Instructions for use

1 Title: Calcium concentration in leaf litter alters the community composition of soil

2 invertebrates in warm-temperate forests.

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15 Running title: Calcium in leaf litter and soil organisms

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33   ABSTRACT

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35   Many studies have shown the effects of aboveground plant species on soil organisms

36   due to differences in litter quality. However, the calcium concentration in soil has

37   received less attention as a controlling factor of soil invertebrate communities, despite

38   its being an essential element for many animals, especially crustaceans. Litter of

39   Japanese cedar (*Cryptomeria japonica*) plantations, which account for 19% of the

40   forested area in Japan, has a higher calcium concentration compared to other taxa such

41   as broad-leaved trees. We predicted that *C. japonica* plantations affect soil invertebrates

42   by altering calcium availability. We compared soil properties including exchangeable

43   calcium concentration and soil invertebrate communities between *C. japonica*

44   plantations and natural broad-leaved forests. Exchangeable calcium was significantly

45   higher in soil from cedar plantations than in that from broad-leaved forests. The

46   invertebrate community composition differed between the two forest types and was best

47   explained by the exchangeable calcium concentration. In particular, two major taxa of

48   soil crustaceans (Talitridae and *Ligidium japonicum*) were found only in cedar

49   plantations. Our results suggest that calcium concentrations in soil are altered in *C.*

50   *japonica* plantations and that this affects soil invertebrate communities.

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Introduction

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67   Soil organisms can be affected by differences in aboveground vegetation (Bardgett

68   and Wardle 2010), often driven by the quality of the litter types (Swift et al. 1979; Berg

69   and McClaugherty 2003). Differences in litter quality among plant species can influence

70   the chemical properties of soil and act as determinants of the community structure of

71   soil invertebrates (Widden and Hsu 1987; Wardle et al. 2006). Because calcium is a

72   major structural component of the proteins forming animals, ambient calcium

73   concentration related to the animal densities in calcium poor environment (Alstad et al.

74   1999; Hessen et al. 2000; Ohta et al. 2014). Similarly, soil calcium concentrations can

75   have an important influence on soil invertebrate communities (Springett and Syers

76   1984). For example, the abundance of some soil invertebrates increase with the

77   available soil calcium concentration (Hotopp 2002; Reich et al. 2005; Skeldon et al.

78   2007). Global pattern of soil calcium concentration is governed by geological change,

79   acid deposition and annual precipitation (Potter and Conkling 2012; Binkley and Fisher

80   2013). For example, low rainfall areas (central North America) tend to have grater soil

81   calcium than humid Eastern United States (Potter and Conkling 2012). Calcium

82   availability and cycling in regional scale are governed by numerous factors including

83   forest vegetation dynamics, atmospheric deposition, soil mineral weathering, and losses

84   due to leaching (Likens et al. 1998; McLaughlin and Wimmer 1999; Dijkstra and Smits

85   2002). However, much research over the last half century has focused on the leaching of

86   calcium due to acid deposition (Likens et al. 1996; Driscoll et al. 2001), with much less

87   emphasis on other factors, such as changes in forest vegetation, even though the calcium

88   concentration in leaf litter varies greatly among tree species.

89   Litter of members of the Cupressaceae has a higher concentration of calcium

90   compared with other plant families (Kiilsgaard et al. 1987; Ohta et al. 2014). In this

91   study, we focused on Japanese cedar (*Cryptomeria japonica*, Cupressaceae) because its

92   leaf litter contains ~3% calcium (Xue and Luo 2002; Baba et al. 2004), more than three

93   times the amount in many other taxa, such as fir (*Abies* spp.) and many broad-leaved

94   trees (Kiilsgaard et al. 1987; Reich et al. 2005; Ohta et al. 2014). Japanese cedar

95   plantations cover 12% of the total land area and 19% of the forested area in Japan

96   (Forestry Agency 2011). Because soil organic matter in forests is derived mainly from

97   plant litter, the chemical properties of litter affect soil chemical properties (Reich et al.

