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Trampling, Litter Removal, and Variations in the Composition and Relative Abundance of Soil Arthropods in a Subtropical Hardwood Forest

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Ya-Fu Lee, Yen-Min Kuo, Sheng-Shan Lu, Duen-Yuh Chen, Hao-Jiang Jean, and Jung-Tai Chao (2009) Trampling, litter removal, and variations in the composition and relative abundance of soil arthropods in a subtropical hardwood forest. *Zoological Studies* **48**(2): 162-173. Relationships of human trampling and litter removal with physicochemical properties and arthropod diversity of forest soils were studied in a secondary hardwood forest in northern Taiwan. In 4 sampling sessions, 360 soil cores were extracted from 24 randomly chosen replicate plots, representing soil samples from (1) densely vegetated areas, (2) bare trails as a result of non-mechanical trampling, and (3) ground underneath nylon-mesh litter traps set up on trails. We collected 7 classes and at least 17 orders of arthropods, with an estimated mean density of 13,982 ind./m^2. The Collembola and Acari were the most common groups. The former dominated in abundance, comprising 8 families (2.5 ± 0.1 per core), followed by the Acari (e.g., oribatids) with at least 37 families (2.2 ± 0.1 per core). The density and number of taxa of arthropod overall, as well as the density and number of families of springtails and oribatids in particular, were highest in soil samples from vegetated areas. Soil samples beneath litter traps were in between, whereas the lowest taxon numbers and densities consistently occurred in soils from bare trails. These patterns were correlated with a trend of significantly more-compacted soils on bare trails than on trails beneath litter traps and an even greater difference when compared to soils of vegetated areas. While the moisture content and temperature of soils tended to vary in response to local weather conditions, soil samples in vegetated areas contained higher carbon and nitrogen contents and slightly lower pH values than those from bare trails. Trampling and litter removal did not affect the frequency of occurrence of the major taxa; yet dramatic declines occurred in relative abundances of the predominant collembolans and Acari, from over 20% to about 90%. At the family level, however, trampling and litter removal appeared to cause larger changes in the composition of the Acari than in collembolans. http://zoolstud.sinica.edu.tw/Journals/48.2/162.pdf

Key words: Arthropods, Biodiversity, Litter, Soil, Trampling.

Soil and soil inhabitants comprise crucial components fundamental to the dynamics and complexity of food webs in forest ecosystems. Various factors can influence the composition, relative abundances, and dynamics of soil faunas (see reviews in Petersen and Luxton 1982). These include biotic interactions such as competition (Ferguson and Joly 2002) and predation (e.g., Niemela et al. 1992, Oliver and Beattie 1996, but see Lenoir et al. 2003); the presence or absence of organic matter (Bengtsson et al. 1998, Eaton et al. 2004); physical features of the soil environment such as temperature, moisture, compaction (Mitchell 1978, Bouwman and Arts 2000, Larsen et al. 2004), and acidity (Athias-Binche 1979, Schaefer 1990, Filser 2002); as well as chemical

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features of soils (Hågvar and Abrahamsen 1984, Moldenke and Thies 1996).

With the trend of increasing human populations and land use intensity, a better understanding of the effects of human activities on soil quality and soil fauna at different spatial-temporal scales is critically important to the conservation of global biodiversity. As a major fraction of the meso- and macro-faunas of soils in terms of both diversity and abundance, arthropods are also likely to be greatly impacted by human activities (Dindal and Norton 1979, Krivolutsky 1979). For instance, Lasebikan (1975) indicated a reduction in the number of taxa and mean densities of most taxa of soil arthropods 6 mo after forest clearing. Lagerlof and Wallin (1993) found that naturally vegetated fields maintain more-diverse and -abundant soil arthropods than do cultivated areas.

