interactions through changes to habitat and food availability and quality (Bondi 2015). Terrestrial crustaceans and molluscs are critical components of the detrital community in forest ecosystems and play a major role in calcium cycling to higher trophic levels (Gärdenfors et al. 1995, Ormerod and Rundle 1998, Skeldon et al. 2007). The high calcium demands of these invertebrates make them particularly sensitive to changes in calcium availability in forest soils and leaf litter, and they thus represent powerful biological indicators of environmental conditions (Hamburg et al. 2003, Lovett et al. 2009, Bondi et al. 2019). However, relatively little research has focused on the effects of soil acidification and calcium decline on terrestrial crustaceans and molluscs. Of the 31 papers reviewed in this study, 17 examined effects on land snails and/or isopods, and six examined effects on snails, isopods, and birds, for a total of 23 papers focused on this topic over the last 50 years (1969-2019). Prior to 2002, all studies reviewed were conducted in Europe, however, since that time an equal number have come from eastern North America (although none from Canada).

The literature review indicated that snails and isopods respond negatively to acidification and calcium leaching, and positively to enriched calcium availability (either through natural calcium-rich soil conditions or experimental liming). Numerous studies documented changes in snail abundance, species richness, and density in relation to calcium availability in soil or litter. The few studies available for isopods showed that calcium availability affected their distribution, and growth and mortality rates. Calcium depletion and its impacts on these invertebrate taxa may affect higher trophic levels, such as birds, both directly (e.g., through effects on eggshell formation) and indirectly (e.g., through increased exposure to toxic metals; Ormerod and Rundle 1998). Studies in North America suggest that calcium limitation may be widespread for the avian community, but relatively undetected because of its subtle effects (Pabian and Brittingham 2011).

The impacts of soil acidification and calcium decline on forest biota remain largely unknown. While calcium availability appears to be a strong driver of forest communities at multiple trophic levels, other factors, including soil and litter moisture, availability of other elements, and forest type and age, likely interact with, and influence the importance of, calcium levels (Hotopp 2002, Hamburg et al. 2003, Beier et al. 2012). More research is needed to better understand the effects of soil acidification and calcium decline on terrestrial forest biota, particularly in forests of eastern Canada.

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