98   2005). Indeed, the soil in Japanese cedar plantations has a calcium content that is three

99   to four times higher than that in evergreen broad-leaved forests in some parts of Japan

100   (Tsutsumi 1987; Ohta et al. 2014). Ohta et al. (2014) showed that the calcium

101   concentration in soil and streams, and the density and survival of dominant aquatic

102   crustaceans, were significantly higher in *C. japonica* plantations compared with

103   evergreen broad-leaved forests. However, Ohta et al. (2014) did not assess the effects of

104   forest vegetation on soil animal community through alteration of calcium availability.

105   Soil crustaceans that are frequently dominant decomposers in soil systems (O'hanlon

106   and Bolger 1999), and contain large amount of calcium in their body (Greenaway 1985).

107   Terrestrial crustaceans mainly take calcium from their food (e.g. leaf litter) and soil

108   water. Therefore, we anticipate that the calcium concentration in litter affects the

109   community structure of soil organisms in calcium-poor environment.

110   Addition of inorganic calcium often increases soil pH (Likens et al. 1996; Driscoll

111   et al. 2001; Warby et al. 2009), and therefore, higher calcium concentrations in soil due

112   to differences in forest vegetation are also likely to increase soil pH (Reich et al. 2005).

113   Alteration of soil pH also causes changes in the abundance of soil invertebrates (Hågvar

114   1990; Myrold 1990; Kaneko and Kofuji 2000). Therefore, plantations of *C. japonica*

115   may affect the community structure of soil invertebrates via increased soil pH.

116   We examined the effect of Japanese cedar (*C. japonica*) plantations on the

117   community structure of soil invertebrates, particularly the density of crustaceans. We

118   conducted field surveys in six plots that differed in surrounding forest vegetation. We

119   predicted (1) that the calcium concentration and soil pH would be higher in *C. japonica*

120   plantations compared to evergreen broad-leaved forests, and (2) that crustacean density

121   would be higher in *C. japonica* plantations than in evergreen broad-leaved forests.

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123   **Methods**

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125   *Study area*

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127   We conducted field surveys in the Wakayama Experimental Forest of Hokkaido

128   University (33°40'N, 135°40'E; 428 ha; annual mean temperature: 15.2ºC) on the

129   Southern Kii Peninsula of Japan. The geological structure in this region consists of

130   sandstone and mudstone formed during the middle Tertiary (Tateishi 1976). Because of

131   the highly acidic soil and high annual rainfall (~4000 mm), the area is extremely poor in

132   calcium (Kihira et al. 2005). The forest soils are extremely thin, nearly exposing the

133   bedrock. Japanese cedar was planted in much of the area beginning in the 1960s, and

134   remnant natural evergreen broad-leaved forests are patchy.

135   We established a sampling plot (50 × 50 m) in each of six different catchments of

136   the Wakayama Experimental Forest. The plots were located on relatively flat forest

137   floors and separated by 0.2–1.5 km. Three of the six catchments were mostly covered

138   by evergreen broad-leaved forests 'evergreen', and the other three were covered by

139   Japanese cedar plantations 'cedar'. Forests in the 'evergreen' plots were dominated by

140   *Quercus acuta*, *Quercus myrsinifolia*, *Quercus sessilifolia*, *Neolitsea aciculata*, *Eurya*

141   *japonica*, and *Machilus thunbergii* (Ohta et al. 2014). The *C. japonica* trees in the

142   'cedar' plots were planted 30–82 years prior to this study. Calcium concentration in the

143   litter of *C. japonica* (3.4%) is about three times higher than in the evergreen

144   broad-leaved species (0.8–1.5%) at this study site (Ohta et al. 2014). Carbon, nitrogen,

145 phosphorus, and magnesium concentrations do not differ significantly among the

146 species, whereas potassium is about three times lower in *C. japonica* compared to the

147 broad-leaved species (Ohta et al. 2014).