While many of those factors can be correlated to one another (Gersper and Challinor 1975), soil compaction has been suggested to be one of the most significant causes of soil degradation (Brais 2001). Soil compaction may result directly or indirectly from human activities, such as cultivation, and vegetation or litter removal, or both; its effects on soil animals, however, are not universally consistent. Kevan et al. (1995) found that tracks caused by human vehicles in the high Arctic tundra reduce carbon and phosphorus in the soil, and the abundance, but not the diversity, of soil arthropods. While Battigelli et al. (2004) found that soil compaction causes a shift in composition from oribatids to prostigmatids and mesostigmatids, Eaton et al. (2004) indicated a decrease in springtail populations caused by organic matter removal and vegetation control, but no significant effect from soil compaction.

Most previous studies investigating the effects of compaction on soil arthropods focused on mechanical forces from farm machinery or vehicles (e.g., Challinor and Gersper 1975, Kevan et al. 1995, Olander et al. 1998, Horn et al. 2004), and mostly on arable soils or cultivated areas (e.g., Bouwman and Arts 2000, Larsen et al. 2004), or soils of temperate forests (e.g., Battigelli et al. 2004, Godefroid and Koedam 2004). Tropical and subtropical forests often exhibit high biological diversity and endemism, including of arthropods (e.g., Kitching et al. 2001). Many areas in such regions, such as East and Southeast Asia, are under the greatest threat by increases in human populations and development (UN 2006), but these issues remain largely unstudied. The composition, diversity, and relative abundances of soil arthropods in tropical and subtropical forests may differ from those in temperate zones (Petersen and Luxton 1982, Takeda and Abe 2001). It is not clear if the processes of soil compaction and litter removal, or different degrees of these processes have similar or even worse effects in subtropical and tropical regions. In addition, studies on the effects resulting from compaction due to human trampling on the composition, relative abundances, and spatiotemporal variations of arthropods in forest soils of the majority of tropical and subtropical regions, at least to our knowledge, are still lacking.

The present study examined the composition and relative abundances of soil arthropods in a mid-elevation subtropical hardwood forest in Taiwan. Soils with treatments of trampling and reduced litter were examined to test the hypothesis that these 2 factors alter the physicochemical properties of the soils thereby affecting the composition and diversity of soil arthropods. We predicted that (1) forest soils from areas with no or less trampling would have more-diverse and -abundant arthropods than soils with more trampling and correspondingly higher degrees of compaction; (2) forest soils containing a litter layer would have more-diverse and -abundant arthropods than soils bare of litter; and (3) trampling and reduced litter would alter the relative abundances of soil arthropods in accordance with their variable tolerances to different levels of soil compaction (Mitchell 1979, Kevan et al. 1995).

MATERIALS AND METHODS

Study site

Field work took place in a secondary broadleaf forest (at 700 m elevation) located within the Fushan Experimental Forest (121°35'E, 24°45'N; 1098 ha in total size), Taiwan Forest Research Institute (TFRI), Ilan County. This is a typical mid-elevation hardwood forest of northeastern Taiwan, and is one of the main study sites for Long-Term Ecological Research (LTER) on the island. Fushan is characterized by red to yellowish-brown acidic sandy clay (Lin et al. 1996), an annual rainfall of above 3600 mm (mean monthly rainfall of 293.8 ± 81.5 mm), and monthly mean temperatures below 15°C in the coldest months (Dec. to Feb.) and around 22-24°C from June to Aug. (Fushan Station weather data, TFRI). Dominant tree species at the

site include long-leaved chinquapin *Castanopsis carlesii* (Hemsl.) Hayata, yellow basket willow *Engelhardtia roxburghiana* Wall., incense nanmu *Machilus zuihoensis* Hayata, Chinese meliosma *Meliosma squamulata* Hance, and Nanto actinodaphne *Litsea acuminata* (Blume) Kurata. Major herbaceous plants include *Alocasia odora* (Roxb.) K. Koch, *Elatostema lineolatum* Wight, and various fern species (Chang et al. 1998).

