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Original paper

Top-down cascade effects of the long-clawed shrew (*Sorex unguiculatus*) on the soil invertebrate community in a cool-temperate forest

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Abstract. In a soil ecosystem, bottom-up control is generally considered more influential than top-down control, although some empirical studies have suggested that predators have a trophic cascade effect on soil animals at lower trophic levels. In the present study, the effects of the long-clawed shrew, a mammalian predator at a high trophic level, on the soil invertebrate community and litter decomposition were investigated in a field experiment using enclosures. In the presence of the shrew, the population densities of earthworms, isopods and spiders tended to decrease, whereas that of large springtails and centipedes appeared to increase. This result might have been caused by the shrew's direct predation on the former invertebrates and the release from predation by spiders on springtails. The reason of the increase of centipedes was unknown. Shrew had no effects on litter decomposition rates both by litter trap analysis and litter-bag test. The top-down effects of shrews on litter decomposition might have been diluted through a complex food-web and the observing period of the present study might be too short to detect litter decomposition process. Experiment for longer time might demonstrate more explicit effect of the shrew on the soil ecosystem.

Key words: enclosure, field experiment, invertebrate community, litter decomposition, soil ecosystem.

A cascading top-down effect sometimes determines and/or sustains the community structure of organisms (Chapin et al. 2000). For instance, in an aquatic ecosystem, such a cascading effect of predators on primary producers via lower consumers often determines the community structure of the producers (Currie et al. 1999; Carpenter et al. 2001). On the other hand, a food web is usually more complex in a terrestrial ecosystem than in an aquatic one, and it is generally suggested that such complexity should dilute predators' direct and indirect effects on the community structure of lower trophic level organisms (Shurin et al. 2006).

The food web of a soil ecosystem on a forest floor is so complex that the effect of predators on lower trophic level organisms is diluted due to multiple factors (Scheu and Setala 2002; Wardle 2002; Walton et al. 2006). In addition, one theoretical study proposed that the bottom-up force usually dominates the top-down force in a soil ecosystem (Ponsard et al. 2000). Vertebrate predators, such as amphibians, reptiles, birds, and mammals, have been thought to have less an effect on trophic interactions among organisms of forest floor, because the small total biomass and sporadic occurrence of those vertebrates on the forest floor initiate less of a cascading effect on organisms at lower trophic levels (Setala et al. 1998). However, some empirical studies suggest that not only macro-invertebrate predators (Kajak 1995; Wise 2004; Miyashita and Niwa 2006) but also mega-vertebrate predators potentially have a trophic cascade effect on soil animals at a lower trophic level and eventually on rates of decomposition and nutrient cycling (Wyman 1998; Rooney et al. 2000; Beard et al. 2002; Walton et al. 2006; Dunham 2008). Thus, it is still worthwhile to investigate the top-down effects of high trophic level vertebrates on soil ecosystems.

Soricine shrews (Mammalia, Soricidae) feed on invertebrates on the forest floor and/or in the soil and are considered to be a top predator of a soil food web in cool-temperate forests. In general, they have a high metabolic rate and thus a high food requirement (McNab 1991). For example, the common shrew (*Sorex araneus*) consumes approximately 80–100% of its body weight in food a day (Churchfield 1982). Hence, predation by shrews might have a considerable impact on soil invertebrate popula-

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tions and their community structure (Churchfield et al. 1991; Shvarts et al. 1997). Thus shrew can be an appropriate model animal for showing the top-down effect in a soil ecosystem. Several studies emphasized that shrews decreased the population densities of some forest pests, such as caterpillars and sawflies (Buckner 1966, 1969; Hanski and Parviainen 1985). Furthermore, since shrews and other small mammals have a wide range of diets, their effects could extend to various species of prey in the soil invertebrate community. However, such a top-down effect of shrews on a soil ecosystem has not been experimentally verified yet.

In the present study, a field experiment using the enclosure and exclosure of shrews was conducted in a cool-temperate forest in Hokkaido, northern Japan, with the long-clawed shrew (*Sorex unguiculatus*) as a top predator. The long-clawed shrew is the largest and most abundant shrew species in Hokkaido (Ohdachi and Maekawa 1990a; Ohdachi 1995a; Ohdachi et al. 2015). This species has a semi-subterranean habit and constructs tunnel systems up to approximately 30 cm in depth (Yoshino and Abe 1984; Ohdachi 1995b). It feeds mainly on earthworms (Haplotaxida) and underground or epigeal arthropods such as coleopteran and lepidopteran larvae, spiders, harvestmen, centipedes, and isopods (Ohdachi 1995a). Thus, the long-clawed shrew potentially has a top-down effect on populations of macro-invertebrates, such as the earthworm and isopod, which act as detrivores (litter transformers and ecosystem engineers) in soil ecosystems. Earthworms and isopods transform litter into feces which then encourages microbial activity. This microbial activity further accelerates the rate of litter decomposition, and in turn facilitates the population growth of some soil invertebrates that feed on fungi and bacteria (Lavelle et al. 1997; Wardle 2002; Zimmer 2002). In addition, shrew predation on some macro-invertebrates such as spiders, centipedes, and coleopteran beetles relaxes predation pressure on the macro-invertebrates' prey of meso-invertebrates, many of which are litter decomposition enhancers and feed on litter and microbes (Bardgett and Wardle 2010). Thus, the top-down effect of the shrew could cascade down to the litter decomposition process. To understand the overall role of a top predator on food web components and the whole ecosystem, it is important to specify each cascading process and to evaluate its relative importance by field experiment.