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149 *Sampling*

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151   On 24 July 2012, we collected five samples at each plot from the litter and soil layers

152 using core samplers (soil layer: 50 mm in diameter and 50 mm in height, litter layer:

153 113 mm in diameter and 40 mm in height) to measure soil chemical properties and mass

154 of the litter layer. To determine the soil crustacean density, we established five sampling

155 quadrats separated by over 10 m in each plot. We collected crustaceans within the

156 sampling quadrats (25 × 25-cm) to a depth of 3 cm (including litter and surface soil

157 layers) on 17 May and 21 September 2013. Soil crustaceans were separated from soil by

158 hand-sorting and placed in 99% ethanol. To examine the community structure of

159 ground-dwelling macroinvertebrates, we established two subplots (20 × 20 m) in each

160 plot. We collected ground-dwelling invertebrates using five pitfall traps (8 cm in

161   diameter and 6 cm in depth) per subplot. We placed the pitfall traps in each subplot ~2

162   m apart on 17 May, 19 July, 19 October, and 18 November 2013, and collected them 3

163   days later. We counted and identified all invertebrates found in the traps at least to the

164   ordinal level following Aoki (1999) and Ueno et al. (1985).

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166   *Sample processing*

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168   To measure soil nitrate and exchangeable calcium, we shook (160 rev min^{-1}) a 0.5 g

169   (air-dried mass) subsample of each soil sample in 100 ml of 1 M KCl solution for 1 h,

170   filtered the sample through filter paper (No. 5C; Advantec, Tokyo, Japan), and then

171   stored the suspension at –30ºC until analysis. We analyzed the soil extracts for calcium

172   and nitrate concentration per unit air-dried mass using an inductively coupled plasma

173   (ICP) atomic emission spectrometer (ICPE-9000; Shimadzu, Kyoto, Japan) and the

174   absorptiometric method (Sakata 2000). We placed a 5-g (air-dried mass) subsample of

175   each soil sample in 25 ml 1 M KCL and measured the pH using a pH meter (TOA-DKK,

176   HM-30V; TOA Electronics, Tokyo, Japan). We dried soil subsamples in a drying oven

177   at 60ºC for 24 h and then analyzed 50-mg dried soil samples for carbon and nitrogen

178   concentrations per dry mass using a CN analyzer (Sumigraph NC-900; Sumika

179   Chemical Analysis Service, Osaka, Japan). We dried a 1-g fresh subsample at 60ºC for

180   48 h to calculate the soil water content as the difference in mass before and after

181   desiccation.

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183   *Statistical analysis*

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185   The soil properties (mass of the litter layer, water content, pH, C:N ratio,

186   exchangeable calcium, total carbon, total nitrogen, and nitrate concentration) were fit to

187   linear mixed models with forest vegetation type as a fixed factor and plot identity as a

188   random factor. The statistical significance of the effect of the fixed factor in each model

189   was evaluated by a likelihood ratio test ($\alpha = 0.05$).

190   We performed canonical correspondence analysis (CCA) to explore the

191   relationships between the soil invertebrate composition and soil properties. The

192   invertebrate data from the five pitfall traps on all four sampling dates were pooled for

193   each subplot. Before conducting the CCA ordination, the abundance data for each taxon

194   were standardized to unit variance, and the most important explanatory variables from

195   all soil properties were determined by forward stepwise selection based on Akaike's

196   information criteria and Monte Carlo permutation tests. All statistical analyses were

197   conducted with R version 2.9.2 software (R Development Core Team 2011).

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199   **Results**

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201   Soil exchangeable calcium concentration (likelihood ratio test: χ^2 = 9.13, d.f. = 1, P

202   = 0.002) and C:N ratio (likelihood ratio test: χ^2 = 8.90, d.f. = 1, P = 0.003) were

203   significantly higher, and nitrate concentration (likelihood ratio test: χ^2 = 8.53, d.f. = 1, P

204   = 0.003) was significantly lower in 'cedar' than 'evergreen'. In particular, soil in 'cedar'

205   plots had ~2.5 times more exchangeable calcium than the 'evergreen' plots (Table 1,

206   Fig. 1). The other soil properties including the mass of litter layer that was selected

207   explainatory variable in community composition of soil invertebrates did not differ

208   significantly between the forest types although soil pH was marginally higher in 'cedar'

209   than 'evergreen' (likelihood ratio test: $\chi^2 = 3.05$, d.f. = 1, $P = 0.08$). We found two taxa

210   of crustaceans, Talitridae (Amphipoda) and *Ligidium japonicum* (Isopoda: Ligiidae) in

211   'cedar' plots by hand-sorting, but we found no crustaceans in 'evergreen' plots (Fig. 2).

