Soil depth distribution and the patterns of alpha- and beta-diversity of families of soil Collembola in cool-temperate deciduous natural forests and larch plantations of northern Japan

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Abstract The relationships between habitat partitioning and the patterns of species diversity of collembolan families in relation to horizontal and to soil depth distributions have not been understood yet. The relationships between soil depth distribution and alpha diversity within a forest stand or beta diversity among forest stands in Simpson's diversity index for 9 family groups of soil Collembola were studied in 6 natural broad-leaved forests and 5 larch plantations of cool temperate zone in northern Japan. Studied forests were on wide range of environmental gradients including two forest types, deciduous broad-leaved natural forests and larch plantation, on south and north facing slopes, and from upper ridge to bottom of the slopes. Collembolan species were classified into 9 family groups. The percentages of organic layer dwellers to total abundance for a family group (%OL) of Tomoceridae, Entomobryidae, Neelidae and Sminthroidea were significantly higher than the other families. The standard deviation of weighted mean of %OL (SDW) of Isotomidae and Onychiuridae/Tullbergiidae were significantly higher than the other families, suggesting that Isotomidae and Onychiuridae/Tullbergiidae should have the widest range of habitat in soil depth distribution. Based on Simpson's D, alpha diversities of Isotomidae and that of Onychiuridae/Tullbergiidae were high, whereas those of Hypogastruridae and of Oncopoduridae were low. Beta diversities of Hypogastruridae and Tomoceridae were high, whereas those of Isotomidae and of Oncopoduridae/Tullbergiidae were low. The significant positive correlation between the SDW and alpha diversity and between SDW and contribution of alpha diversity to gamma diversity of family groups were found, indicating that the range of soil depth distribution among species within a family related with local diversity of collembolan family. The %OL and beta diversity were not significantly correlated. Negative correlation between alpha and beta diversities of family groups was found, indicating that families with high local diversity within a forest stand had low turnover diversity among forest stands in this site.

Key words: alpha diversity, beta diversity, eastern Hokkaido, horizontal and vertical distribution, Simpson's diversity index

Introduction

The factors that determine patterns of species richness have been interest to ecologists for long time, and are of fundamental importance to the management and preservation of biodiversity and its functions (Mittelbach *et al.*, 2001). Regional (gamma) species diversity of community is determined by the combination of its local (alpha) diversity and turnover (beta) diversity components (Whitterker, 1960). For the application of biodiversity conservation, fundamental

understanding both the patterns of alpha and beta diversities is important.

Collembola are important soil arthropods in terms of both abundance and species diversity in forest soil ecosystems (Hopkin, 1997). Species of Collembola share with their habitat niche in vertical and in horizontal distributions. Niche differentiation of species in vertical habitat distributions of collembolan species, that is, soil depth distributions, preferences for leaf litter decomposition processes and of humus distributions as well as feeding guilds and life histories has been well known (Hågvar, 1983; Takeda, 1987; Hasegawa and Takeda, 1995: Ponge, 2000; Hishi et al., 2007). In addition, they suggested that the niche differentiations among species in depth distribution should contribute alpha diversity of Collembola (Takeda, 1987), because a lot of species of the group can be packed into same area. On the other hand, horizontal distribution patterns, that is, species turnover among different vegetation (Deharveng, 1996), composition of leaf litter (Takeda, 1987), topography (Takeda, 1981), humus types (Chagnon et al., 2000; Ponge et al., 2003), openness by vegetation, soil moisture, acidity (Ponge, 1993), slope aspects (Broza et al., 2004) and macrofaunal distribution (Eisenhauer et al., 2007), have been investigated. These studies showed that there are turnover of collembolan species among different forest sites. However, there are few studies about the relationships between beta diversity and distribution patterns of Collembola. In relation to soil depth distribution and the species turnover among sites, correspondence analysis of collembolan communities in 679 soil samples including various vegetation types and soil depth gradients in France by Ponge (1993) showed that the epigeic and hemi-edaphic species were primarily diverged into distant positions among axes of vegetation and soil humidity, and then, euedaphic species converged into a similar position among axes of vegetation and soil humidity. That means that epigeic species tend to have higher turnover than euedaphic species, in relation to different vegetation or soil humidity. This suggests that epigeic species may highly contribute to beta diversity, as compared with the euedaphic species.