So far, there have been only several experiments conducted to evaluate the top-down effect of high tropic level predators in microcosms in laboratories (Walton and Steckler 2005; Walton et al. 2006) and mesocosms in the field (Wyman 1998; Lawrence and Wise 2000, 2004). However, the results of those experiments seem to be distorted because the environmental variables were simplified into unnatural conditions. On the other hand, a large-scale field experiment can simulate more realistic environmental variables, although detection of phenomena might be more difficult. Despite this, such a large-scale field experiment on the top-down effect has not been conducted in a soil ecosystem. In the present study, the field experiment was conducted in the natural spatial condition of the shrew. Therefore, the experiment detailed in the present study is expected to have simulated more natural conditions.

The present study was designed to answer two questions. First, does a single species (the shrew) as a top predator actually induce a cascading effect in a soil food web? Second, does the cascading effect, if present, reach down to the level of litter decomposition?

Materials and methods

Research site

This study was conducted in Tomakomai Experimental Forest (TOEF; 42°43'N, 141°36'E, ca. 90 m a.s.l.), Hokkaido, Japan. The natural vegetation there is that of a cool-temperate forest. A survey of the canopy trees at the research site indicated that the heartleaf hornbeam *Carpinus cordata* (32% of the total number of trees), the maples *Acer mono* (8%), *Acer amoenum* (7%) and *Acer palmatum* (6%), the oak *Quercus crispula* (7%), and the whitebeam *Aria alnifolia* (6%) are dominate, with a floor of the bamboo *Sasa nipponica*, the wood fern *Dryopteris crassirhizoma* and saplings of the dominant tree species. Canopy height ranges from 10 to 15 m. Annual precipitation is 1,450 mm and the average monthly temperature is –3.2°C to 19.2°C with an annual average of 5.6°C (Hiura 2001). The forest is formed on 2 m deep volcanic ash, which was accumulated during the eruptions of Mt. Tarumae in 1669 and 1739, and has a very shallow humus (Igarashi 1987; Sakuma and Sato 1987). The depth of the humus is approximately 10 cm. Leaves making up the litter mainly consist of canopy tree leaves (mostly oak, maple, hornbeam, and whitebeam leaves) and the sasa bamboo leaves. In TOEF, three species of shrews —*Sorex unguiculatus*, *S. caecutiens*, and *S. gracillimus*— occur, the former two being dominant. Additionally, *Apodemus argenteus*, *A. speciosus*, and *Myodes rufocanus*, are common murid species.

Shrews

The long-clawed shrew (*Sorex unguiculatus*) is a common species in TOEF. In Hokkaido, newly born shrews remain immature during their birth year, but sexually mature after wintering (Ohdachi and Maekawa 1990b). In overwintered, mature individuals, the male is easily identified by the descended testes and the female by the enlarged mammae. Sexing of young individuals is difficult based on external features (Inoue 1988). In this study, the sex of young individuals was determined, using the DNA marker by Matsubara et al. (2001), when samples are available. The home range of *S. unguiculatus* in Hokkaido is, on average, 188.3 ± 54.5 *SE* m^2 ($n = 7$: one adult male, one adult female, and five unsexed young) (Ohdachi 1992). *Sorex unguiculatus* has a subterranean habit and it mainly feeds on earthworms and small terrestrial arthropods (see Introduction).

Explanation of the experimental design and investigation

To elucidate the effects of the long-clawed shrew on soil invertebrate communities and the decomposition of litter, two experimental blocks (Blocks A and B) were established. Each had two experimental treatment plots: the enclosure of shrews (with shrews, WS) and the exclosure of shrews (no shrews, NS), as well as an open control plot (OC). The population densities of soil macro- and meso-invertebrates and the amount of leaf-litter were measured once a month from early summer (July) to autumn (September or October) during 2006, 2007, and 2008.

Experimental plots and the introduction of the shrew

The enclosure and the exclosure plots (15 m × 15 m) were surrounded by corrugated galvanized iron fences (see Appendix 1). The area (225 m^2) of an enclosure/exclosure was suitable for one or two long-clawed shrews in natural conditions (Ohdachi 1992). The galvanized iron fence stood 1 m high and delved 50 cm deep into the ground. The shrew cannot surmount a fence of such a height nor dig soil to such a depth (Ohdachi 1995b). Therefore, the fence of the enclosure/exclosure prevents the shrew from escaping one pen and entering another. Also, the fence largely prevents surface invertebrates from wandering in or out of the plots. The open control plot was a 15 m × 15 m open area without a fence. There were not any small mammals including shrews captured in WS and NS plots by 10 Sherman traps (S type) the three nights before the experiment although shrews and rodents are common in TOEF. Probably, during the experimental period, small mammal populations happened to be in low density. This means that there were less shrews inhabiting the research plot; therefore, the OC plots included less (or even no) shrews in the present experiment. The experimental and control plots of Block A were replicated in Block B. The blocks were established close to each other, approximately 200 m apart. Block A was established on May 24, 2006 and Block B on July 20, 2007. The composition of the canopy and undergrowth plant species were basically the same in both blocks. In WS plots, shrews were introduced as follows. Shrews were first captured in other areas of TOEF, the Yufutsu Moor (approximately 15 km away from TOEF) or Sapporo (approximately 40 km away from TOEF) by the slightly modified method of Ohdachi (1992). One to three shrews were released into an enclosure as soon as possible after their capture. When necessary to shortly keep the captured shrews caged for transportation, earthworms and/or mealworms (*Tenebrio molitor*) were given to them to reduce the mortality rate. To monitor the survival of the introduced shrew(s) in the enclosures, the foot-print method of King and Edgar (1977) was used. If no foot-prints were recorded for more than three weeks, another one to three shrews were immediately introduced. In addition, an automatic camera system (Okabe and Agetsuma 2007) was used to supplement monitoring the survival of the shrews in the enclosures. The shrews introduced into the enclosures are summarized in Table 1.