212   Abundances of Talitridae and *L. japonicum* did not differ significantly among 'cedar'

213   plots between the two sampling months (generalized linear models assuming Poisson

214   distribution and likelihood ratio tests: $P > 0.05$).

215   Crustaceans, spiders, ants, beetles, lepidopteran larvae, and millipedes accounted for

216   23, 19, 9, 19, 10, and 9%, respectively, of the total invertebrates captured by pitfall traps

217   (Table 2). Crustaceans (mainly Talitridae and *L. japonicum*) dominated the

218   ground-dwelling invertebrate communities in 'cedar' plots, while they were remarkably

219   scarce, and millipedes (Paradoxosomatidae) and beetles were relatively abundant in

220   'evergreen' plots. Talitridae and *L. japonicum* were only collected in 'cedar' plots using

221   pitfall traps, and a few individuals of *Venezillo* sp. (Isopoda: Armadillidae) were

222   collected not only in 'cedar' but also 'evergreen' plots (Table 2). Taxonomic

223   compositions of ground invertebrates differed distinctively between 'cedar' and

224   'evergreen' plots (Table 2, Fig. 3). From all the soil properties, exchangeable calcium

225   concentration and mass of the litter layer explained the most variation among the 12

226   subplots in invertebrate community composition as determined through the forward

227   selection process of CCA. The first and second axes explained 17.17 and 14.04%,

228   respectively, of the variation in community composition (Monte Carlo permutation test:

229    $P < 0.05$). The CCA ordination showed that community composition in the 'cedar' plots

230   was distinctively different from that in the 'evergreen' plots along the first CCA axis,

231   which corresponded to the gradient of exchangeable calcium concentration, and the

232   'cedar' plots had much lower variation than the 'evergreen' plots (Fig. 3).

233   Compositional difference within 'evergreen' was distinctively indicated by second axis,

234   which weakly correlated with mass of litter layer (Fig. 3). Talitridae and *L. japonicum*

235   had large negative values on the first axis, and their high abundance characterized the

236   'cedar' community.

237

238   **Discussion**

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240   Our results show that forest vegetation might affect the community structure of soil

241   invertebrates by altering calcium availability. Our field survey showed that soil

242   exchangeable calcium was ~2.5 times higher and soil pH was not significantly higher in

243   *C. japonica* plantations compared with that in evergreen broad-leaved forests (these

244   partly supported prediction 1). The major taxa of soil crustaceans (Talitridae and *L.*

245   *japonicum*) were found only in *C. japonica* plantations, whereas only a few individuals

246   of a minor crustacean species (*Venezillo* sp.) occurred in broad-leaved forests

247   (supporting prediction 2). The community structure of soil invertebrates varied with

248   forest vegetation types, and calcium in the soil layer was the most important

249   environmental variable explaining the variation in community composition (supporting

250   prediction 2). Furthermore, both intra- and inter-plot variation in the soil invertebrate

251   community structure in *C. japonica* plantations were lower than in natural broad-leaved

252   forests, suggesting that the homogeneous environment created by the monoculture

253   plantation caused a large decrease in micro- and local-scale β-diversity of soil

254   invertebrates. This might be caused by uniform increase in the abundance of Talitridae

255   and *L. japonicum* in *C. japonica* plantations and difference in the mass of litter layer

256   within 'evergreen' plots (Table 1, Fig. 3).

257   The difference in calcium concentration in leaf litter produces significant

258   differences in soil calcium (Morrison 1985; Kloeppel and Abrams 1995). In fact, Ohta

259   et al. (2014) showed that the calcium concentration in *C. japonica* litter was about three

260   times higher than that of dominant evergreen broad-leaved trees in Wakayama

261   Experimental Forest. We found that total calcium in the litter layer and

262   water-extractable calcium in the soil at 'cedar' sites were three to four times higher than

263   at 'evergreen' sites. These results support our finding that calcium supplied by *C.*

264   *japonica* litter increased the calcium concentration in the soil of our study plots.