Basically, each family or super-family may have different spectrum of niche from the others in soil depth distribution patterns. For example, Tomoceridae and Entomobrydae, which include the most of species with large body and pigmented, are generally epigeic (Hasegawa and Takeda, 1995; Ponge, 2000). Onychiuridae/Tullbergiidae, which are mostly white and without eyes and furca, are mostly hemi- or euedaphic

(Ponge, 2000). Isotomidae, which includes species with wide range of body size, pigmentation and number of eyes, have wide range of habitats, from epigeic to euedaphon (Takeda, 1987; Ponge, 2000). Odontellidae/Neanuridae, having piercing sucking mandible without a molar plate, suggesting sucking feeders, opportunistic herbofungivore or predators, are mostly hemiedaphic (Ponge, 2000; Berg et al., 2004). Neelidae, which includes species with very small body and without eyes, are mostly euedaphic (Hasegawa and Takeda, 1995; Lauga-Reyrel and Deconchat, 1999). Sminthroidea, which includes species with round body, large and pigmented body, are generally atomophilic or epigeic (Lauga-Reyrel and Deconchat, 1999; Berg et al., 2004; Chahartaghi et al., 2005). These suggest that families of Collembola should have different diversity patterns because depth distribution may relate with species diversity patterns. However, there have been few studies to compare quantitatively the relationships between habitats and the patterns of diversities of families in Collembola.

Because of the differences of family groups in habitat preferences, the alpha and beta diversities of the family groups and these balances may relate with their depth distributions. Collembolan species share their habitats along with soil depth (Hasegawa and Takeda, 1995; Ponge, 2000; Hishi et al., 2007). When some collembolan group widely differentiates among soil depth as Isotomidae, it may have high alpha diversity because a lot of species of the group can be packed into same area. In addition, the heterogeneous distribution of various litters converges into homogeneous quality with advance of decomposition in chemical or physical structure (Mellilo et al., 1989; Osono and Takeda, 2005). Then, the epigeic groups, such as Sminthroidea, Tomoceridae or Entomobryidae, may share their habitats more horizontally among forest stands, and have higher beta diversity than euedaphic groups, such as Neelidae and Onychiuridae/ Tullbergiidae.

The study site is Ashoro Research Forest (ARF), Hokkaido in Japan. Larch plantations and deciduous broad-leaved natural forests with topographic gradients on the slope facing southwest and northeast are there. These forests in ARF include the wide range of vegetation both in over- and in understory, or litter components (Maeda et al., 2010; Table 1) and soil aspects (Hishi et al., 2010; Table 1). The range of soil pH is from 4.3 to 6.3 (Table 1). The range of soil pH includes pH 5, which is the threshold of change in community structures of Collembola (Ponge, 1993). Therefore, the study

Table 1. Topographic status, soil properties and vegetation types for the 11 sites in this study. Soil pH, C/N ratio and A_0 depth represent mean ± standard deviation for each forest stand (n=3).

	Aspect (slope degree)	Position[a]	pH (H_2O)	Soil C/N	A_0 (cm)	Stand age (yr)	Basal area (m^2/ha)	Dominant Species[b] (% dominance)
Natural	SW (20.3)	Upper	4.8 ± 0.4	17.4 ± 1.8	9.6 ± 1.4	>180	24.6	*Quercus crispula* (92)
	SW (25.5)	Middle	4.9 ± 0.3	16.7 ± 0.6	7.5 ± 3.0	>180	44.3	*Q. crispula* (89)
	NNE (22.6)	Upper	5.2 ± 0.1	14.8 ± 1.1	3.1 ± 1.1	>180	38.5	*Q. crispula* (29), *Acer pictum subsp. mono* (19), *Kalopanax pictus* (17)
	NNE (18.2)	Middle	6.3 ± 0.1	13.1 ± 1.0	3.2 ± 2.1	>180	25.4	*Tilia japonica* (71), *Ostrya japonica* (17)
	SW (23.1)	Lower	5.5 ± 0.2	12.3 ± 0.5	3.2 ± 0.9	>180	18.4	*Ulmus davidiana var. japonica* (28), *Fraxinus mandshurica* (21) *Maackia amurensis* (15)
	NE (11.8)	Lower	5.3 ± 0.2	12.6 ± 0.2	1.6 ± 0.8	>180	29.4	*U. davidiana var. japonica* (44), *F. mandshurica* (33)
Plantation	SW (24.4)	Upper	4.3 ± 0.1	20.0 ± 0.3	12.5 ± 0.5	51	15.8	*Larix kaempferi* (53), *Q. crispula* (42)
	SSE (37.5)	Middle	5.0 ± 0.1	15.7 ± 0.3	10.1 ± 1.9	51	23.1	*L. kaempferi* (75), *A. pictum mono* (16)
	NNE (21.7)	Upper	5.1 ± 0.3	14.7 ± 0.7	6.2 ± 1.6	51	23.6	*L. kaempferi* (84)
	NE (22.9)	Middle	4.8 ± 0.2	12.2 ± 0.4	3.2 ± 2.1	43	29.4	*L. kaempferi* (89)
	SSW (6.5)	Lower	5.2 ± 0.2	14.4 ± 0.7	3.0 ± 0.5	51	27.4	*L. kaempferi* (78)

[a] Upper, middle and lower indicates upper, middle and lower slopes near a river, respectively.