The density of shrews could not be controlled completely in WS treatment due to frequent disappearance of shrews. However, density of shrews was definitely higher in WS than NS/OC treatments.

Before the first shrews were introduced into the enclosures, a census of soil invertebrates was done (June 2006 in Block A and July 2007 in Block B) to establish the initial condition of the invertebrate fauna.

Sampling macro-invertebrates and leaf-litter

A sample was taken once a month from June to September during 2006, 2007, and 2008. Litter and soil to a depth of 10 cm was sampled with a 25 cm × 25 cm frame quadrat. Nine replicating samples were randomly taken in each experimental and open control plot. The samples were put in plastic bags and carried to the laboratory. Soil invertebrates (earthworms, spiders, coleopteran larvae, large-sized springtails, etc.) more than about 2 mm in body length were manually sorted from the samples and preserved in 70% ethanol. In June 2006, however, only the earthworms were collected. Earthworms were identi-

Table 1. Introduced dates and collection sites of the individuals of *Sorex unguiculatus* introduced into the enclosure treatment plots

Block	Date	Age class[1]	Sex[2]	Collection locality	Body weight (g)
A	20 Jun 2006	Y	M	Yufutsu	9.2
	21 Jun 2006	Y	M	Yufutsu	8.7
	21 Jun 2006	Y	M	Yufutsu	9.0
	23 Jul 2006	Y	F	TOEF	8.9
	23 Jul 2006	Y	M	TOEF	8.6
	31 Jul 2006	Y	M	TOEF	9.4
	28 Aug 2006	Y	M	TOEF	8.1
	2 Jun 2007	OW	M	TOEF	13.1
	27 Jun 2007	OW	F	TOEF	10.6
	3 Aug 2007	OW	M	Yufutsu	15.6
	11 Sep 2007	Y	unk	Yufutsu	10.2
	14 Jul 2008	Y	unk	Sapporo	8.3
	17 Jul 2008	OW	M	Sapporo	14.5
	17 Jul 2008	OW	M	Sapporo	17.9
	28 Aug 2008	Y	unk	Yufutsu	9.9
B	1 Aug 2007	OW	M	TOEF	16.7
	3 Aug 2007	Y	un	Yufutsu	9.6
	14 Jul 2008	OW	F	Sapporo	13.0
	16 Jul 2008	Y	unk	Sapporo	8.7
	27 Aug 2008	Y	unk	Yufutsu	9.2
	27 Aug 2008	OW	F	Yufutsu	12.4

[1] Y: young, OW: over wintered (mature).

[2] M: male, F: female, unk: unknown.

fied at the species level. The other macro-invertebrates were identified at the order level and the number of organisms per order was counted using a binocular microscope. After collecting the invertebrates, the leaf-litter was segregated from the soil in each sample, dried at 60°C in an oven for two days, and then weighed to the nearest 0.01 g.

Sampling meso-invertebrates

In June, July, and September of 2006 as well as in September of 2008, 15 samples of soil and leaf-litter were taken from randomly chosen places within each experimental and open control plot in Block A (2006 and 2008) and B (2008), using a 100-ml soil core sampler (DIK-1801, Daiki co., Saitama, Japan). Soil meso-invertebrates were extracted from each core sample using Tullgren funnel extractors. The Tullgren extractors were operated for three days and the extracted meso-invertebrates were preserved in 70% ethanol. These collected invertebrates were observed under a binocular microscope. The present study is concerned only with mites (Acari) and springtails (Collembola), so the number of individuals in each of these groups was counted separately.

Measuring the leaf-litter decomposition rate

In addition to weighing litter samples every month, the rate of litter decomposition was measured using two types of litter bags, both 15 cm × 15 cm in size. The fiberglass mesh bags had small openings 1.8 mm in size and prevented large invertebrates such as earthworms and isopods from affecting the litter decomposition process. The nylon mesh bags had large openings of 9.0 mm in size and allowed both macro- and meso-invertebrates access to the litter inside the bags. In the experimental blocks, the oak (*Quercus crispula*) and the hornbeam (*Carpinus cordata*) are the most dominant tree species. Each litter bag was filled with approximately 2 g (1.95–2.15 g) of either fallen oak or hornbeam leaves, which had been collected from around the research plots, and dried in an oven at 60°C for two days. A set of four bags (two tree species × two mesh sizes) was placed on the ground and covered with a steel mesh sheet (1 m × 2 m) with openings 50 mm in size to prevent the bags from being blown away or disturbed by large animals (e.g., the deer *Cervus nippon*, the raccoon *Procyon lotor*, and large birds). Twelve replicate sets were placed within each experimental and control plot in late November, 2006 (Block A) and 2007 (Block A and B). Half of the 12 replicate sets were collected in early July, 2007 and 2008 (eight months after their placement) and the remaining half in late November, 2007 and 2008 (one year after their placement). After collecting them, the litter samples were dried at 60°C for two days and then weighed to the nearest 0.01 g.

