Title: Calcium concentration in leaf litter alters the community composition of soil invertebrates in warm-temperate forests.

Authors: Tamihisa Ohta[1], Shigeru Niwa[2], Naoki Agetsuma[3] and Tsutom Hiura[1]

Affiliations:

[1]Tomakomai Research Station, Field Science Center for Northern Biosphere, Hokkaido University, Takaoka, Tomakomai, Hokkaido 053-0035, Japan

[2]Network Center of Forest and Grassland Survey in Monitoring Sites 1000 Project, Japan Wildlife Research Center, Takaoka, Tomakomai, Hokkaido 053-0035, Japan

[3]Wakayama Experimental Forest, Field Science Center for Northern Biosphere, Hokkaido University, Hirai, Kozagawa-cho Higashimuro-gun, Wakayama, 649-4563, Japan

Running title: Calcium in leaf litter and soil organisms

*Corresponding Author: Email: tammyohta@gmail.com Phone: +81-0144-33-2171,
Fax: +81-0144-33-2173
Email:
S. Niwa: sniwa@fsc.hokudai.ac.jp
N. Agetsuma: agetsuma@fsc.hokudai.ac.jp
T. Hiura: hiura@fsc.hokudai.ac.jp

ABSTRACT

Many studies have shown the effects of aboveground plant species on soil organisms due to differences in litter quality. However, the calcium concentration in soil has received less attention as a controlling factor of soil invertebrate communities, despite its being an essential element for many animals, especially crustaceans. Litter of Japanese cedar (*Cryptomeria japonica*) plantations, which account for 19% of the forested area in Japan, has a higher calcium concentration compared to other taxa such as broad-leaved trees. We predicted that *C. japonica* plantations affect soil invertebrates by altering calcium availability. We compared soil properties including exchangeable calcium concentration and soil invertebrate communities between *C. japonica* plantations and natural broad-leaved forests. Exchangeable calcium was significantly higher in soil from cedar plantations than in that from broad-leaved forests. The invertebrate community composition differed between the two forest types and was best explained by the exchangeable calcium concentration. In particular, two major taxa of soil crustaceans (Talitridae and *Ligidium japonicum*) were found only in cedar plantations. Our results suggest that calcium concentrations in soil are altered in *C. japonica* plantations and that this affects soil invertebrate communities.

Keywords: Evergreen broad-leaved trees, *Cryptomeria japonica*, forest management, crustaceans, *Ligidium japonicum*, Talitridae

Introduction

Soil organisms can be affected by differences in aboveground vegetation (Bardgett and Wardle 2010), often driven by the quality of the litter types (Swift et al. 1979; Berg and McClaugherty 2003). Differences in litter quality among plant species can influence the chemical properties of soil and act as determinants of the community structure of soil invertebrates (Widden and Hsu 1987; Wardle et al. 2006). Because calcium is a major structural component of the proteins forming animals, ambient calcium concentration related to the animal densities in calcium poor environment (Alstad et al. 1999; Hessen et al. 2000; Ohta et al. 2014). Similarly, soil calcium concentrations can have an important influence on soil invertebrate communities (Springett and Syers 1984). For example, the abundance of some soil invertebrates increase with the available soil calcium concentration (Hotopp 2002; Reich et al. 2005; Skeldon et al. 2007). Global pattern of soil calcium concentration is governed by geological change, acid deposition and annual precipitation (Potter and Conkling 2012; Binkley and Fisher 2013). For example, low rainfall areas (central North America) tend to have grater soil calcium than humid Eastern United States (Potter and Conkling 2012). Calcium availability and cycling in regional scale are governed by numerous factors including forest vegetation dynamics, atmospheric deposition, soil mineral weathering, and losses due to leaching (Likens et al. 1998; McLaughlin and Wimmer 1999; Dijkstra and Smits 2002). However, much research over the last half century has focused on the leaching of calcium due to acid deposition (Likens et al. 1996; Driscoll et al. 2001), with much less emphasis on other factors, such as changes in forest vegetation, even though the calcium concentration in leaf litter varies greatly among tree species.

Litter of members of the Cupressaceae has a higher concentration of calcium compared with other plant families (Kiilsgaard et al. 1987; Ohta et al. 2014). In this study, we focused on Japanese cedar (*Cryptomeria japonica*, Cupressaceae) because its leaf litter contains ~3% calcium (Xue and Luo 2002; Baba et al. 2004), more than three times the amount in many other taxa, such as fir (*Abies* spp.) and many broad-leaved trees (Kiilsgaard et al. 1987; Reich et al. 2005; Ohta et al. 2014). Japanese cedar plantations cover 12% of the total land area and 19% of the forested area in Japan (Forestry Agency 2011). Because soil organic matter in forests is derived mainly from plant litter, the chemical properties of litter affect soil chemical properties (Reich et al. 2005). Indeed, the soil in Japanese cedar plantations has a calcium content that is three to four times higher than that in evergreen broad-leaved forests in some parts of Japan (Tsutsumi 1987; Ohta et al. 2014). Ohta et al. (2014) showed that the calcium concentration in soil and streams, and the density and survival of dominant aquatic crustaceans, were significantly higher in *C. japonica* plantations compared with evergreen broad-leaved forests. However, Ohta et al. (2014) did not assess the effects of forest vegetation on soil animal community through alteration of calcium availability. Soil crustaceans that are frequently dominant decomposers in soil systems (O'hanlon and Bolger 1999), and contain large amount of calcium in their body (Greenaway 1985). Terrestrial crustaceans mainly take calcium from their food (e.g. leaf litter) and soil water. Therefore, we anticipate that the calcium concentration in litter affects the community structure of soil organisms in calcium-poor environment.

Addition of inorganic calcium often increases soil pH (Likens et al. 1996; Driscoll et al. 2001; Warby et al. 2009), and therefore, higher calcium concentrations in soil due to differences in forest vegetation are also likely to increase soil pH (Reich et al. 2005).