Soil sampling

Soil samples were extracted every 3 mo between Nov. 2001 and Aug. 2002. For each sampling, we collected 30 cores (5 cm in diameter × 5 cm deep) of soil samples from 6 different randomly chosen replicate plots of 10 × 10 m each, representing soils from (1) naturally and densely vegetated areas where little or no trampling occurred and litter was allowed to accumulate naturally, and from (2) bare trails. Plots were about 30-50 m from each another. Trails, generally about 50-80 cm in width, passed by or between plots in a roughly north to south direction. Prior to the study, vegetation sampling and long-term monitoring of forest dynamics by various research teams caused trampling in these human-frequented trails over years of use (Chang et al. 1998, FC Ma pers. comm.). Thus, the trails were bare of vegetation, but litter had accumulated. For our 3rd set of samples, we took an additional 30 soil cores, 5 from each of the 6 plots from the trail directly beneath a nylon-mesh litter trap (1 × 1 m in size, and 1 m high). These litter traps had been set up on the trail in the winter of 1994 while establishing these site plots (Chang et al. 1998). Therefore, soil beneath the litter traps was free from trampling, but the vegetation remained and was nearly bare of litter compared to vegetated areas. In the latter, a mean litterfall of 123.84 ± 11.87 g/m^2 dry mass/3 mo had accumulated (data of 1994-2005; F.C. Ma pers. comm.). In total, 360 core samples (with a mean dry mass of 25.9 ± 0.7 g/core) were taken from 24 sampled plots (90 cores over 6 plots in each sampling sessions).

In the field, we measured soil temperature (°C) of each soil sample with a temperature probe (TES-1319, TES Electronics Crop., Taipei, Taiwan). We also used Yamanaka's soil hardness tester (Kiya Seisakusho, Kawagoe-shi, Japan) to measure the resistance value of the soil (mm), which can be converted to the degree of soil compaction (1.96 N/mm). The fresh soil mass of each core was weighed in the Fushan Research Center, immediately after sampling, using an electronic balance. Soil samples were placed in Tullgren funnels in the laboratory for 5 d to collect soil animals, after which they were oven-dried at 55°C overnight and weighed again for the dry mass. We obtained soil moisture by subtracting the net dry soil mass from the original wet mass, and estimated the ratio of water (g) to the dry soil mass (Schinner et al. 1996). We ignored the weight of soil animals except for large macro- or mega-fauna, e.g., earthworms and molluscs, which occurred only occasionally; yet we might have overestimated the soil moisture in samples that contained high numbers of soil arthropods. We followed the procedures of Page (1983) to determine pH values, and carbon and nitrogen contents of each soil sample.

Soil animals

We set up 90 Tullgren funnel extractors in the laboratory, with a 25-W bulb for each extractor, and followed Coleman et al.'s procedure (1999) for collecting soil animals. Arthropods were sorted and identified under microscopes, mostly to order, or families whenever possible, based on Triplehorn and Johnson (2005). We treated the Formicidae (ants) as a separate taxon from other hymenopterans because of their relatively higher abundances and close association with soils (Toda and Kitching 1999). We additionally sorted the most abundant taxa, springtails (Collembola) and oribatid mites (Acari), into families when possible, using the keys in Krantz (1978), Balogh and Balogh (1992), Hopkin (2002), and Bellinger et al. (2007). All specimens were categorized, submersed in 75% alcohol in individually labeled vials, and stored in the Entomological Museum, TFRI.

Data analysis

We present data as the mean ± standard error (S.E.), and determined all statistical tests at a significance level of 0.05, using STATISTICA 6.0 for Windows 2000 (StatSoft, 2001), unless otherwise noted. We measured the relative frequency of occurrence (RF) and relative abundance (RA) of each arthropod taxon identified. The former was calculated as the number of soil cores in which a particular taxon was identified, divided by the total numbers of soil cores that contained each identified taxon. This provides a standardized measure, ranging from 0% to 100%,

of the commonness of each taxon in the sample array. We defined each taxon as predominant, abundant, less abundant, and rare as comprising ≥ 50%, 10% to < 50%, 1% to < 10%, and < 1%, respectively, of the arthropod individuals present in a sample. We additionally used the arithmetic mean of the RF and RA, adopted from Curtis and McIntosh (1951), to obtain an estimate of the relative importance index (RI) of each arthropod taxon.