[b] Dominant plant species with more than 10% basal-area are listed.

site has sufficient wide range of forest and soil environments for collembolan community.

This study focused on collembolan community at family level, and investigated the mean and range of soil depth distributions of species within each family or superfamily in cool temperate deciduous forest and plantation stands in Hokkaido, northern Japan. In addition, the relationships between the vertical distribution patterns and alpha diversity within a stand or beta diversity among stands on different vegetation and on topographic sequence of species richness and that of Simpson's diversity index were examined.

Materials and Methods

Study site

This study was carried out in deciduous broad-leaved natural forests and deciduous conifer plantations at Ashoro Research Forest of the Kyushu University Forest, near the town of Ashoro (43°15'N, 143°33'), Hokkaido, Japan. The climate is cool temperate, with an annual precipitation averaging 800 mm and a mean temperature of 6 °C over the past 10 years.

In the natural broad-leaved deciduous forests, the stand age is more than 150 years and plant species compositions differ by topographic gradient and slope direction (Okano,

1994; Maeda *et al.*, 2010; Table 1). In the plantations, Japanese larch (*Larix kaempferi*) is planted, and the stand age is about 50 years. The understories in all natural and plantation stands are covered with *Sasa nipponica*. In this study, six 20 x 20 m plots were established in natural broad-leaved forests, and five 20 x 20 m plots were established in larch plantations within 2 km of one another. These 11 plots included a broad range of gradients in topography, vegetation, and soil properties within both natural forests and plantations (Table 1). These 11 study plots are within 2 km in distance.

The soil parent material was volcanic ash. The soil characteristics of both natural forests and plantations were different among the topographic gradients and slope directions (Table 1; Hishi *et al.*, 2010). Soils on south-facing upper slopes were lower in pH and the depth of the A-horizon and were higher in organic accumulation and in C/N ratio than on north-facing slopes and lower elevations. Soil pH (1:5 H₂O) ranged from 4.3 to 6.3. Vegetation in natural forests was different among slope directions and topographic zones, i.e., *Quercus crispula* dominated upper or middle south-facing slopes, *Acer pictum* subsp. *mono* and *Tilia japonica* were dominant on north-facing slopes, and *Ulmus davidiana* var. *japonica* and *Fraxinus mandshurica* dominated on lower slopes with mesic conditions.

Extraction of Collembola

Sampling collection was carried out in August, 2008. In each plot, organic layers were taken from three points randomly selected within the plot for the extraction of Collembola. The size of the organic layers was 5 cm x 5 cm. Three mineral-soil samples were also taken with a cylindrical soil core sampler (25 cm² in area, 5 cm in depth) adjacent to the organic layer sampling locations. Collembola were extracted using a modified Tullgren funnel (Hasegawa and Takeda, 1995) at 35 °C for 96 h. Collembola were identified to species level and classified into one of the following nine taxonomic groups: Hypogastruridae, Odontellidae/Neanuridae, Onychiuridae/Tullbergiidae, Isotomidae, Tomoceridae, Oncopoduridae, Entomobryidae, Neelidae and Sminthuroidea. Systematics of Collembola followed Deharveng (2004) and the web site of Frans Janssens (http://www.collembola.org/, last updated 30 April, 2012).

Calculations of indices and statistical analyses

Each species of Collembola in both the organic layer and the mineral soil layer was counted. The numbers found in organic and in mineral soil layers from three samples within each of the 11 plots were pooled. Total number of individuals of some taxon was the numbers in organic layer plus those in mineral layer for each plot. To evaluate the weighted mean soil depth distribution, the percentages of individuals that were found in the organic layer to total individuals (%OL) across all species and for each family group were averaged after weighted based on relative abundance of species for each plot as follow:

$$\%OL_{mean} = \sum_{i=1}^{n} w_i \%OL_i$$

where $\%OL_{mean}$ is the weighted mean of a certain family group for each plot based on relative abundance of species, w_i is the relative abundance as weight, and $\%OL_i$ is the $\%OL$ of i-th species.

To evaluate the range of soil depth distribution of each family group, standard deviation of the weighted sample mean of %OL (SDW) of species based on relative abundance as weights within a taxonomic group was calculated for each forest stand. SDW is defined as follow:

$$SDW = \sqrt{\sum_{i=1}^{n} w_i (\%OL_i - \%OL_{mean})^2}$$

where n, w_i and $\%OL_i$ are number of species in a some family group weight and %OL of the i-th species and $\%OL_{mean}$ is the weighted mean of the family group based on relative abundance of the species (Sokal and Rohlf, 1995). The sum of w_i equals to 1. Large SDW of %OL indicates that a family group includes wide range of habitat in soil depth among species, whereas small SDW of %OL indicates that a family includes narrow range of that.