Alteration of soil pH also causes changes in the abundance of soil invertebrates (Hågvar 1990; Myrold 1990; Kaneko and Kofuji 2000). Therefore, plantations of *C. japonica* may affect the community structure of soil invertebrates via increased soil pH.

We examined the effect of Japanese cedar (*C. japonica*) plantations on the community structure of soil invertebrates, particularly the density of crustaceans. We conducted field surveys in six plots that differed in surrounding forest vegetation. We predicted (1) that the calcium concentration and soil pH would be higher in *C. japonica* plantations compared to evergreen broad-leaved forests, and (2) that crustacean density would be higher in *C. japonica* plantations than in evergreen broad-leaved forests.

Methods

Study area

We conducted field surveys in the Wakayama Experimental Forest of Hokkaido University (33°40’N, 135°40’E; 428 ha; annual mean temperature: 15.2ºC) on the

Southern Kii Peninsula of Japan. The geological structure in this region consists of sandstone and mudstone formed during the middle Tertiary (Tateishi 1976). Because of the highly acidic soil and high annual rainfall (~4000 mm), the area is extremely poor in calcium (Kihira et al. 2005). The forest soils are extremely thin, nearly exposing the bedrock. Japanese cedar was planted in much of the area beginning in the 1960s, and remnant natural evergreen broad-leaved forests are patchy.

We established a sampling plot (50 × 50 m) in each of six different catchments of the Wakayama Experimental Forest. The plots were located on relatively flat forest floors and separated by 0.2–1.5 km. Three of the six catchments were mostly covered by evergreen broad-leaved forests ‘evergreen’, and the other three were covered by Japanese cedar plantations ‘cedar’. Forests in the ‘evergreen’ plots were dominated by *Quercus acuta*, *Quercus myrsinifolia*, *Quercus sessilifolia*, *Neolitsea aciculata*, *Eurya japonica*, and *Machilus thunbergii* (Ohta et al. 2014). The *C. japonica* trees in the ‘cedar’ plots were planted 30–82 years prior to this study. Calcium concentration in the litter of *C. japonica* (3.4%) is about three times higher than in the evergreen broad-leaved species (0.8–1.5%) at this study site (Ohta et al. 2014). Carbon, nitrogen, phosphorus, and magnesium concentrations do not differ significantly among the species, whereas potassium is about three times lower in *C. japonica* compared to the broad-leaved species (Ohta et al. 2014).

Sampling

On 24 July 2012, we collected five samples at each plot from the litter and soil layers using core samplers (soil layer: 50 mm in diameter and 50 mm in height, litter layer: 113 mm in diameter and 40 mm in height) to measure soil chemical properties and mass of the litter layer. To determine the soil crustacean density, we established five sampling quadrats separated by over 10 m in each plot. We collected crustaceans within the sampling quadrats (25 × 25-cm) to a depth of 3 cm (including litter and surface soil layers) on 17 May and 21 September 2013. Soil crustaceans were separated from soil by hand-sorting and placed in 99% ethanol. To examine the community structure of ground-dwelling macroinvertebrates, we established two subplots (20 × 20 m) in each plot. We collected ground-dwelling invertebrates using five pitfall traps (8 cm in diameter and 6 cm in depth) per subplot. We placed the pitfall traps in each subplot ~2 m apart on 17 May, 19 July, 19 October, and 18 November 2013, and collected them 3 days later. We counted and identified all invertebrates found in the traps at least to the ordinal level following Aoki (1999) and Ueno et al. (1985).

Sample processing

To measure soil nitrate and exchangeable calcium, we shook (160 rev min^{-1}) a 0.5 g (air-dried mass) subsample of each soil sample in 100 ml of 1 M KCl solution for 1 h, filtered the sample through filter paper (No. 5C; Advantec, Tokyo, Japan), and then stored the suspension at –30ºC until analysis. We analyzed the soil extracts for calcium and nitrate concentration per unit air-dried mass using an inductively coupled plasma (ICP) atomic emission spectrometer (ICPE-9000; Shimadzu, Kyoto, Japan) and the absorptiometric method (Sakata 2000). We placed a 5-g (air-dried mass) subsample of each soil sample in 25 ml 1 M KCL and measured the pH using a pH meter (TOA-DKK, HM-30V; TOA Electronics, Tokyo, Japan). We dried soil subsamples in a drying oven at 60ºC for 24 h and then analyzed 50-mg dried soil samples for carbon and nitrogen concentrations per dry mass using a CN analyzer (Sumigraph NC-900; Sumika Chemical Analysis Service, Osaka, Japan). We dried a 1-g fresh subsample at 60ºC for 48 h to calculate the soil water content as the difference in mass before and after desiccation.

Statistical analysis

The soil properties (mass of the litter layer, water content, pH, C:N ratio, exchangeable calcium, total carbon, total nitrogen, and nitrate concentration) were fit to linear mixed models with forest vegetation type as a fixed factor and plot identity as a random factor. The statistical significance of the effect of the fixed factor in each model was evaluated by a likelihood ratio test ($\alpha = 0.05$).

We performed canonical correspondence analysis (CCA) to explore the relationships between the soil invertebrate composition and soil properties. The invertebrate data from the five pitfall traps on all four sampling dates were pooled for each subplot. Before conducting the CCA ordination, the abundance data for each taxon were standardized to unit variance, and the most important explanatory variables from all soil properties were determined by forward stepwise selection based on Akaike's information criteria and Monte Carlo permutation tests. All statistical analyses were conducted with R version 2.9.2 software (R Development Core Team 2011).