Statistical analysis

To elucidate the effect of the experimental treatments (the presence or the absence of the shrews and the fence) on soil invertebrate populations and litter biomass, a generalized linear mixed model (GLMM) was applied. The effect on each taxon group of macro- and meso-invertebrates was examined separately. Ants were excluded from the analysis due to a potentially strong sampling bias; the number of ants could be heavily affected by the presence of a colony in or near the sampling quadrat. As response variables, the number of invertebrate individuals was assumed to have a negative binomial error structure with a log link function, and the litter dry mass was to have a normal error structure with an identity link function. A unit of analyzed data corresponds to a sample of nine (frame quadrat) or 15 (core) sampling replications taken from each plot at a time. The presence (WS) or the absence of shrews (NS and OC), that of the fence, and when the sample was taken (month and year) were used as factors with fixed effects. The analysis for the litter-bag test was made separately for each of the four (two tree species × two mesh sizes) treatments. The dry weight of the re-sampled litter, offset by the initial weight, was the response variable. The presence or the absence of shrews, that of the fence, as well as what year the data was taken (2007 and 2008) and the length of time in months from when the litter bags were first placed to when they were collected were incorporated into the models as factors with fixed effects. The significance of the effect of each factor was tested using a one-tailed log-likelihood ratio chi-square test (Venables and Ripley 2002). In the present experiment, sampling was conducted by the nested pseudo replication, which several samplings were conducted in each plot. Therefore, sampling plot was treated as a random factor in GLMM, taking account of the variance of each sampling plot. All analyses were conducted using *R*: language and environment for statistical computing, version 2.10.1 (R Development Core Team 2011) with lme4 and aod packages.

Results

Effect on macro-invertebrates

Invertebrates collected in the 25 cm × 25 cm frame quadrat survey were classified into 19 orders. Hymenoptera (ant: 4,747 individuals), Collembola (springtail: 4,147), Chiropoda (centipede: 1,960), Araneae (spider: 2,067), Coleoptera (953), Haplotaxida (earthworm: 675), and Isopoda (*Ligidium japonicum*: 645) occupied more than 95% of the total invertebrate individuals sampled. Earthworms collected were *Amynthas vittatus*, *Metaphire hilgendorfi* and *Am. yunoshimaensis* of the family Megascolecidae, and *Eisenia japonica* of the family Lumbricidae.

All of the six major macro-invertebrate groups (excluding ants) showed significant temporal (seasonal and yearly) fluctuation in population size (likelihood ratio test, $\alpha = 0.05$, Fig. 1).

A significant negative effect due to shrews was detected on the population densities of earthworms, isopods, and spiders, but a positive effect was detected on centipedes and springtails (Table 2). The effect of the fence was sig-