265   Field manipulations at the Hubbard Brook Experimental Forest in the northeastern

266   United States indicated that adding $CaSiO_3$ to a catchment area increased calcium

267   concentrations in soil (Juice et al. 2006; Minocha et al. 2010; Nezat et al. 2010) and

268   altered the community structure of terrestrial snails, which have high demand for

269   calcium (Skeldon et al. 2007). Hotopp (2002) showed that the abundance of sugar

270   maple, a calciphilic species (Likens and Bormann 1970), was positively correlated with

271   terrestrial snail density. As in snails, crustaceans must ingest a lot of calcium

272   (Greenaway 1985). Because terrestrial crustaceans lose 20% of their body calcium

273   through exuviae (Ziegler et al. 2007), they need adequate calcium to calcify their

274   exoskeleton rapidly after exuviation. Terrestrial crustaceans in soil get calcium from

275   soil water and litter (Greenaway 1985; Glötzner and Ziegler 2000). Therefore, the

276   'cedar' plots, which have high calcium levels in their litter and soil layers, are well

277   suited for the survival of crustaceans (Figs. 1, 2). Indeed, both natural and artificial *C.*

278   *japonica* forests in central Japan have high densities of crustaceans (Ikeda at al. 2005).

279   Calcium addition to acidic soil increases soil pH (Groffman et al. 2006; Groffman

280   and Fink 2011). However, our result showed the soil pH was not significantly higher in

281   *C. japonica* plantations that increase the calcium concentration of the soils (Table 1).

282   Although previous studies showed soil pH may also affect the structure of invertebrate

283   communities by altering forest vegetation (e.g. Kaneko and Kofuji 2000), forward

284   selection of the CCA analysis selected exchangeable soil calcium concentration and not

285   pH in our result. Calcium concentration may have a greater impact on the community

286   structure of soil invertebrates in our study site.

287   The litter of other members of Cupressaceae, such as *Chamaecyparis* and

288   *Sequoiadendron*, also have high calcium content comparable to that of *C. japonica*

289   (Kiilsgaard et al. 1987; D'Amore et al. 2009). This might mean change in soil system

290   through difference in calcium concentration in leaf litter is caused in other forest types.

291   Furthermore, Reich et al. (2005) showed that exchangeable calcium in soils and the

292   density of earthworms were significantly higher in forests dominated by *Acer*

293   *pseudoplatanus* and *Tilia cordata* compared to forests dominated by *Larix* and *Pinus*,

294   even though calcium concentrations were ~40% lower in the litter of *A. pseudoplatanus*

295   and *T. cordata* than in *C. japonica*. This implies that the change in soil systems is

296   caused by the alteration of forest vegetation with low calcium content relative to *C.*

297   *japonica*.

298   Soil crustaceans, such as Talitridae and *L. japonicum*, are powerful litter

299   decomposers (Zimmer 2002). Their existence influences litter decomposition rates

300   (O'Hanlon and Bolger 1999), and their abundance can lead to increased turnover rates

301   of organic matter. Furthermore, soil crustaceans affect the dynamics of organic matter

302   by incorporating organic material from the forest floor into deeper soil horizons

303   (Mattson 2012) and may also enhance microbial biomass (Escher et al. 2000). Reich et

304   al. (2005) showed that plantations of tree species with high calcium concentrations in

305   their litter cause an increase in exchangeable soil calcium and earthworm densities.

306   Therefore, especially in calcium-poor environments, transformation of forest vegetation

307   might change the densities of key decomposers such as crustaceans and earthworms,

308   thereby affecting the decomposition rates of soil organic matter and nutrient dynamics.

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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	**

485   Table 2 Abundance (5 traps^{-1} 12 days^{-1}; mean ± SE) of ground-dwelling

486   macroinvertebrates sampled by pitfall traps. 'cedar' and 'evergreen' mean cedar

487   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

488

489   Fig. 1 Concentration (mean ± SE) of exchangeable calcium in soil in each plot. White

490   and black bars indicate evergreen broad-leaved forests (evergreen) and cedar plantations

491   (cedar), respectively. Significant differences between vegetation types are denoted by

492   different letters (likelihood ratio tests, $P < 0.05$).

493

494   Fig. 2 Abundance (mean ± SE) of Talitridae (a) and *Ligidium japonicum* (b) in each plot

495   by the hand-sorting method. White and black bars indicate evergreen broad-leaved

496   forests (evergreen) and cedar plantations (cedar), respectively.