Simpson's diversity index evaluates both species richness and evenness of community, and can accurately evaluate alpha, beta and gamma diversity regardless of sample size (Lande, 1996; Lande *et al.*, 2000). Therefore, in this study, Simpson's D was calculated to evaluate the diversities of family groups within the Collembolan community. Simpson's D is calculated as follows:

$$D = 1 - \sum_{i=1}^{S} p_i^2$$

where p_i is the relative abundance of species i in the community and S is the total number of species in the community. Simpson's D of the community pooled across all

11 plots (both natural forests and plantations) was calculated as the gamma diversity index (D_γ).

The alpha diversity index (D_α) is the mean local diversity weighted by the number of collembolans (Lande, 1996).

$$D_\alpha = 1 - \sum_{j=1}^{N} q_j^2 \sum_{i=1}^{S} p_{ij}^2$$

where p_{ij} is the relative abundance of the i-th species in the j-th stand, q_j is the ratio of individuals in j-th stand to total abundance in all plots, and N is the number of study plots (11 in this study), except that individuals of some family was zero. The beta diversity index (D_β) is the difference in community structure among different local communities, and is defined by the following equation:

$$D_\beta = D_\gamma - D_\alpha$$

In this study, D_α and D_β were calculated for each family group. D_α / D_γ were calculated to evaluate contribution of alpha to gamma diversity, and D_α / D_γ plus D_β / D_γ is 1.

One-way ANOVA and Tukey-Kramer's HSD test as post-hoc were used for comparing the %OL$_{mean}$ and SDW among the family groups. The liner relationship between alpha diversity of whole collembolan community and SDW of whole Collembola in each plot, and between each diversity index and %OL or SDW of family groups were examined using Pearson's correlation analysis. Statistical analyses were performed using JMP ver. 9.0 (SAS Institute Inc.).

Results

In total, we obtained 2580 individuals representing 80 species (including some that could only be identified to genus) in nine taxonomic groups of Collembola (Table 2). The mean alpha, beta and gamma diversity of whole collembolan community was 0.916, 0.039 and 0.955, respectively. Alpha diversities of plots did not significantly correlated with SDW of plots for whole collembolan communities (n=11 sites, r=-0.124, P=0.717).

Abundances of the family groups of Collembola were ranked as follows (Table 2): Isotomidae (49% of total Collembola) > Onychiuridae/Tullbergiidae (15%) > Hypogastruridae (9%) > Entomobryidae (6%) > Neanuridae (6%) > Neelidae (5%) > Tomoceridae (5%) > Sminthuridae (3%) > Oncopoduridae (1%).

%OL$_{mean}$ of Neelidae, Sminthroides, Tomoceridae and Entomobryidae were significantly higher than those of Neanuridae, Isotomidae, Onychiuridae/Tullbergiidae, Oncopoduridae and Hypogastruridae (Table 3; One-way ANOVA, F=8.69, P<0.0001).

The SDW of %OL$_{mean}$ of Onychiuridae/Tullbergiidae and Isotomidae were significantly higher than those of Neelidae and Oncopoduridae (Table 3; One-way ANOVA, F=6.82, P<0.0001).

The rank of D_α for family groups (Table 4) was Isotomidae (0.80) > Onychiuridae/Tullbergiidae (0.64) > Entomobryidae (0.55), Sminthuridae (0.55) > Tomoceridae (0.49) > Odontellidae/Neanuridae (0.47) > Neelidae (0.30) > Oncopoduridae (0.00). The rank of D_β for family groups (Table 4) was Hypogastruridae (0.23) > Tomoceridae (0.22) > Odontellidae/Neanuridae (0.14), Neelidae (0.14), Sminthuroidea (0.14) > Entomobryidae (0.12) > Onychiuridae (0.11) > Isotomidae (0.08) > Oncopoduridae (0.00). The ranking pattern for D_γ was similar to that of D_α. The contributions of alpha diversities to gamma diversity (D_α/D_γ) of family groups were ranked as Isotomidae (0.91) > Onychiuridae/ Tullbergiidae (0.85) > Entomobryidae (0.82) > Sminthroidea (0.80), Odontellidae/Neanuridae (0.79) > Tomoceridae (0.69) > Neelidae (0.68) > Hypogastruridae (0.57).

Population density was not significantly correlated to D_α or D_β (data not shown). D_α was positively correlated with the mean SDW (Fig. 1, n=9 family groups, r=0.934, P=0.0002). The correlation between D_β and %OL$_{mean}$ was not significant (Fig. 2, n=9 family groups, r=0.318, P=0.4049). The significant negative correlation between D_α and D_β was found (n=8, r=-0.737, P=0.0369). The significant positive correlation between D_α/D_γ and SDW (Fig. 3; r=0.712, P=0.0496; excluding Oncopoduridae, which is impossible to calculate D_α/D_γ) was found, meaning that the significant negative correlation between D_β/D_γ and SDW (n=8, r=-0.712, P=0.0496) was found. The D_α/D_γ was not significantly correlated with %OL$_{mean}$ (n=8, r=-0.065, P=0.8788).