Results

Soil exchangeable calcium concentration (likelihood ratio test: $\chi^2 = 9.13$, d.f. = 1, $P = 0.002$) and C:N ratio (likelihood ratio test: $\chi^2 = 8.90$, d.f. = 1, $P = 0.003$) were significantly higher, and nitrate concentration (likelihood ratio test: $\chi^2 = 8.53$, d.f. = 1, $P = 0.003$) was significantly lower in 'cedar' than 'evergreen'. In particular, soil in 'cedar' plots had ~2.5 times more exchangeable calcium than the 'evergreen' plots (Table 1, Fig. 1). The other soil properties including the mass of litter layer that was selected explainatory variable in community composition of soil invertebrates did not differ significantly between the forest types although soil pH was marginally higher in 'cedar' than ‘evergreen’ (likelihood ratio test: $\chi^2 = 3.05$, d.f. = 1, $P = 0.08$). We found two taxa of crustaceans, Talitridae (Amphipoda) and *Ligidium japonicum* (Isopoda: Ligiidae) in ‘cedar’ plots by hand-sorting, but we found no crustaceans in ‘evergreen’ plots (Fig. 2). Abundances of Talitridae and *L. japonicum* did not differ significantly among ‘cedar’ plots between the two sampling months (generalized linear models assuming Poisson distribution and likelihood ratio tests: $P > 0.05$).

Crustaceans, spiders, ants, beetles, lepidopteran larvae, and millipedes accounted for 23, 19, 9, 19, 10, and 9%, respectively, of the total invertebrates captured by pitfall traps (Table 2). Crustaceans (mainly Talitridae and *L. japonicum*) dominated the ground-dwelling invertebrate communities in ‘cedar’ plots, while they were remarkably scarce, and millipedes (Paradoxosomatidae) and beetles were relatively abundant in ‘evergreen’ plots. Talitridae and *L. japonicum* were only collected in ‘cedar’ plots using pitfall traps, and a few individuals of *Venezillo* sp. (Isopoda: Armadillidae) were collected not only in ‘cedar’ but also ‘evergreen’ plots (Table 2). Taxonomic compositions of ground invertebrates differed distinctively between ‘cedar’ and ‘evergreen’ plots (Table 2, Fig. 3). From all the soil properties, exchangeable calcium concentration and mass of the litter layer explained the most variation among the 12 subplots in invertebrate community composition as determined through the forward selection process of CCA. The first and second axes explained 17.17 and 14.04%, respectively, of the variation in community composition (Monte Carlo permutation test: $P < 0.05$). The CCA ordination showed that community composition in the 'cedar' plots was distinctively different from that in the 'evergreen' plots along the first CCA axis, which corresponded to the gradient of exchangeable calcium concentration, and the 'cedar' plots had much lower variation than the 'evergreen' plots (Fig. 3). Compositional difference within 'evergreen' was distinctively indicated by second axis, which weakly correlated with mass of litter layer (Fig. 3). Talitridae and *L. japonicum* had large negative values on the first axis, and their high abundance characterized the 'cedar' community.

Discussion

Our results show that forest vegetation might affect the community structure of soil invertebrates by altering calcium availability. Our field survey showed that soil exchangeable calcium was ~2.5 times higher and soil pH was not significantly higher in *C. japonica* plantations compared with that in evergreen broad-leaved forests (these partly supported prediction 1). The major taxa of soil crustaceans (Talitridae and *L. japonicum*) were found only in *C. japonica* plantations, whereas only a few individuals of a minor crustacean species (*Venezillo* sp.) occurred in broad-leaved forests (supporting prediction 2). The community structure of soil invertebrates varied with forest vegetation types, and calcium in the soil layer was the most important environmental variable explaining the variation in community composition (supporting prediction 2). Furthermore, both intra- and inter-plot variation in the soil invertebrate community structure in *C. japonica* plantations were lower than in natural broad-leaved forests, suggesting that the homogeneous environment created by the monoculture plantation caused a large decrease in micro- and local-scale β-diversity of soil invertebrates. This might be caused by uniform increase in the abundance of Talitridae and *L. japonicum* in *C. japonica* plantations and difference in the mass of litter layer within 'evergreen' plots (Table 1, Fig. 3).

The difference in calcium concentration in leaf litter produces significant differences in soil calcium (Morrison 1985; Kloeppel and Abrams 1995). In fact, Ohta et al. (2014) showed that the calcium concentration in *C. japonica* litter was about three times higher than that of dominant evergreen broad-leaved trees in Wakayama Experimental Forest. We found that total calcium in the litter layer and water-extractable calcium in the soil at ‘cedar’ sites were three to four times higher than at ‘evergreen’ sites. These results support our finding that calcium supplied by *C. japonica* litter increased the calcium concentration in the soil of our study plots.

Field manipulations at the Hubbard Brook Experimental Forest in the northeastern United States indicated that adding $CaSiO_3$ to a catchment area increased calcium concentrations in soil (Juice et al. 2006; Minocha et al. 2010; Nezat et al. 2010) and altered the community structure of terrestrial snails, which have high demand for calcium (Skeldon et al. 2007). Hotopp (2002) showed that the abundance of sugar maple, a calciphilic species (Likens and Bormann 1970), was positively correlated with terrestrial snail density. As in snails, crustaceans must ingest a lot of calcium (Greenaway 1985). Because terrestrial crustaceans lose 20% of their body calcium through exuviae (Ziegler et al. 2007), they need adequate calcium to calcify their exoskeleton rapidly after exuviation. Terrestrial crustaceans in soil get calcium from soil water and litter (Greenaway 1985; Glötzner and Ziegler 2000). Therefore, the ‘cedar’ plots, which have high calcium levels in their litter and soil layers, are well suited for the survival of crustaceans (Figs. 1, 2). Indeed, both natural and artificial *C. japonica* forests in central Japan have high densities of crustaceans (Ikeda at al. 2005).

Calcium addition to acidic soil increases soil pH (Groffman et al. 2006; Groffman and Fink 2011). However, our result showed the soil pH was not significantly higher in *C. japonica* plantations that increase the calcium concentration of the soils (Table 1). Although previous studies showed soil pH may also affect the structure of invertebrate communities by altering forest vegetation (e.g. Kaneko and Kofuji 2000), forward selection of the CCA analysis selected exchangeable soil calcium concentration and not pH in our result. Calcium concentration may have a greater impact on the community structure of soil invertebrates in our study site.