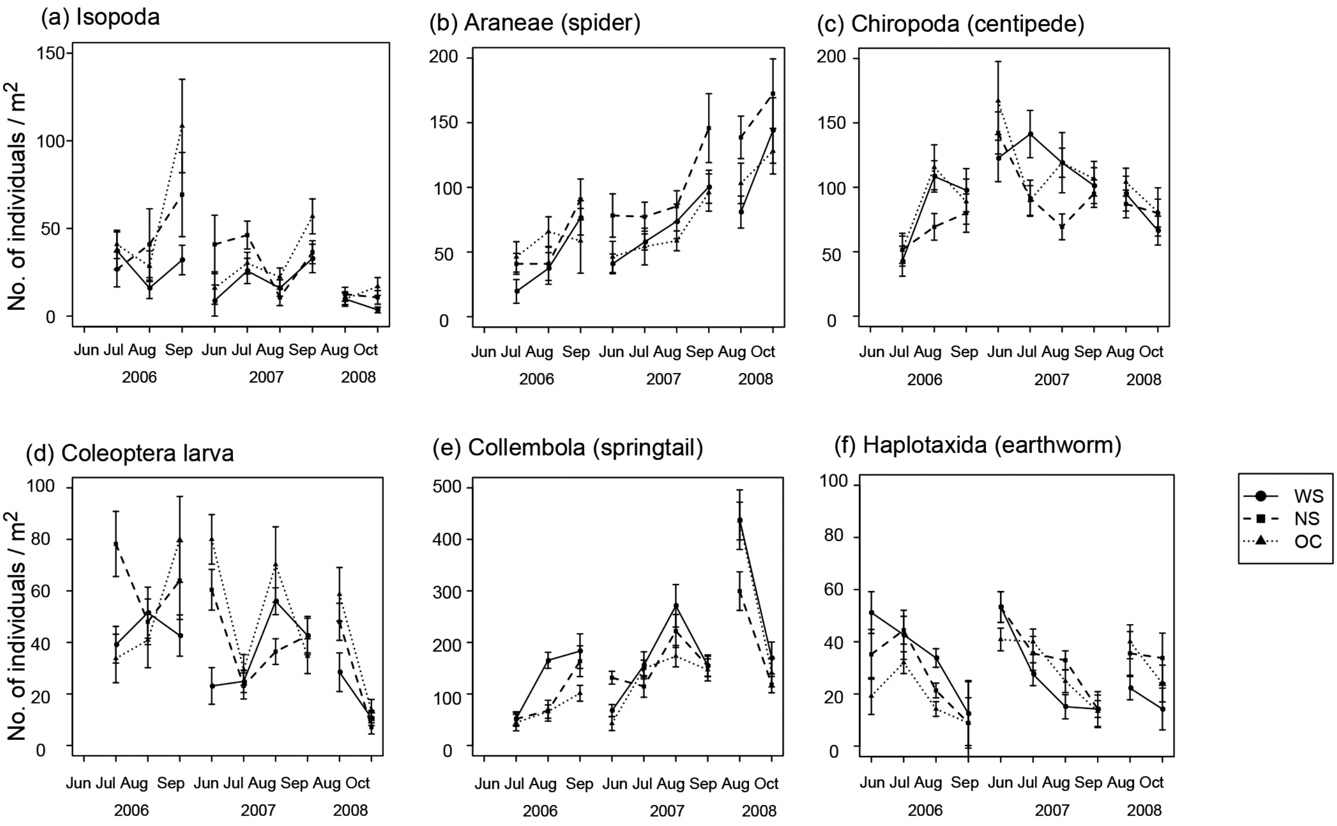


Fig. 1. Temporal change in population densities of six macro-invertebrate orders at the shrew enclosure (WS), exclosure (NS), and open control (OC) plots during the course of the field experiment in TOEF. Error bars represent standard errors.

Table 2. Estimated effect of four factors on the abundance of macro-invertebrates and litter dry weight in the quadrat survey based by GLMMs

	Shrew				Fence				Annual change					Seasonal change				
	Coefficient	*SD*	*df*	*P*	Coefficient	*SD*	*df*	*P*	Year	Coefficient[1]	*SD*	*df*	*P*	Month	Coefficient[2]	*SD*	*df*	*P*
Isopoda	–0.39	0.17	1	<0.01	–0.07	0.14	1	0.07	2007	–0.45	0.17	2	<0.01	Jul	–0.30	0.25	4	<0.01
									2008	0.04	0.12			Aug	–0.47	0.20		
														Sep	–0.36	0.16		
														Oct	–0.80	0.14		
Araneae (spider)	–0.35	0.09	1	<0.01	0.32	0.09	1	<0.01	2007	0.60	0.10	2	<0.01	Jul	0.62	0.13	4	<0.01
									2008	–0.02	0.07			Aug	–0.07	0.10		
														Sep	–0.21	0.10		
														Oct	–0.13	0.09		
Collembola (large springtail)	0.19	0.08	1	0.02	0.05	0.08	1	0.58	2007	0.92	0.09	2	<0.01	Jul	0.09	0.13	4	<0.01
									2008	0.03	0.06			Aug	–0.90	0.11		
														Sep	–0.21	0.10		
														Oct	0.02	0.08		
Chilopoda (centipede)	0.18	0.07	1	0.01	–0.21	0.07	1	0.01	2007	0.10	0.08	2	<0.01	Jul	–0.28	0.11	4	<0.01
									2008	–0.19	0.06			Aug	0.08	0.09		
														Sep	–0.22	0.08		
														Oct	0.09	0.07		
Coleoptera larvae	–0.14	0.09	1	0.09	–0.13	0.10	1	0.24	2007	–0.27	0.10	2	<0.01	Jul	–0.86	0.17	4	<0.01
									2008	0.09	0.08			Aug	–0.58	0.14		
														Sep	–0.68	0.11		
														Oct	0.07	0.09		
Haplotaxida (earthworm)	–0.03	0.12	1	0.01	0.15	0.11	1	0.11	2007	0.26	0.12	2	<0.01	Jul	–0.78	0.15	4	<0.01
									2008	0.02	0.09			Aug	0.18	0.12		
														Sep	0.35	0.12		
														Oct	0.16	0.12		
Litter weight	4.09	2.97	1	0.08	2.09	2.97	1	0.31	2007	–2.88	1.07	2	<0.01	Jul	–18.04	1.36	4	<0.01
									2008	6.90	0.76			Aug	0.04	1.06		
														Sep	0.83	1.00		
														Oct	–3.15	0.93		

[1] Coefficent to 2006. [2] Coefficient to June.

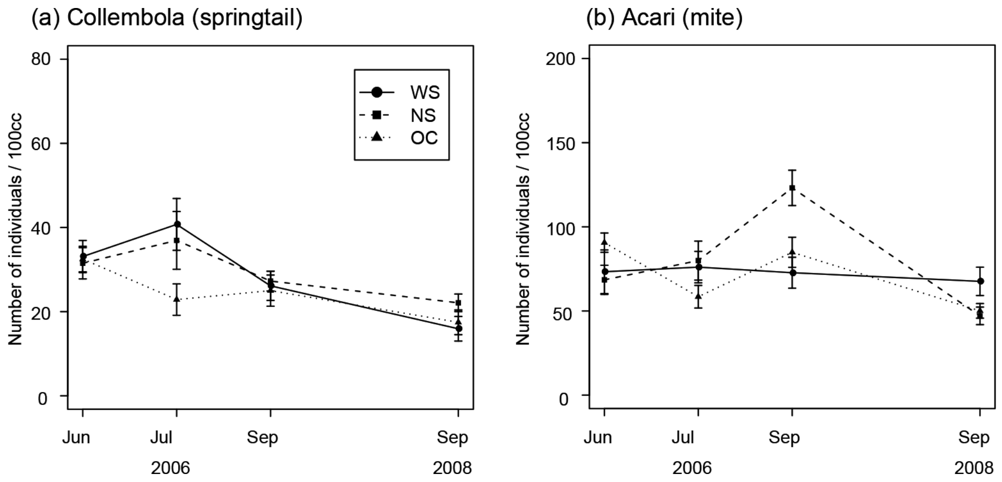


Fig. 2. Temporal variation in population densities (the number of individuals collected in litter/soil core samples 20 cm^2 in area and 5 cm in depth) of two meso-invertebrate orders during the course of field experiment in TOEF (see Fig. 1 for further explanation).