497

498   Fig. 3 Canonical correspondence analysis (CCA) ordination of soil invertebrate

499   community composition in 12 subplots by the pitfall trap method. Explanatory variables

500   selected by forward selection are shown as arrows: Ca, exchangeable calcium

501   concentration and Litter, mass of the litter layer. White and black symbols indicate

502   subplot scores (mean ± SE) of evergreen broad-leaved forests (evergreen) and cedar

503   plantations (cedar), respectively. Invertebrate taxa are abbreviated by alphabets: G,

504   Gastropoda; H, Haplotaxida; P, Paradoxosomatidae; Xs, *Xystodesmus* sp.; As,

505   *Anaulaciulus* sp.; A, Araneae; T, Talitridae; Lj, *Ligidium japonicum*; Vs *Venezillo* sp.;

506   L, Lepidoptera (larva); Pc, *Pachycondyla chinensis*; Af, *Aphaenogaster famelica*; Pf,

507   *Paratrechina flavipes*; Fh, *Formica hayashi*; Co, *Camponotus obscuripes*; C,

508   Coleoptera (larva); Pp, *Panelus parvulus*; On, *Onthophagus nitidus*; Pl, *Phelotrupes*

509   *laevistriatus*; Pa, *Phelotrupes auratus*; Bs, *Bolitobius* sp.; St, Staphylininae; Ci,

510   *Carabus iwawakianus*; Cc, *Chlaenius costiger*; Sp, *Stomis prognathous*; Ps,

511   *Pterostichus* (*Rhagadus*) sp.; Rj, *Rupa japonica*; Syp, *Synuchus picicolor*; M,