Discussion

Soil depth plays a key role in resource partitioning for collembolan communities (Hågvar, 1983; Ponge, 2000; Takeda, 1987; Hishi et al., 2007). The SDW of whole collembolan community did not significantly correlated with alpha diversity of plots, suggesting that habitat partitioning in soil depth might not relate diversity of whole collembolan community in this site. This might be partly because each functional or family group of Collembola has different patterns for depth distribution and alpha or beta diversities, as

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Table 2. Total numbers of collembolans found in organic and mineral soil habitats.

Taxonomic Group	Species[a]	O	M	total
Hypogastruridae		37	202	239
	Ceratophysella denisana	17	133	150
	C. communis	4	7	11
	C. tergilobata	2	4	6
	C. wrayia	10	50	60
	Hypogastrura itaya	1	1	2
	Hypogastrura sp.	0	1	1
	Xenylla brevispina	2	6	8
	Xenylla sp.	1	0	1
Odontellidae/Neanuridae		71	80	151
	Superodontella sp.	2	7	9
	Anurida sp.	2	0	2
	Ceratrimeria sp.	1	0	1
	Friesea japonica	42	42	84
	Granurida tuberculata	3	1	4
	Micranurida sp1	4	10	14
	Micranurida sp2	6	2	8
	Neanura ezomontana	0	1	1
	Neanura fodinarum	0	1	1
	Paranura sp.	2	4	6
	Pseudachorutes sp.	9	12	21
Onychiuridae/Tullbergiidae		214	183	397
	Mesaphorura spp.	39	102	141
	Protaphorura longisensillatus	26	16	42
	Protaphorura okaffii	9	7	16
	Protaphorura uenoi	2	1	3
	Allonychiurus flavescens	80	26	106
	Allonychiurus japonica	15	12	27
	Onychiurus folsomii	43	19	62
Isotomidae		598	660	1258
	Dagamaea flavescens	1	10	11
	D. morei	0	1	1
	Desoria albella	0	1	1
	D. hyonosenensis	20	2	22
	D. notabilis f. pallida	74	29	103
	D. notabilis	29	5	34
	D. trispinata	4	11	15
	D. gracilliceta	2	1	3
	D. occulata	2	5	7
	D. sensibilis	5	0	5
	Desoria sp.	17	47	64
	Folsomia octoculata	175	119	294
	F. reguralis	33	78	111
	F. inoculata	16	65	81
	F. fimetalia	5	31	36

	F. bidentata	6	0	6
	F. hidakana	2	46	48
	Folsomides parvurus	0	10	10
	Heteroisotoma carpenteri	38	30	68
	Isotoma viridis	1	0	1
	Isotomiella minor	115	143	258
	Micrisotoma acrotoma	0	1	1
	Proisotoma subminuta	0	1	1
	Proisotoma sp1	9	3	12
	Proisotoma sp2	39	20	59
	Pseudanurophorus arcticus	5	0	5
	Pteronychella spatiosa	0	1	1
Entomobriidae		94	70	164
	Coecobrya tibiotarsalis	30	44	74
	Entomobrya sp1	12	0	12
	Entomobrya sp2	0	2	2
	Homidia sp.	12	1	13
	Lepidocyrtus sp1	35	21	56
	Lepidocyrtus sp2	1	1	2
	Sinella umesaoi	4	1	5
Tomoceridae		104	16	120
	Aphaenomurus interpositus	1	0	1
	Plutomurus belozerovi	6	0	6
	Pogonognathellus fravescens	7	0	7
	P. borealis	6	0	6
	Tomocerus varius	55	6	61
	T. aokii	15	3	18
	T. ocreatus	1	2	3
	T. violaceus	1	1	2
	T. jezonicus	9	0	9
	T. lamelliferus	2	4	6
	T. ishibashii	1	0	1
Oncopoduridae		10	24	34
	Oncopodura japonica	10	24	34
Neelidae		110	23	133
	Megarothorax minimus	71	18	89
	Neelus minutus	39	5	44
Sminthuroidea		71	12	83
	Arrhopalites minutus	37	4	41
	Arrhopalites sp	1	0	1
	Dycyrtoma sp	11	2	13
	Ptenothrix sp	8	4	12
	Sphaeridia sp	0	1	1
	Sminthurinus sp.	5	0	5
	Sminthurus sp	9	1	10
Total		1311	1269	2580

Table 3. Means and standard deviations of the weighted average of %OL (%OL$_{mean}$) and its standard deviation of %OL$_{mean}$ (SDW) of a forest stand for each family group.