We adopted the converted Simpson index, $1 - D = 1 - \Sigma (p_i^2)$, to assess the heterogeneity (SH) and Simpson's measure of evenness, $E_{1/D} = (1/D)/s$, to estimate the evenness (S.E.) of the soil arthropod composition (Magurran 2004); where p_i is the relative abundance of a particular taxon i (i = 1 to n, n being the total number of arthropod taxa identified). A higher SH value indicates a more-diverse composition with a more-even distribution in abundance, and the 95% confidence intervals (CIs) of the latter index were estimated using the jackknife technique (Magurran 2004). We also applied Morisita's index, $C_\lambda = 2\Sigma X_{ij}X_{ik}/(\lambda_1 + \lambda_2)N_jN_k$, to measure the overall similarity in the composition among samples from the 3 types of soils (Krebs 1999); where X_{ij} and X_{ik} are the numbers of arthropods of taxon i in samples j and k, $\lambda_1 = \Sigma[X_{ij}(X_{ij} - 1)]/N_j (N_j - 1)$, $\lambda_2 = \Sigma[X_{ik}(X_{ik} - 1)]/N_k(N_k - 1)$, and N_j and N_k are the total numbers of arthropods in samples j and k, respectively.

We used analysis of variance (ANOVA) to examine the effects of soil types and sampling sessions on the dry mass and physicochemical properties of the soils. A simple linear regression was used to determine the relationship of dry soil mass to the numbers of arthropod taxa and individuals present in each sample, respectively. In addition, we used multiple linear regressions, with t values testing for partial regression coefficients (β), to determine the relationships of the physicochemical properties of the soils to arthropod density and numbers of arthropod taxa present in each sample (Zar 1999). We adopted the R × C G-test (Zar 1999) to examine if the distributions of the RF among the 3 types of soils and sampling sessions deviated from randomness, and Levene's test (F) to measure the homogeneity of the variance in abundances for the 4 most-dominant arthropod taxa. We also applied a multivariate analysis of variance (MANOVA) with Pillai's *trace* values and F transformation to examine the effects of soil types on the variance in numbers of arthropod taxa and individuals present, and the variation among sampling sessions. For the above analysis, soil samples were standardized per unit of dry soil mass to adjust for differences in soil volume sampled per core. When significant differences occurred, we conducted additional post hoc multiple-range comparisons using Tukey's honest significant difference (HSD) test for equal sample sizes to pinpoint the differences (Zar 1999).

RESULTS

Composition and relative abundances of soil arthropods

Our samples contained a total of 9801 arthropods from 7 classes and 17 orders, including 3 orders in the Arachnida (Acari, Araneae, and Pseudoscorpiones), Isopoda of the Malacostraca, 12 orders in the Hexapoda, Scolopendromorpha (Chilopoda), Diplopoda, Pauropoda, and Symphyla, and some unidentified arthropod larvae (comprising < 1% in total abundance) (Fig. 1). We also found a small proportion of other invertebrates, e.g., earthworms (Annelida), snails (Mollusca), and nematodes (Nematoda). The numbers of taxa found per soil core, primarily resolved to order level, varied from 0 to 11 (mean 4.1 ± 0.1), with 83.4% of samples contained 2-6 taxa. The densities of arthropods per 100 g of dry soil fluctuated (range 0-1366; mean 135.2 ± 8.7). The dry mass of soil samples from bare trails was heavier (28.97 ± 1.27 g; with a bulk density of 0.3 ± 0.01 g/cm^3) than those from vegetated areas (23.59 ± 0.99 g; with a bulk density of 0.24 ± 0.01 g/cm^3; $F_{(2, 356)} = 5.45$, $p < 0.005$). The soil dry mass, however, also varied among types of habitats where these soil samples were collected (ANOVA: $F_{(2, 347)} = 12.68$, $p < 0.001$) and over the 4 sampling sessions ($F_{(3, 347)} = 149.37$, $p < 0.001$) with a factor × factor interaction ($F_{(6, 347)} = 6.37$, $p < 0.001$). Thus, both the numbers of arthropod taxa ($r = 0.14$, $F_{(1, 337)} = 4.73$, $p < 0.05$) and the densities ($r = 0.32$, $F_{(1, 342)} = 36.2$, $p < 0.001$) were little or only slightly correlated with the dry mass of soils.