Table 3. Estimated effect of four factors on the abundance of meso-invertebrates in the soil core sampling based on GLMMs

	Shrew				Fence				Annual change					Seasonal change				
	Coefficient	*SD*	*df*	*P*	Coefficient	*SD*	*df*	*P*	Year	Coefficient[1]	*SD*	*df*	*P*	Month	Coefficient[2]	*SD*	*df*	*P*
Collembola (small springtail)	–0.24	0.11	1	0.79	–0.08	0.10	1	0.68	2008	–0.34	0.11	1	<0.01	Jul	0.11	0.13	2	0.5
														Sep	–0.19	0.13		
Acari (mite)	–0.14	0.09	1	0.12	0.04	0.10	1	0.01	2008	–0.59	0.10	1	<0.01	Jul	–0.13	0.12	2	<0.01
														Sep	0.17	0.12		

[1] Coefficent to 2006. [2] Coefficient to June.

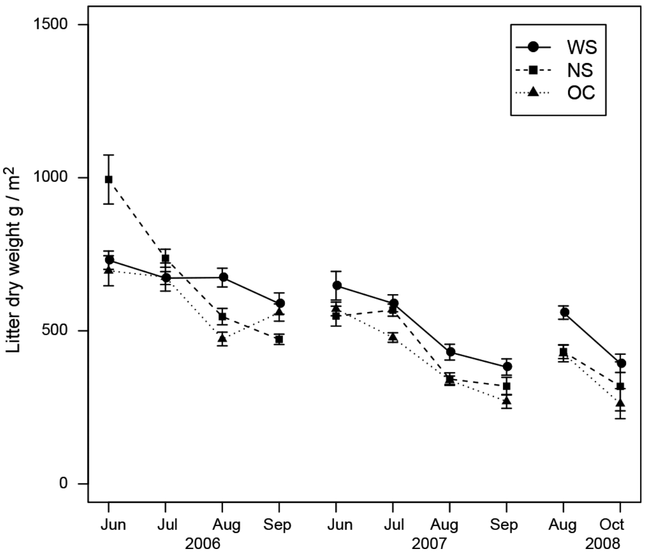


Fig. 3. Temporal variation in litter biomass during the course of the field experiment in TOEF (see Fig. 1 for further explanation).

nificantly positive on spiders but negative on centipedes (Table 2).

Effect on meso-invertebrates

In total, 14,695 mites (mainly fungivorous) and 5,320 springtails were collected from the soil-core samples taken in 2006 and 2008. Both groups showed significant temporal (seasonal and yearly) fluctuation in population size (likelihood ratio test, $\alpha = 0.05$; Fig. 2). However, there was no significant detectable effect due to the shrew or fence in either group (Table 3).

Litter decomposition

The amounts of litter sampled in June 2006 before introducing shrews in the enclosure did not significantly differ among the three experimental plots (ANOVA, $F = 0.11$, $P = 0.90$, Fig. 3). In addition, after introducing the shrew, no significant positive effect on the litter biomass was detected for the factors of both the shrew and the fence in GLMM (Table 2).

In the litter-bag test, the decomposition rate during winter and early summer (from November to July) was nearly the same for both the oak and hornbeam leaves, approximately 20% of their dry weight having been lost in the eight months after litter bags were placed. During summer and autumn (from July to November), however, the rates differed among the treatments, the dry weight of the hornbeam leaves in the bags of large mesh being reduced to approximately 40%, while the other treatments were reduced to approximately 20% (Fig. 4).

In the GLMM test for each treatment, no significant effect of shrews on the decomposition rate were detected in all types of mesh-bag (Table 4). A significant yearly variation was detected in oak and hornbeam leaves with small mesh (Table 4), and the decomposition rates in the litter-bag of small mesh were higher in 2007 than in 2008 (Table 4, Fig. 4).

Discussion

Effect of shrews on soil invertebrates

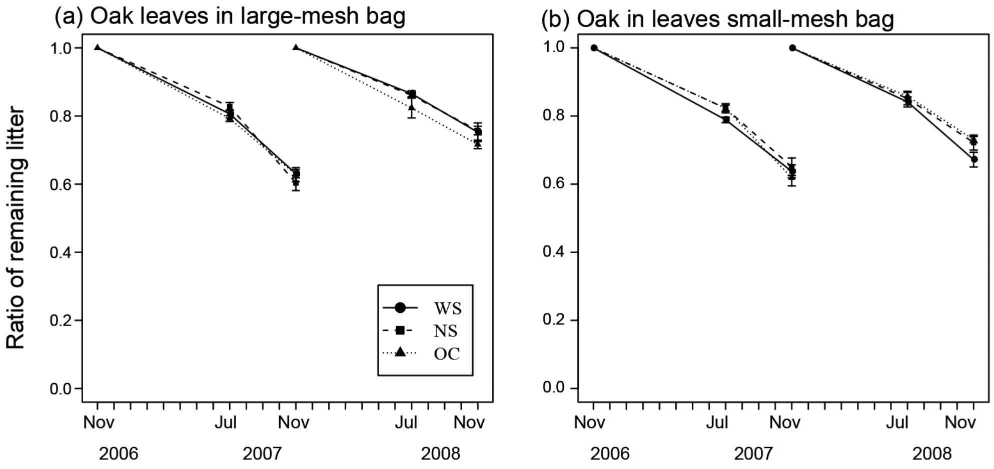
In general, top-down regulation has been considered to have less effect than bottom-up regulation in soil ecosystems (Scheu 2002; Wardle 2002). Only a few studies have indicated that vertebrate predators can have a top-down effect on lower trophic level organisms (Churchfield et al. 1991; Wyman 1998; Walton et al. 2006; Dunham 2008). One reason for smaller top-down effects of predators in soil is that the effect is diluted due to complexity of food-web (Scheu and Setala 2002; Wardle 2002; Shurin et al. 2006; Walton et al. 2006).