Family group	%OL$_{mean}$	SDW
Hypogastruridae	27.4 ± 25.8 C	15.9 ± 7.7 AB
Odontellidae/Neanuridae	44.2 ± 31.5 BC	17.3 ± 9.8 AB
Onychiuridae/Tullbergiidae	36.9 ± 17.4 BC	25.8 ± 7.4 A
Isotomidae	41.0 ± 21.1 BC	24.6 ± 6.5 A
Entomobryidae	64.1 ± 21.5 AB	19.2 ± 9.1 AB
Tomoceridae	78.5 ± 23.1 A	18.6 ± 10.3 AB
Oncopoduridae	30.1 ± 33.5 BC	0.0 ± 0.0 C
Neelidae	80.8 ± 21.9 A	12.7 ± 9.7 B
Sminthuridae	80.8 ± 19.7 A	15.8 ± 11.0 AB

Table 4. Number of species, Simpson's alpha, beta and gamma diversity indices, and contribution of alpha diversity to gamma diversity for family groups of Collembola.

Taxonomic group	No. of species	D_γ	D_α	D_β	D_α / D_γ
Hypogastruridae	8	0.54	0.31	0.23	0.57
Odontellidae/Neanuridae	11	0.65	0.52	0.14	0.79
Onychiuridae/Tullbergiidae	7	0.76	0.64	0.11	0.85
Isotomidae	27	0.87	0.80	0.08	0.91
Entomobryidae	7	0.67	0.55	0.12	0.82
Tomoceridae	11	0.70	0.49	0.22	0.69
Oncopoduridae	1	0.00	0.00	0.00	n.c.
Neelidae	2	0.44	0.30	0.14	0.68
Sminthuridae	7	0.69	0.55	0.14	0.80

n.c.: not calculated

Hasegawa *et al.* (2006) who had stated that species diversity in each functional group was related with environmental valuables, though species diversity of whole community of Collembola was stable among a different sere of secondary succession.

This study is the first report to examine quantitatively the relationships between soil depth distribution and alpha or beta diversity for collembolan families. Here, we tested two hypotheses: (1) that the alpha diversity of a family with a wide range of habitats will be higher than that of a family with a narrow range, and (2) that the beta diversity of a family living in shallow soil layers will be higher than that of a family in deep layers. Epigeic groups, such as Tomoceridae, Sminthuroidea and Neelidae, had lower alpha diversity and higher beta diversity than Isotomidae or Onychiuridae. On the

other hand, the groups that occupied wide range soil depth, such as Isotomidae, Entomobryidae, Odontellidae/Neanuridae and Onychiuridae, had higher alpha diversity. Consistent with our hypothesis, the SDW of the family groups correlated with D_α (Fig. 1) and with contribution of alpha diversity to gamma diversity (Fig. 3). Contrary to our expectations, %OL$_{mean}$ of a family group did not significantly correlate with D_β (Fig. 2).

Soil depth distribution patterns of family groups

This study showed that Tomoceridae, Neelidae and Sminthroidea were epigeic, Hypogastruridae and Oncopoduridae was euedaphic, and Onychiuridae/ Tullbergiidae and Isotomidae had wide habitat range (Table 3). These confirmed previous studies reported without Hypogastruridae recognized as aerophilic or hemiedaphic and
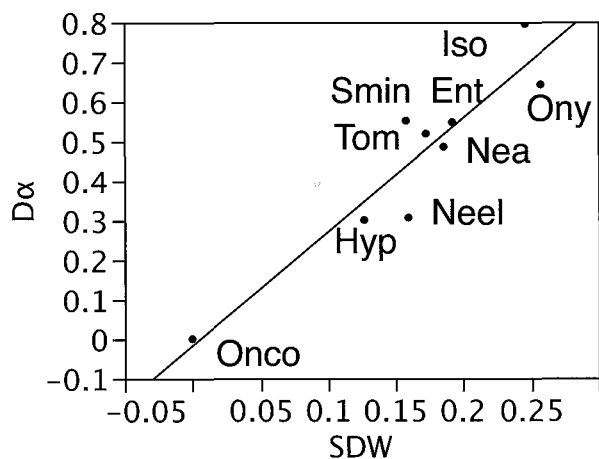
Fig. 1. Relationship between the standard deviation of the weighted mean of organic layer population to total population (SDW) and alpha diversity (D_α) for family groups of Collembola. The solid line indicates the regression between SDW and D_α. Hyp, Hypogastruridae; Nea, Odontellidae/Neanuridae; Ony, Onychiuridae/Tullbergiidae; Iso, Isotomidae; Ent, Entomobryidae; Tom, Tomoceridae; Onco, Oncopoduridae; Neel, Neelidae; Smin, Sminthuroidea.
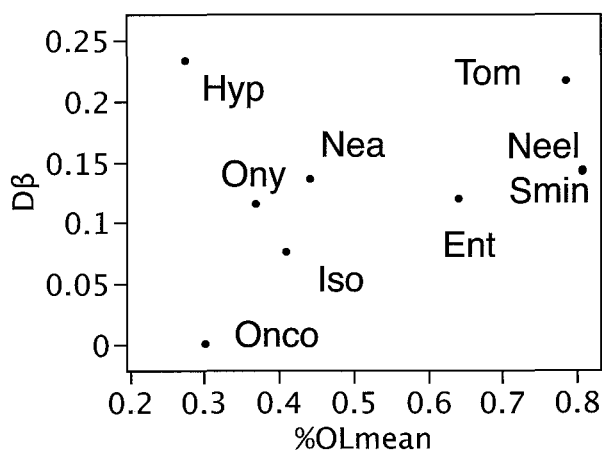