Springtails and mites each accounted for > 20% of the relative frequency of occurrence (RF). The former also predominated in the relative abundance (RA), followed by the Acari, accounting for 55.7% and 30.1% of the total abundance, respectively. Beetles (e.g., carabids, curculionids, and staphylinids), ants, and symphylans followed, and these 5 taxa accounted for nearly 60% of

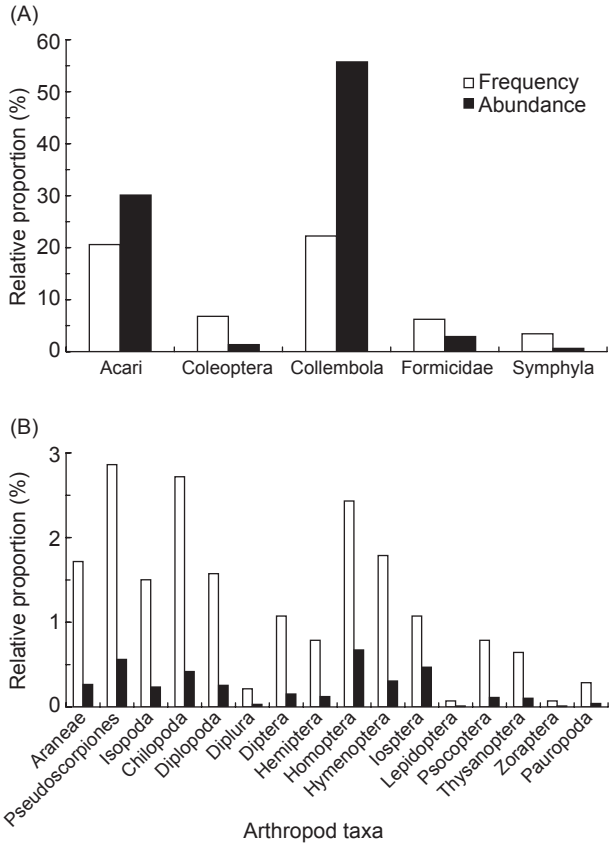

Fig. 1. Frequencies of occurrences and relative abundances of (A) the top 5 arthropod taxa with the highest values, and (B) the other 16 taxa sampled in 3 types of soils (bare trail, underneath litter traps, and vegetated areas) in the Fushan Experimental Forest, Taiwan Forest Research Institute.

the RF (Fig. 1). Ants (2.9%) and beetles (1.4%), however, were much less abundant compared to springtails and mites, and all other taxa were rare and each contributed < 1% to the total abundance. Overall, the 4 most important taxa, springtails (% relative importance, RI = 39.0), mites (RI = 25.4), ants (RI = 4.6), and beetles (RI = 4.1), comprised > 80% of the abundance in all samples, except for those of the Aug. session from bare trails, where they accounted for 65%. We identified 8 families of springtails (mean 2.5 ± 0.1 per core); isotomids predominated, followed by onychiurids and entomobryids (Table 1). The Acari was mostly comprised of oribatids, and then mesostigmatids and prostigmatids (e.g., tetranychids). We recorded 37 families of oribatids (mean 2.2 ± 0.1); nanhermanniids, haplozetids, and malaconothrids were the most common and abundant, followed by lohmanniids, tectocepheids, and xylobatids (Table 2).