In the present study, shrews caused a top-down impact on some soil invertebrate populations. The effect of the shrews varied depending on the invertebrate group. Earthworms, isopods, and spiders had a significant decrease in their population sizes when shrews were introduced into the enclosure plot (Table 2). The decrease in earthworm and spider populations should be attributed

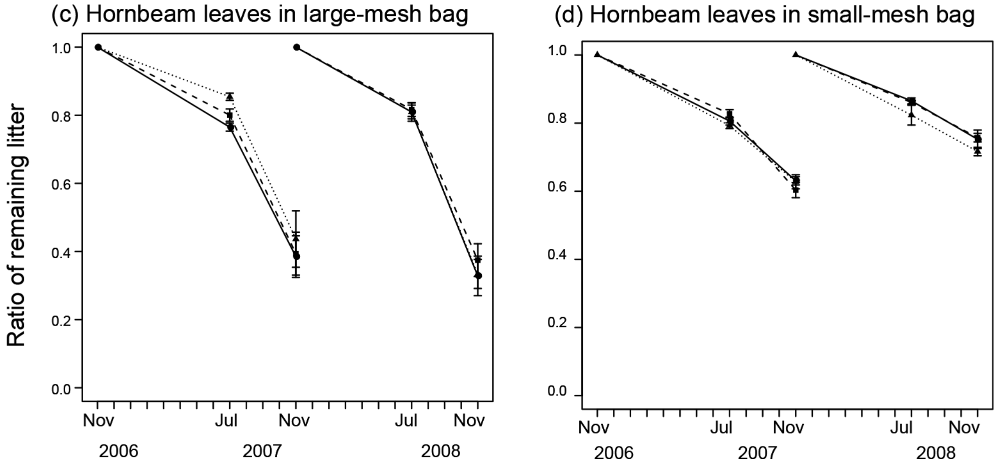
Table 4. Estimated effect of four factors on the ratio of litter remaining in the litter-bag test by GLMMs

	Shrew				Fence				Annual change				Seasonal change			
	Coefficient	*SD*	*df*	*P*	Coefficient	*SD*	*df*	*P*	Coefficient[1]	*SD*	*df*	*P*	Coefficient[2]	*SD*	*df*	*P*
Oak in large mesh	–0.08	0.06	1	0.12	0.07	0.06	1	0.17	0.10	0.04	1	0.02	–0.48	0.04	1	<0.01
Oak in small mesh	–0.05	0.07	1	0.29	0.02	0.07	1	0.77	0.10	0.02	1	<0.01	–0.31	0.02	1	<0.01
Hornbeam in large mesh	–0.07	0.13	1	0.45	0.03	0.13	1	0.87	–0.11	0.06	1	0.20	–0.90	0.05	1	<0.01
Hornbeam in small mesh	–0.01	0.05	1	0.97	0.07	0.05	1	0.08	0.18	0.03	1	<0.01	–0.27	0.02	1	<0.01

[1] Total coefficent of 2007 to 2006 and 2007 to 2008. [2] Coefficient of November, 2007 to July, 2007.


(a) Oak leaves in large-mesh bag

(b) Oak in leaves small-mesh bag


(c) Hornbeam leaves in large-mesh bag

(d) Hornbeam leaves in small-mesh bag

Fig. 4. Litter decomposition process measured for oak (*Quercus crispula*) and hornbeam (*Carpinus cordata*) leaves put in bags of large (9.0 mm) or small (1.8 mm) mesh and placed at the study plots of TOEF in July, 2006 and 2007 (see Fig. 1 for further explanation).

to the consumption by the shrews, since these invertebrates are the main food of the long-clawed shrew (Ohdachi 1995a). The shrews in Tomakomai region ate isopods, such as *Ligidium japonicum*, without hesitation under captivity (personal observation) although no isopod was found in the stomach contents of long-clawed shrews in central Hokkaido (Inoue and Maekawa 1990) and northern Hokkaido (Ohdachi 1995a). Thus, the shrews introduced into the enclosures must have consumed enough isopods to decrease their population size. No significant effect due to the shrew was detected on coleopteran larvae (Table 2), which are main prey of long-clawed shrews in Hokkaido (Inoue and Maekawa 1990; Ohdachi 1995a). The reason for no effect on coleopteran larvae could not be clarified, but it might have been caused by over abundance of these invertebrates as food resource for the shrew.

The results of previous field experiments on the direct top-down effect of vertebrate predators on soil macro-invertebrates have not always been consistent with one another. Chen and Wise (1999) investigated the effect of vertebrate predators such as lizards, birds, and mammals including the shrew on the wolf spider (*Schizocosa* sp.), using exclosures on the floor of a deciduous forest in North America, but detected no significant effect. In contrast, Churchfield et al. (1991) demonstrated that the population density of ground spiders decreased when small mammals (shrews and mice) were excluded from grassland in England. Likewise, Dunham (2008) observed that the exclusion of insectivorous vertebrates such as birds, lizards, and the white-toothed shrew decreased the populations of forest-floor invertebrates in a tropical forest.