The litter of other members of Cupressaceae, such as *Chamaecyparis* and *Sequoiadendron*, also have high calcium content comparable to that of *C. japonica*

(Kiilsgaard et al. 1987; D'Amore et al. 2009). This might mean change in soil system through difference in calcium concentration in leaf litter is caused in other forest types. Furthermore, Reich et al. (2005) showed that exchangeable calcium in soils and the density of earthworms were significantly higher in forests dominated by *Acer pseudoplatanus* and *Tilia cordata* compared to forests dominated by *Larix* and *Pinus*, even though calcium concentrations were ~40% lower in the litter of *A. pseudoplatanus* and *T. cordata* than in *C. japonica*. This implies that the change in soil systems is caused by the alteration of forest vegetation with low calcium content relative to *C. japonica*.

Soil crustaceans, such as Talitridae and *L. japonicum*, are powerful litter decomposers (Zimmer 2002). Their existence influences litter decomposition rates (O'Hanlon and Bolger 1999), and their abundance can lead to increased turnover rates of organic matter. Furthermore, soil crustaceans affect the dynamics of organic matter by incorporating organic material from the forest floor into deeper soil horizons (Mattson 2012) and may also enhance microbial biomass (Escher et al. 2000). Reich et al. (2005) showed that plantations of tree species with high calcium concentrations in their litter cause an increase in exchangeable soil calcium and earthworm densities. Therefore, especially in calcium-poor environments, transformation of forest vegetation might change the densities of key decomposers such as crustaceans and earthworms, thereby affecting the decomposition rates of soil organic matter and nutrient dynamics.

Acknowledgments

We thank staff members of Wakayama Experimental Forest, Hokkaido University, for their support during the study. This study was partly supported by Grant-in-Aid from JSPS (12J07244 to TO and 2566011103, 25281053 to TH) and from the Ministry of Environment (S-9-3 to TH).

References

Alstad, N.E.W., Skardal, L., Hessen, D.O., 1999. The effect of calcium concentration on the calcification of Daphnia magna. Limnol. Oceanogr. 44, 2011-2017.

Aoki, J., 1990. Soil Animals of Japan: Manual with Keys and Illustrations (in Japanese). Tokai University Press, Tokyo.

Baba, M., Kato, M., Sugiura, T., Kobayashi, H., 2004. Calcium accumulation alleviates soil acidification in Japanese cedar (*Cryptomeria japonica*) stands. Soil Sci. Plant Nutr. 50, 403-411.

Bardgett, R.D., Wardle, D.A., 2010. Aboveground-Belowground Linkages. Biotic Interactions, Ecosystem Processes and Global Change. Oxford university press, Oxford.

Berg, B., McClaugherty, C., 2003. Plant litter: Decomposition, Humus Formation and Carbon Sequestration. Springer, Berlin.

Binkley, D. Fisher R.F., 2013. Ecology and Management of Forest Soils 4th ed. Wiley-Blackwell, New York.

D'Amore, D.V., Hennon, P.E., Schaberg, P.G., Hawley, G.J., 2009. Adaptation to exploit nitrate in surface soils predisposes yellow-cedar to climate-induced decline while enhancing the survival of western redcedar: A new hypothesis. Forest Ecol. Manag. 258, 2261-2268.

Dijkstra, F.A., Smits, M.M., 2002. Tree species effects on calcium cycling: The role of calcium uptake in deep soils. Ecosystems 5, 385-398.

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

Escher, N., Käch, B., Nentwig, W., 2000. Decomposition of transgenic *Bacillus thuringiensis* maize by microorganisms and woodlice *Porcellio scaber* (Crustacea: Isopoda). Basic Appl. Ecol. 1, 161-169.

Forestry Agency, 2011. 2011 Forestry Census. Forestry Agency, Tokyo.

Glötzner, J., Ziegler, A., 2000. Morphometric analysis of the calcium-transporting sternal epithelial cells of the terrestrial isopods *Ligia oceanica*, *Ligidium hypnorum*, and *Porcellio scaber* during molt. Arthropod Struct. Dev. 29, 241-257.

Greenaway, P., 1985. Calcium balance and molting in the crustacea. Biol. Rev. 60, 425-454.

Groffman, P.M., Fisk, M.C., 2011. Calcium constrains plant control over forest ecosystem nitrogen cycling. Ecology 92, 2035-2042.

Groffman, P.M., Fisk, M.C., Driscoll, C.T., Likens, G.E., Fahey, T.J., Eagar, C., Pardo, L.H., 2006. Calcium additions and microbial nitrogen cycle processes in a northern hardwood forest. Ecosystems 9, 1289-1305.

Hågvar, S., Abrahamsen, G., 1990. Microarthropoda and Enchytraeidae (Oligochaeta) in naturally lead-contaminated soil - a gradient study. Environ. Entomol. 19, 1263-1277.

Hessen, D.O., Alstad, N.E.W., Skardal, L., 2000. Ca limitation in Daphnia magna. J. Plankton Res. 22, 553-568.

Hotopp, K.P., 2002. Land snails and soil calcium in central Appalachian Mountain Forest. Southeast Nat. 1, 27-44.

Ikeda, H., Homma, K., Kubota, K., 2005. Biotic and abiotic factors affecting the structures of ground invertebrate communities in Japanese cedar dominant forests. Eur. J. For. Res. 8, 1-13.

Juice, S.M., Fahey, T.J., Siccama, T.G., Driscoll, C.T., Denny, E.G., Eagar, C., Cleavitt, N.L., Minocha, R., Richardson, A.D., 2006. Response of sugar maple to calcium addition to Northern Hardwood Forest. Ecology 87, 1267-1280.

Kaneko, N., Kofuji, R., 2000. Effects of soil pH gradient caused by stemflow acidification on soil microarthropod community structure in a Japanese red cedar plantation: An evaluation of ecological risk on decomposition. J. For. Res. 5, 157-162.