Trampling, litter removal, and soil arthropods

Both higher numbers of taxa (5.1 ± 0.2) and densities of arthropods (237.6 ± 20.1) per unit of soil occurred in vegetated areas. Soils beneath the litter traps were in between (taxa 4.4 ± 0.2, density 133.5 ± 10.9), and the lowest taxon numbers and densities occurred in soils from bare trails (taxa 2.9 ± 1.4, density 43.1 ± 4.9; MANOVA: Pillai's *trace* = 0.07, $F_{(6, 654)} = 3.68$, $p < 0.005$). Similar patterns were observed for springtails and oribatids at the family level, where higher numbers of families and

Table 1. Mean density (± S.E.) of each family of springtails per 100 g of dry soil, and its respective relative importance (RI), for each of the 3 types of soil samples collected at the Fushan Experimental Forest. A superscript letter with an asterisks (*) indicate a significantly higher mean density of a specified family in that particular soil type than for the other soil types with a letter but no asterisk. Superscript numbers indicate the 3 most abundant families, with the highest important values, by their ranks

Family/Soil	Bare		Underneath the trap		Vegetated	
	Density	RI	Density	RI	Density	RI
Entomobryidae	1.03 ± 0.21[a]	9.92[3]	4.61 ± 0.77[a***]	14.5[3]	5.43 ± 0.91[a***]	13.3[2]
Hypogastruridae	0.22 ± 0.1	2.50	0.59 ± 0.21	2.55	0.71 ± 0.2	3.06
Isotomidae	18.90 ± 3.4[a]	64.3[1]	38.45 ± 5.72	55.5[1]	77.27 ± 8.93[a***]	60.3[1]
Neanuridae	0.15 ± 0.12[a]	0.89	1.01 ± 0.35 [a*]	3.0	0.51 ± 0.13	3.13
Onychiuridae	1.81 ± 0.48[a]	11.3[2]	5.20 ± 0.71[a***]	14.9[2]	4.90 ± 0.79[a**]	12.9[3]
Pseudachorutidae	0.05 ± 0.03	0.21	0.37 ± 0.21	1.1	0.16 ± 0.13	0.56
Sminthuridae	0.86 ± 0.22	7.33	1.49 ± 0.35	5.23	1.19 ± 0.26	4.88
Tomoceridae	0.11 ± 0.06[a]	1.21	0.65 ± 0.18[a*]	2.98	0.37 ± 0.12	1.84

*$p < 0.05$, **$p < 0.01$, *** $p < 0.001$.

densities occurred in soils from vegetated areas (springtails, family, 2.8 ± 0.1 and density, 90.6 ± 9.9; oribatids, family, 3.2 ± 0.2 and density, 63.7 ± 8.4; MANOVA: Pillai's *trace* = 0.362, $F_{(8, 560)} = 15.44$, $p < 0.001$) and beneath the litter traps (springtails, family, 2.8 ± 0.1 and density, 52.4 ± 6.4; oribatids,

Table 2. Mean density (± S.E.), and respective relative importance (RI), of each family of oribatids per 100 g of dry soil, for each of the 3 types of soil samples collected in the Fushan forest. A superscript letter with an asterisks (*) indicates a significantly higher mean density of a specified family in that particular soil type than in the other soil types with the same letter but no asterisk. Superscript numbers indicate the families with the top 5 highest importance values by ranks in each soil type