In the present study, a significant positive effect due to the shrew was detected on large-sized springtails and centipedes (Table 2). Wise (2004) found that the removal of wandering spiders promoted population increase in six families of springtails (mainly Tomoceridae and Entomobryidae). This implies that spiders' predation pressure is strong enough to control springtail populations. In this context, the increase of springtails observed in the shrew-enclosure plots of the present study could be interpreted as an indirect effect of the shrew's predation through the decreased populations of macro-invertebrate predators (mainly spiders). The long-clawed shrew sometimes preys on springtails, but much less than it does on spiders, centipedes, or harvestmen (Ohdachi 1995a). Therefore, the indirect positive effect might have overcome the direct negative effect of the shrew on the springtail. The introduction of shrews had an opposite effect on spiders as it did on centipedes, a negative and positive effect, respectively (Table 2), although both of them are the shrew's prey and are predators to meso-invertebrates such as the springtail (Salmon et al. 2005). Spiders and centipedes had similar population densities in the present study site (Fig. 1), and hence it is somewhat difficult to explain this different effect. It might be related to the shrew preferring one over the other, but it remains a topic for further study.

With regard to soil meso-invertebrates, the shrew had no detectable effect on either the mite or the small-sized springtail (Table 3), although a positive indirect effect was detected on the large-sized springtail (Table 2). These soil meso-invertebrates might be too small for predatory spiders and centipedes to eat. Walton (2005) observed that the red-backed salamander (*Plethodon cinereus*) decreased populations of soil meso-invertebrates (springtails) by predation. Contrarily, Walton and Steckler (2005) reported that the salamanders increased the abundance of mite and springtail in a laboratory microcosm by freeing them from their competitors and/or predators. Thus, the response of meso-invertebrates to such high trophic-level predators like the salamander and shrew varies case by case. The reason for the inconsistency of the effect on small springtails among different experiments might be related with their response to the invertebrate predator of them.

Effect of the shrew on litter decomposition

In the present study, the presence of shrews did not change litter mass (Table 2). It could be interpreted that shrews decreased the populations of earthworms and isopods (detrivores) by directly eating them, which could eventually retarded litter decomposition. However, litter did not decrease in the presence of shrew. In addition, the shrews had no detectable effect on litter loss on all types of litter-bags (Table 4).

Thus, in the present study, shrew, a top predator of soil ecosystem in Hokkaido, had no effect on litter decomposition process (Tables 2 and 4). The cascading effect of shrew might have been diluted through a complex food-web and the observing period of the present study might be too short to detect litter decomposition process.

In previous studies, litter decomposition in a soil ecosystem is affected through various pathways in a food web composed of different functional groups, such as micro-floral decomposers (i.g., bacteria and fungi), fungivores (e.g., mites and springtails), detrivores (e.g., earthworms and isopods), invertebrate predators (e.g., spiders and centipedes), and vertebrate predator (e.g., salamanders and shrews). For instance, predation by spiders directly decreases the abundance of fungivores (springtails), resulting in a decrease in the litter decomposition rate (Lawrence and Wise 2000, 2004). In addition, as moderate fungivory by soil invertebrates encourages the activity of microbes and fungi (Kajak 1997), the decrease in population density of such invertebrate fungivores may decelerate the decomposition of litter due to lowered fungous activity. Furthermore, a salamander species that preys on both of detrivores (isopods and millipedes) and macro-invertebrate predators (spiders), releases fungivores (mites and springtails) from predation by those macro-invertebrates (Wyman 1998; Walton and Steckler 2005; Walton et al. 2006). As a result, the effect of the salamander on litter decomposition is not straightforward and seems to depend upon the relative importance of each different pathway in a given circumstance. It is also known that the feces and carcasses of frogs facilitate the nutrient cycling rate and thereby accelerate litter decomposition (Beard et al. 2002, 2003). Thus, litter decomposition is affected in different ways depending on ecological functions of participating soil animals. Shvarts et al. (1997) observed that the number of soil invertebrates (mainly detrivores and decomposers) paradoxically increased through super compensative population growth against the shrew's predation, resulting in greater consumption of litter by invertebrates.

Thus, judging from the previous and the present investigations, the reasons behind vertebrate predator's cascading effect on litter decomposition are not straightforward. These reasons might be determined by the relative ratio of predation on each of the different functional groups.

In the present investigation, the effect of the shrew more or less appears to be seen for some soil invertebrates but not for the litter decomposition process. In addition, the shrew had no clear detectable effect on the bacterial community in the same experimental plots of the present study (Yamamoto et al. 2010), implying that the shrew's effect does not reach down to the microbial decomposing process of the litter.

Shortly summarized the present investigation, through a large scale experiment, it was demonstrated that a top-predator (the long-clawed shrew) could alter the structure of the soil invertebrate community, although the effect of the shrew was not considerably apparent. In addition, the shrew's cascading effect did not reach down to the decomposition process of the litter. In future, longer observation of the top-down effect of vertebrate predators in soil ecosystem should be conducted to determine more detailed role of the predators.

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Appendix 1.

The enclosure (back) and exclosure (front) plots surrounded by tin fences in Block B in autumn, 2007.