Kihira, T., Yoshida, S., Hironishi, M., Miwa, H., Okamato, K., Kondo, T., 2005. Changes in the incidence of amyotrophic lateral sclerosis in Wakayama, Japan. Amyotroph. Lateral. Sc. 6, 155-163.

Kiilsgaard, C.W., Greene, S.E., Stafford, S.G., 1987. Nutrient concentrations in litterfall from some western conifers with special reference to calcium. Plant Soil 102, 223-227.

Kloeppel, B.D., Abrams, M.D., 1995. Ecophysiological attributes of the native *Acer saccharum* and the exotic *Acer platanoides* in urban oak forests in Pennsylvania, USA. Tree Physiol. 15, 739-746.

Likens, G.E., Bormann, F.H., 1970. Chemical analyses of plant tissue from the Hubbard Brook Ecosystem in New Hampshire. Yale Univ. Sch. For. Bull. 79, 1–25.

Likens, G.E., Driscoll, C.T., Buso, D.C., 1996. Long-term effects of acid rain: Response and recovery of a forest ecosystem. Science 272, 244-246.

Likens, G.E., Driscoll, C.T., Buso, D.C., Siccama, T.G., Johnson, C.E., Lovett, G.M., Fahey, T.J., Reiners, W.A., Ryan, D.F., Martin, C.W., Bailey, S.W., 1998. The biogeochemistry of calcium at Hubbard Brook. Biogeochemistry 41, 89-173.

Mattson, W.J., 2012. The Role of Arthropods in Forest Ecosystems (Proceedings in Life Sciences). Springer, Berlin.

McLaughlin, S.B., Wimmer, R., 1999. Tansley Review No. 104 - Calcium physiology and terrestrial ecosystem processes. New Phytol. 142, 373-417.

Minocha, R., Long, S., Thangavel, P., Minocha, S.C., Eagar, C., Driscoll, C.T., 2010.

Elevation dependent sensitivity of northern hardwoods to Ca addition at Hubbard Brook Experimental Forest, NH, USA. Forest Ecol. Manag. 260, 2115-2124.

Morrison, I.K., 1985. Effect of crown position on foliar concentrations of 11 elements in *Acer Saccharum* and *Betula Alleghaniensis* trees on a till soil. Can. J. Forest Res. 15, 179-183.

Myrold, D.D., 1990. Effect of Acidic Deposition on Soil Organisms. In Mechanisms of Forest Response to Acidic Deposition. Lucir A.A. and Haines S.G. (eds.), Springer, New York, pp. 163-187.

Nezat, C.A., Blum, J.D., Driscoll, C.T., 2010. Patterns of Ca/Sr and Sr-87/Sr-86 variation before and after a whole watershed CaSiO3 addition at the Hubbard Brook Experimental Forest, USA. Geochim. Cosmochim. Ac 74, 3129-3142.

O'hanlon, R.P., Bolger, T., 1999. The importance of *Arcitalitrus dorrieni* (Hunt) (Crustacea: Amphipoda: Talitridae) in coniferous litter breakdown. Appl. Soil Ecol. 11, 29-33.

Ohta, T., Niwa, S., Hiura, T., 2014. Calcium concentration in leaf litter affects the abundance and survival of crustaceans in streams draining warm–temperate forests. Freshw. Biol. 59, 748-760.

Potter, K.M., Conkling, B. L., 2012. Forest health monitoring: 2008 national technical report. Gen. Tech. Rep. SRS-158. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station. 179 p.

R Development Core Team, 2011. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Reich, P.B., Oleksyn, J., Modrzynski, J., Mrozinski, P., Hobbie, S.E., Eissenstat, D.M., Chorover, J., Chadwick, O.A., Hale, C.M., Tjoelker, M.G., 2005. Linking litter calcium, earthworms and soil properties: a common garden test with 14 tree species. Ecol. Lett. 8, 811-818.

Sakata, T., 2000. The assay of nitrate nitrogen in the soil extract using the UV absorbance (in Japanese). Jpn. J. For. Environment. 42, 53-55.

Skeldon, M.A., Vadeboncoeur, M.A., Hamburg, S.P., Slum, J.D., 2007. Terrestrial gastropod responses to ecosystem-level calcium manipulation a northern hardwood forest. Can J. Zool. 85, 994-1007.

Springett, J.A., Syers, J.K., 1984. Effect of pH and calcium content of soil on earthworm cast production in the laboratory. Soil Biol. Biochem. 16, 185-189.

Swift, M.J., Heal, O.W., Anderson, J.M., 1979. Decomposition in Terrestrial Ecosystems. Backwell, Oxford.

Tateishi, M., 1976. The Muro Group in the southwestern part of the Muro Belt of the Shimanto Terrain (in Japanese). J. Geol. Soc. Jpn. 82, 395–407.

Tsutsumi, T., 1987. Material Cycling in Forest (in Japanese). University of Tokyo Press, Tokyo.

Ueno, S., Kurosawa, Y., Sato, M., 1985. The Coleoptera of Japan in color, vol. II (in Japanese). Hoikusha Press, Osaka.

Warby, R.A.F., Johnson, C.E., Driscoll, C.T., 2009. Continuing acidification of organic soils across the north-eastern USA: 1984–2001. Soil Sci. Soc. Am. J. 73, 274–284.

Wardle, D.A., Yeates, G.W., Barker, G.M., Bonner, K.I., 2006. The influence of plant litter diversity on decomposer abundance and diversity. Soil. Biol. Biochem.

38, 1052-1062.

Widden, P., Hsu, D., 1987. Competition between Trichoderma Species - Effects of Temperature and Litter Type. Soil Biol. Biochem. 19, 89-93.

Xue, L., Luo, S., 2002. Seasonal changes in the nutrient concentrations of leaves and leaf litter in a young Cryptomeria japonica stand. Scand. J. Forest Res. 17, 495-500.