Fig. 2. Relationship between the weighted mean of percentages of the total population number found in the organic layer (%OL_mean) and beta diversity (D_β) for taxonomic groups of Collembola. Abbreviations are as in Fig. 1.

Fig. 3. Relationship between the SDW and D_α/D_y for family groups of Collembola. The solid line indicates the regression between SDW and D_α/D_y. Abbreviations are as in Fig. 1 and 2.

without Neelidae as euedaphic (Hågvar, 1983; Takeda, 1987; Hasegawa and Takeda, 1995; Ponge, 2000).

Hypogastruridae, which have been reported as epigeic or hemiedaphon (Hågvar, 1983; Hasegawa and Takeda, 1995; Takeda, 1987; Ponge, 2000), preferred mineral soil to organic layer in this study. The group with seasonal migration in depth may not follow to the relationship between habitat
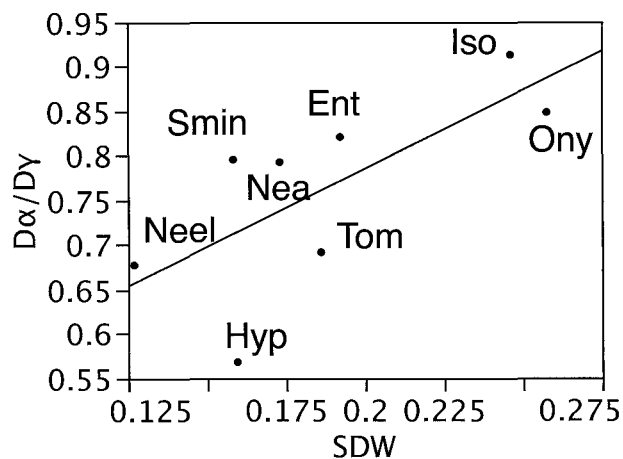
and diversity. Some Hypogastruridae species have been known to aggregate the specific habitats or resources, such as mushrooms or tree trunk, and to migrate frequently from aboveground and deep soil layer. *Ceratophysella denisana*, which often aggregates the mushrooms, moves to deep soil layer for reproduction in spring and aggregate to mushrooms during autumn (Sawahata *et al.*, 2002). *Xenylla brevispina* has constant univoltine life cycle, and habits mineral soil during juveniles with high density (Itoh, 1991). After that, *X. brevispina* simultaneously climb on the tree branches. Therefore, some Hypogastruridae species might occasionally live in mineral soil layer during juveniles in their life cycles in this study. Previous studies showed that various species of Collembola vertically migrate to downward especially in summer dry season (Hågvar, 1983; Takeda, 1987). Unfortunately, this study was carried out for one-time in summer season.

Diversity and soil depth distribution in relation to families of Collembola

Positive correlation between SDW and D_α (Fig. 1) suggested that partitioning the vertical habitat resource among species should enable a family to be co-existed in small area. A family with high species diversity, such as Onychiuridae and Isotomidae (Table 4), can have wide range of life form, and tend to include from epigeic to euedaphic species, whereas that with low species diversity tend to include narrow

range of habitat. This result is not due to the size effect of whole regional species diversity of the families in our site on alpha diversity. Without regard for the effect of gamma diversity, D_a/D_γ positively correlated with SDW of %OL (Fig. 3), and then, the contributions of beta diversity was negatively correlated with SDW. This suggests that families with wider range of habitats in soil depth may have relatively higher alpha diversity to beta diversity within a stand than those with narrow ranges. In addition, families with narrow range of soil depth habitat should have relatively higher beta diversity to alpha diversity than those with wide range.