Family/Soil	Bare		Underneath the trap		Vegetated	
	Density	RI	Density	RI	Density	RI
Ameridae	0.03 ± 0.03	1.53			0.1 ± 0.07	0.65
Astegistidae					0.03 ± 0.03	0.22
Carabodidae					0.02 ± 0.02	0.22
Cepheidae					0.61 ± 0.35	2.30
Damaeidae					0.03 ± 0.03	0.22
Epilohmanni+	0.04 ± 0.04	1.53	0.17 ± 0.08	1.66	0.22 ± 0.09	1.29
Eremobelbidae	0.02 ± 0.02[a]	1.53	0.09 ± 0.06	1.0	0.39 ± 0.15[a*]	2.74
Eremulidae					0.03 ± 0.03	0.22
Euphthiracar+	0.07 ± 0.05	3.70	0.17 ± 0.07	1.99	0.20 ± 0.10	1.23
Galumnidae	0.15 ± 0.09	5.23[5]	0.10 ± 0.06	1.0	0.47 ± 0.23	0.42
Gustaviidae			0.02 ± 0.02	0.33	0.06 ± 0.06	0.22
Haplochthoni+					0.07 ± 0.07	0.22
Haplozetidae	0.27 ± 0.1[a]	12.86[3]	0.71 ± 0.22[b]	6.01[5]	4.47 ± 1.07[ab***]	17.31[2]
Hermanniell+	0.07 ± 0.05	3.05	0.08 ± 0.06	0.66	0.07 ± 0.06	0.43
Hermanniidae	0.18 ± 0.08	7.63[4]	0.52 ± 0.14	5.59	0.40 ± 0.10	4.11
Heterobelbidae			0.02 ± 0.02	0.33	0.04 ± 0.04	0.22
Hypochthoni+			0.08 ± 0.07	0.80	0.98 ± 0.33	4.72
Liodidae			0.10 ± 0.05	1.33		
Lohmanni+	0.03 ± 0.03[a]	1.53	0.83 ± 0.23	7.66[4]	1.36 ± 0.34[a***]	6.5[5]
Malaconothr+	0.75 ± 0.24[a]	28.97[1]	0.89 ± 0.19[b]	9.28[2]	1.88 ± 0.40[ab*]	12.13[3]
Mochlozetidae			0.02 ± 0.02	0.33		
Mycobatidae					0.01 ± 0.01	0.22
Nanhermanni+	0.46 ± 0.21[ab]	19.58[2]	3.43 ± 0.59[a***]	24.32[1]	3.81 ± 0.70[b***]	17.41[1]
Nothridae			0.69 ± 0.26	5.58	0.60 ± 0.18	3.63
Oppiidae			0.64 ± 0.18	5.82	1.55 ± 0.36	7.49[4]
Oribotritiidae					0.06 ± 0.04	0.43
Otocepheidae			0.07 ± 0.05	3.14	0.06 ± 0.04	0.65
Peloppiidae	0.02 ± 0.02	1.53	0.05 ± 0.05	2.81	0.17 ± 0.09	1.08
Perlohmanni+			0.07 ± 0.04	1.0		
Phthiracar+			0.09 ± 0.05	1.0	0.31 ± 0.11	1.94
Prothoplophor+			0.02 ± 0.02	0.33	0.02 ± 0.02	0.22
Scheloribatidae	0.05 ± 0.04[a]	3.05	0.57 ± 0.18[a*]	5.44	0.36 ± 0.15	2.52
Suctobelbidae					0.06 ± 0.06	0.22
Tectocephe+	0.07 ± 0.05[a]	3.05	0.93 ± 0.21[a*b*]	7.81[3]	0.38 ± 0.12[b]	2.23
Xylobatidae	0.08 ± 0.05	5.23[5]	0.51 ± 0.15	4.45	0.64 ± 0.22	3.89
Zetorchestidae					0.18 ± 0.11	0.72

*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$. +Families which names are abbreviated by omitting their ending -idae: Epilohmanniidae, Euphthiracaridae, Haplochthoniidae, Hermanniellidae, Hypochthoniidae, Lohmanniidae, Malaconothridae, Nanhermanniidae, Perlohmanniidae, Phthiracaridae, Prothoplophoridae, Tectocepheidae.

family, 2.9 ± 0.3 and density, 36.6 ± 3.9) than in bare soils (springtails, family, 1.7 ± 0.1 and density, 23.4 ± 3.8; oribatids, family, 0.5 ± 0.1 and density, 8.8 ± 1.3; Tukey's HSD: all p values < 0.001).