Ziegler, A., Hagedorn, M., Ahearn, G.A., Carefoot, T.H., 2007. Calcium translocations during the moulting cycle of the semiterrestrial isopod *Ligia hawaiiensis* (Oniscidea, Crustacea). J. Comp. Physiol. B 177, 99-108.

Zimmer, M., 2002. Nutrition in terrestrial isopods (Isopoda: Oniscidea): an evolutionary-ecological approach. Biological Reviews 77, 455-493.

Table 1 Soil properties (mean ± SE) at each plot. Significant differences between cedar plantations (cedar) and evergreen broad-leaved forests (evergreen) are denoted in the last column: $^{**}P < 0.01$, n.s. $P > 0.05$ (likelihood ratio tests).

Plot name	cedar1	cedar2	cedar3	evergreen1	evergreen2	evergreen3	Significant differences between 'cedar' and 'evergreen' plots
Mass of litter layer (g)	10.42 ± 0.527	11.04 ± 0.561	10.28 ± 1.560	11.70 ± 1.240	7.47 ± 0.569	7.80 ± 0.845	n.s.
Water content (g/g)	0.62 ± 0.025	0.63 ± 0.064	0.57 ± 0.057	0.53 ± 0.045	0.64 ± 0.023	0.60 ± 0.036	n.s.
pH	4.34 ± 0.166	4.81 ± 0.143	5.20 ± 0.217	4.26 ± 0.182	4.55 ± 0.226	3.58 ± 0.085	n.s. ($P = 0.08$)
Exchangeable calcium (mg/g)	1.81 ± 0.256	1.83 ± 0.349	2.21 ± 0.971	0.63 ± 0.183	1.06 ± 0.413	0.43 ± 0.112	**
Total carbon (mg/g)	154.03 ± 23.188	117.63 ± 33.999	174.65 ± 58.206	139.58 ± 28.232	257.24 ± 47.917	201.00 ± 30.483	n.s.
Total nitrogen (mg/g)	10.33 ± 1.823	6.76 ± 1.770	9.90 ± 3.079	9.90 ± 1.908	19.0 ± 3.641	14.15 ± 1.880	n.s.
Nitrate (mg/g)	0.39 ± 0.021	0.52 ± 0.059	0.58 ± 0.047	0.73 ± 0.099	1.01 ± 0.113	0.82 ± 0.081	**
C:N ratio	15.89 ± 1.990	17.00 ± 0.781	17.36 ± 1.140	14.27 ± 0.775	13.52 ± 0.638	14.13 ± 0.473	**

Table 2 Abundance (5 traps^{-1} 12 days^{-1}; mean ± SE) of ground-dwelling macroinvertebrates sampled by pitfall traps. 'cedar' and 'evergreen' mean cedar plantation and evergreen broad-leaved forest.

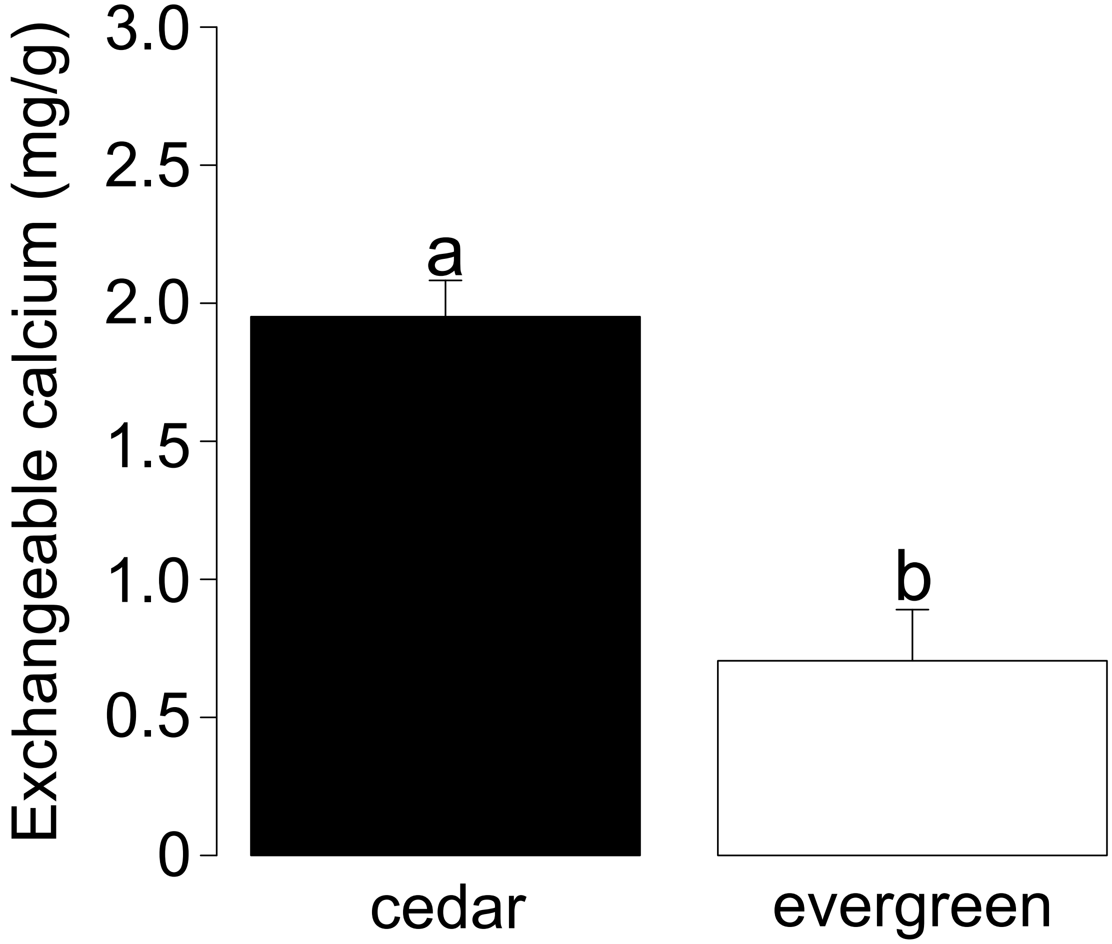
	cedar	evergreen
Gastropoda	0.67 ± 0.67	0.00 ± 0.00
Oligochaeta		
Haplotaxida	0.33 ± 0.33	0.00 ± 0.00
Diplopoda		
Polydesmida		
Paradoxosomatidae	0.00 ± 0.00	3.33 ± 1.76
Xystodesmidae		
Xystodesmus sp.	0.33 ± 0.33	0.00 ± 0.00
Julida		
Julidae		
Anaulaciulus sp.	0.00 ± 0.00	0.33 ± 0.33
Arachnida		
Araneae	4.00 ± 0.58	4.00 ± 1.00
Crustacea		
Amphipoda		
Talitridae	4.33 ± 0.88	0.00 ± 0.00
Isopoda		
Ligiidae		
Ligidium japonicum	4.67 ± 0.88	0.00 ± 0.00
Armadillidae		
Venezillo sp.	0.67 ± 0.33	0.33 ± 0.33
Insecta		
Archaeognatha		
Machilidae	0.33 ± 0.33	0.33 ± 0.33
Orthoptera		
Rhaphidophoridae	0.00 ± 0.00	0.67 ± 0.33
Lepidoptera (larva)	2.33 ± 0.88	2.00 ± 0.00
Hymenoptera		
Formicidae		
Pachycondyla chinensis	0.67 ± 0.67	0.00 ± 0.00
Aphaenogaster famelica	0.33 ± 0.33	1.00 ± 1.00
Paratrechina flavipes	0.33 ± 0.33	0.67 ± 0.67
Formica hayashi	1.00 ± 0.58	0.33 ± 0.33
Camponotus obscuripes	0.00 ± 0.00	0.67 ± 0.67
Coleoptera (larva)	0.00 ± 0.00	0.67 ± 0.67
Coleoptera (adult)		
Geotrupidae		
Phelotrupes laevistriatus	0.33 ± 0.33	0.33 ± 0.33
Phelotrupes auratus	0.33 ± 0.33	0.00 ± 0.00
Scarabaeidae		
Panelus parvulus	0.00 ± 0.00	0.33 ± 0.33
Onthophagus nitidus	0.33 ± 0.33	0.67 ± 0.67
Staphylinidae		
Bolitobius sp.	0.33 ± 0.33	0.33 ± 0.33
Staphylininae	0.00 ± 0.00	0.33 ± 0.33
Carabidae		
Carabus iwawakianus	0.00 ± 0.00	0.67 ± 0.67
Chlaenius costiger	0.67 ± 0.67	0.00 ± 0.00
Stomis prognathus	0.00 ± 0.00	0.33 ± 0.33
Pterostichus (*Rhagadus*) sp.	0.33 ± 0.33	1.33 ± 0.88
Rupa japonica	1.00 ± 0.58	0.33 ± 0.33
Synuchus picicolor	0.00 ± 0.00	0.33 ± 0.33