Beta diversity of collembolan family group among forest stands both in species richness and in diversity index was not significantly related with %OL, whereas the significant positive correlation between D_β and the $\%OL_{mean}$ was found without Hypogastruridae (n=8 taxonomic groups, r=0.877, P=0.0043). Thus, the pattern of Hypogastruridae did not follow our expectations, and this was partly because juveniles of Hypogastruridae, which is basically epigeic or hemiedaphic group, might occasionally aggregate in deep soil layer as above-mentioned. For understanding the relationship between beta diversity and soil depth distribution, the groups with high frequency of vertical migration might be considered other than the means and ranges of depth distribution. Therefore, seasonal migration pattern should be counted into relationship between soil habitat depth and diversity patterns in future study.

Otherwise, mineral soil layer may serve heterogeneous conditions beyond our expectations, in relation to mineral soil acidity, organic contents, disturbance by macro-faunal activity, or mycorrhizal conditions. In this study, Tullbergiidae was classified into one as *Mesaphorura* spp. This might lead misunderstanding the results of this study. Many studies showed that *Mesaphorura* (Tullbergiidae) displays resource partitioning in soil pH, vertical habitats or food (Hågvar, 1983; Ponge, 1993; Ponge, 2000), suggesting that species diversity of Onychiuridae/Tullbergiidae might be under estimation in this study.

Previous studies of depth distribution of Collembola have separated the sample into more detailed layers, 1-2cm in depth range (i.e., Hågvar, 1983; Takeda, 1987; Ponge, 1993), than this study, and have determined the positions and ranges of the niche of species. This study used weighted mean of the percentage of organic layer population to total population as depth of habitat ($\%OL_{mean}$) and its standard deviation of the sample weighted mean (SDW) as the width of habitat of

family group. Though these indices are less informative than the estimations from samples obtained detailed soil layer, these could easily obtain the depth distributions of species of collembolan species only from the sample of organic and mineral soil layers. It should note that SDW tends to be large value when the sample includes large distance from the mean, suggesting that SDW of family group including species at extreme surface or deep layer should be larger than that partitioned continuously the habitat in soil depth.

In ecological sense, this study showed that the species of Collembola partitioned their habitat resource according to horizontal or soil depth within each family of Collembola as previous study had indicated within the class Collembola (i.e. Takeda, 1987), and this assumption should help our understanding the patterns of biodiversity among families of collembolan communities. The negative correlation between D_a and D_β of the families of Collembola indicated that species diversification in each family of Collembola may have been selected among horizontally or among soil depth.

摘　要

菱拓雄 [1,2]・田代直明 [1]・前田由香 [1]・井上幸子 [1]・長慶一郎 [1]・緒方健人 [1]・山内康平 [1]・馬渕哲也 [1]（[1] 九州大学北海道演習林　〒 089-3705 北海道足寄郡足寄町北 5 条 1-85・[2] 九州大学福岡演習林　〒 811-2415 福岡県糟屋郡篠栗町津波黒 394）：北海道東部の落葉広葉樹天然林およびカラマツ人工林における土壌性トビムシの科の α および β 多様性と土壌深度分布との関係

トビムシの科において，水平分布および土壌深度分布に関する住み場所資源の分割と種の多様性の関係はほとんどしられていない．冷温帯上部に位置する北海道東部の森林において，トビムシの分類群ごとに有機物層，鉱質土層の個体数の割合とシンプソンの多様度指数における α，β 多様性の関係を調べた．調査には南北斜面方位の尾根から谷地形を含む十分な環境傾度をもつ，6 つの落葉広葉樹天然林と 5 つのカラマツ人工林を用いた．有機物層に生息する割合（%OL）が最も高かったのはトゲトビムシ科であり，最も低かったのはムラサキトビムシ科であった．%OL の科内における種間でのばらつき（SDW：標本の加重平均標準偏差）は，シロトビムシ

上科およびツチトビムシ科で大きく，最も低かったのはキヌ
トビムシ科であった．シンプソンの多様度指数から計算した
α多様性はツチトビムシ科やシロトビムシ上科で高く，ムラ
サキトビムシ科，キヌトビムシ科で低かった．β多様性はム
ラサキトビムシ科，トゲトビムシ科で高く，ツチトビムシ科，
キヌトビムシ科で低かった．SDWと多様度指数における α
多様性の間には有意な正の相関がみられた．これはトビムシ
の科内における種の土壌深度分布のばらつきが林分内での局
所多様性と関係していることを示している．%OLと林分間の
β多様性の間に有意な相関はみられなかった．またSDWと
α／γの間には正の相関，β／γの間には負の相関がみられた．
また，科のα多様性とβ多様性の間には有意な負の相関が
みられた．これは林分内での局所多様性の大きい科では林分
間での種の入れ替わりが小さいことを示している．

キーワード：α多様性，β多様性，北海道東部，シンプソン
の多様性，水平及び垂直分布

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