512   Machilidae; R, Rhaphidophoridae. Taxa indicated by boldface are crustaceans.

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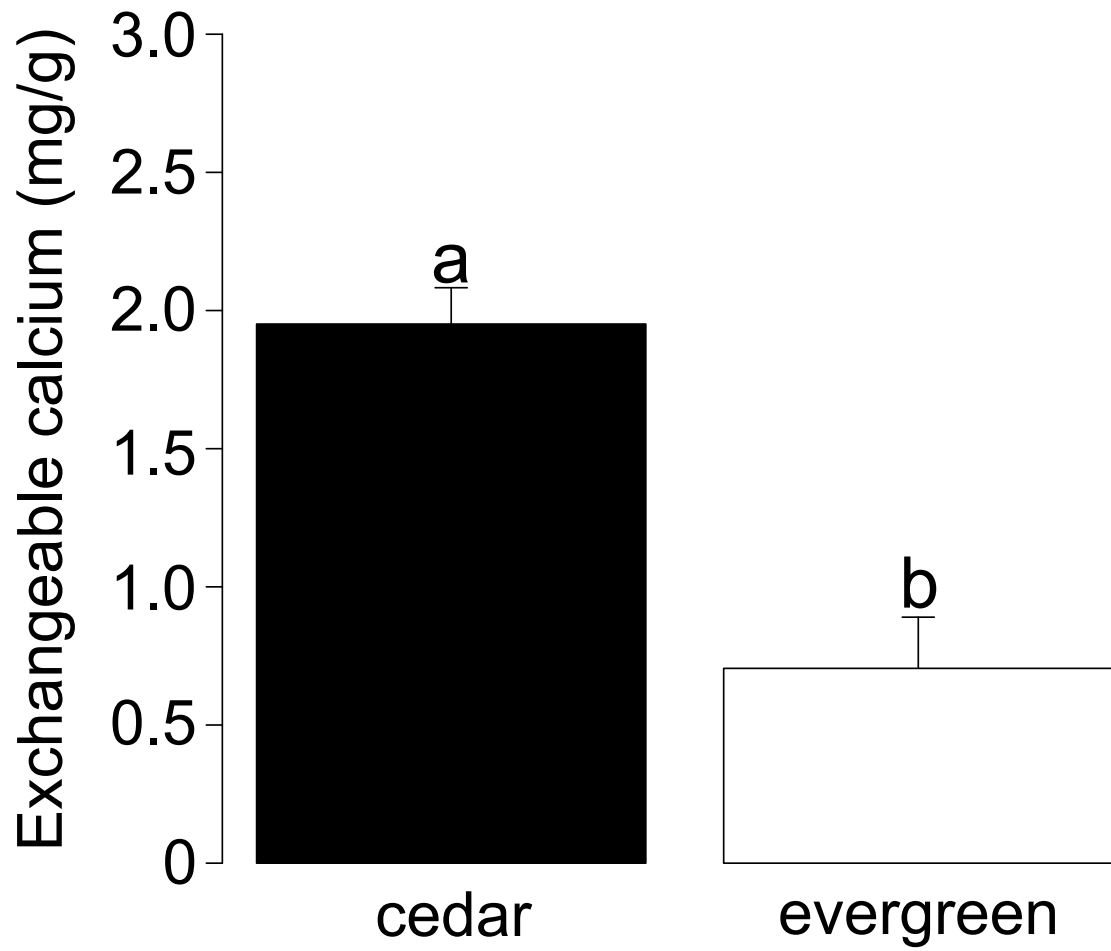
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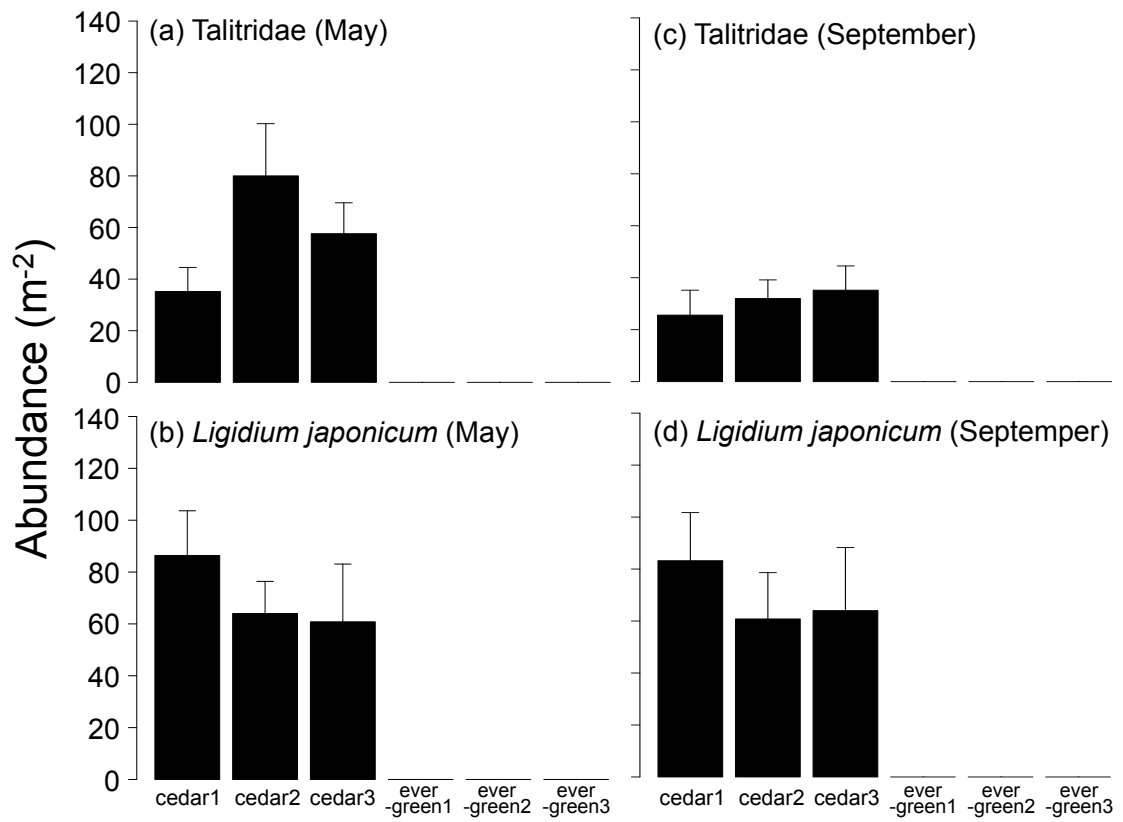
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