Fig. 1 Concentration (mean ± SE) of exchangeable calcium in soil in each plot. White and black bars indicate evergreen broad-leaved forests (evergreen) and cedar plantations (cedar), respectively. Significant differences between vegetation types are denoted by different letters (likelihood ratio tests, $P < 0.05$).

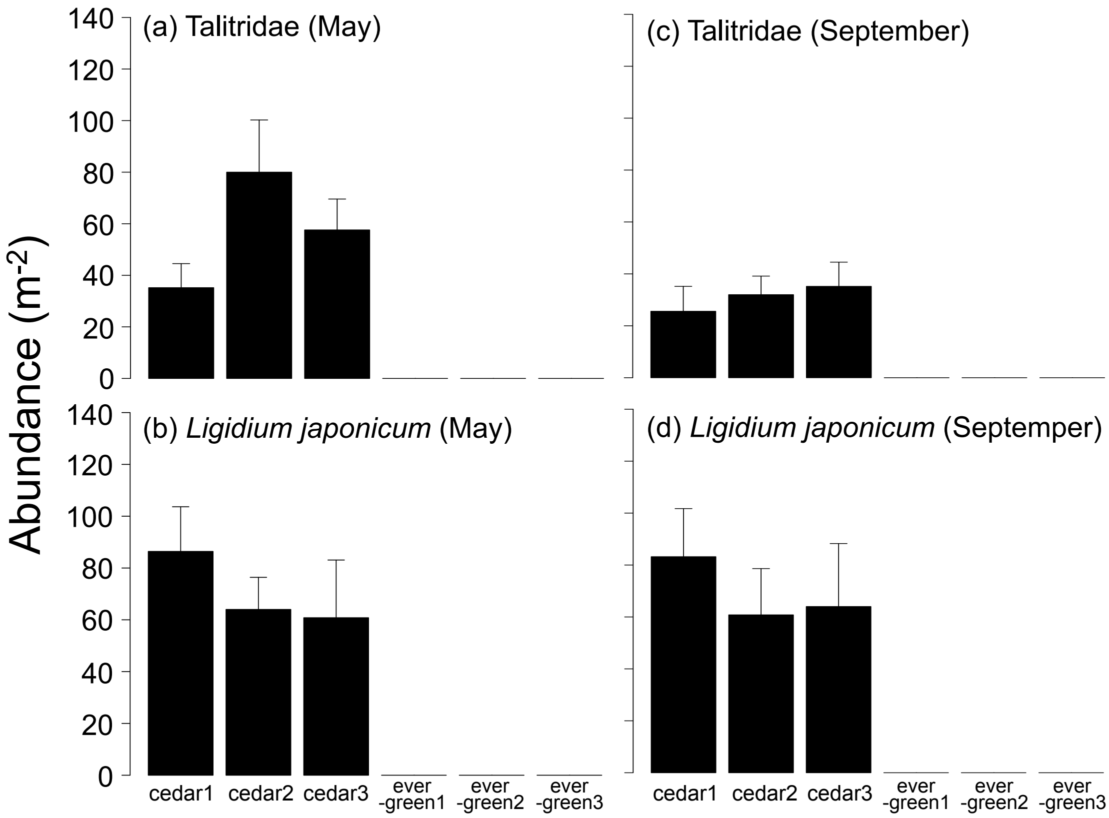
Fig. 2 Abundance (mean ± SE) of Talitridae (a) and *Ligidium japonicum* (b) in each plot by the hand-sorting method. White and black bars indicate evergreen broad-leaved forests (evergreen) and cedar plantations (cedar), respectively.

Fig. 3 Canonical correspondence analysis (CCA) ordination of soil invertebrate community composition in 12 subplots by the pitfall trap method. Explanatory variables selected by forward selection are shown as arrows: Ca, exchangeable calcium concentration and Litter, mass of the litter layer. White and black symbols indicate subplot scores (mean ± SE) of evergreen broad-leaved forests (evergreen) and cedar plantations (cedar), respectively. Invertebrate taxa are abbreviated by alphabets: G, Gastropoda; H, Haplotaxida; P, Paradoxosomatidae; Xs, *Xystodesmus* sp.; As, *Anaulaciulus* sp.; A, Araneae; T, Talitridae; Lj, *Ligidium japonicum*; Vs *Venezillo* sp.; L, Lepidoptera (larva); Pc, *Pachycondyla chinensis*; Af, *Aphaenogaster famelica*; Pf, *Paratrechina flavipes*; Fh, *Formica hayashi*; Co, *Camponotus obscuripes*; C, Coleoptera (larva); Pp, *Panelus parvulus*; On, *Onthophagus nitidus*; Pl, *Phelotrupes laevistriatus*; Pa, *Phelotrupes auratus*; Bs, *Bolitobius* sp.; St, Staphylininae; Ci, *Carabus iwawakianus*; Cc, *Chlaenius costiger*; Sp, *Stomis prognathous*; Ps, *Pterostichus* (*Rhagadus*) sp.; Rj, *Rupa japonica*; Syp, *Synuchus picicolor*; M, Machilidae; R, Rhaphidophoridae. Taxa indicated by boldface are crustaceans.

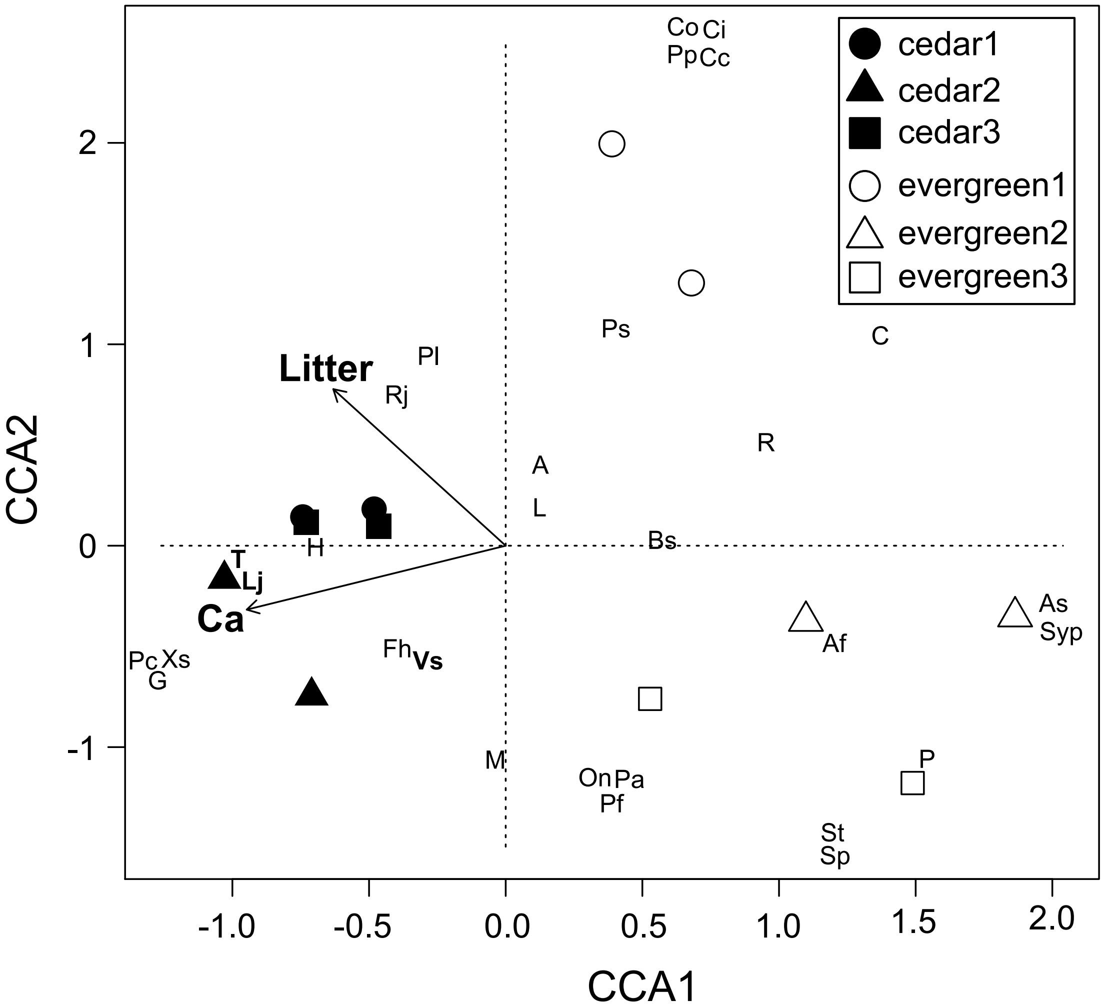
Ohta et al. Fig. 1



Ohta et al. Fig. 2



555 Ohta et al. Fig. 3



556