None of the 4 most important taxa, i.e., springtails (G = 2.77, $d.f.$ = 6, p > 0.5), Acari (G = 2.14, $d.f.$ = 6, p > 0.5), ants (G = 6.96, $d.f.$ = 6, p > 0.5), or beetles (G = 7.88, $d.f.$ = 6, p > 0.5), deviated from randomness in their frequency distributions of occurrence among soil types and sampling sessions. Bare trails, however, contributed the smallest proportion of abundance to all 4 samplings for all 4 of these taxa (springtails: G = 94.3, $d.f.$ = 6, p < 0.001; Acari: G = 212.1, $d.f.$ = 6, p < 0.001; ants: G = 13.1, $d.f.$ = 6, p < 0.05; beetles: G = 54.7, $d.f.$ = 6, p < 0.001; Fig. 2). Values of soil arthropod heterogeneity, based on the converted Simpson index of the relative abundances of taxa, and the evenness values, were lower in samples from vegetated areas than in samples from the other 2 types of soils. A similar pattern was observed for the indices measured for springtails; yet in oribatids, the heterogeneity value was higher in vegetated soils than in soils beneath litter traps (Fig. 3).

Composition of springtails at the family level in the 3 soil types were largely similar. Overall, vegetated areas were only slightly less similar to soils beneath litter traps (Morisita's C_λ = 0.986) than either of them was to bare soils (C_λ = 0.988 and 0.993, respectively). The 4 most dominant families with the highest RI values were the same among soil types, together accounting for over 90% of the RI, and in nearly the same ranking order (Table 1). For oribatid mites, however, soils from vegetated areas were more similar to soils beneath litter traps (C_λ = 0.794) than either of them was to bare soils (C_λ = 0.704 and C_λ = 0.692, respectively), and differences between C_λ values were larger in oribatids that that in springtails (2.4-, 7.5-, and 14.6-fold, respectively). The compositions of the dominant families in the 3 soil types differed from each other, with only 14 of the total 37 identified families (38%) occurring in all the 3 soil types (Table 2). The importance of non-oribatid mites increased from 31.4% in vegetated areas to 37.4% in soils beneath litter traps and 41% in bare soils.

Variances in the abundances of springtails ($F_{(11, 348)}$ = 11.98), Acari ($F_{(11, 348)}$ = 8.97), beetles ($F_{(11, 348)}$ = 12.47), and ants ($F_{(11, 348)}$ = 4.38) in soils all deviated from homogeneity (Levene's tests, all p < 0.001). Their relative abundances fluctuated both among soil types (Pillai's *trace* = 0.26, $F_{(8, 654)}$ = 12.93, p < 0.001) and sampling sessions (MANOVA: Pillai's *trace* = 0.24, $F_{(12, 654)}$ = 7.47, p < 0.001; factor × factor effect: Pillai's *trace* = 0.11, $F_{(24, 654)}$ = 1.68, p < 0.05). Post hoc comparisons, however, revealed no differences in the abundances of ants (Tukey's HSD; p > 0.05), and only moderate differences in those of beetles (e.g., vegetated samples > bare trail samples in Aug. and Nov.; Tukey's HSD; p < 0.05) among samples. In contrast, dramatic declines in abundances of the Acari occurred between soils of vegetated areas and those of bare trails ranging from 63.5% in May samples to 91.8% in Nov. samples, and between soils of vegetated areas and those of trails beneath litter traps, declines ranged from 20.8% in

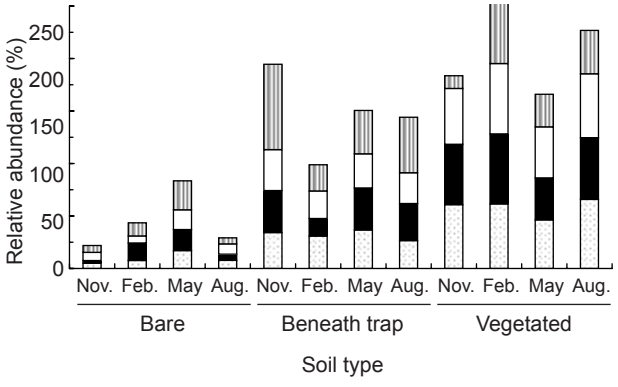

Fig. 2. Relative abundances of each of the 4 major arthropod groups, Acari (▒), beetles (■), springtails (□), and ants (‖), present in the 3 types of soils sampled over 4 sampling sessions from 2001 to 2002.

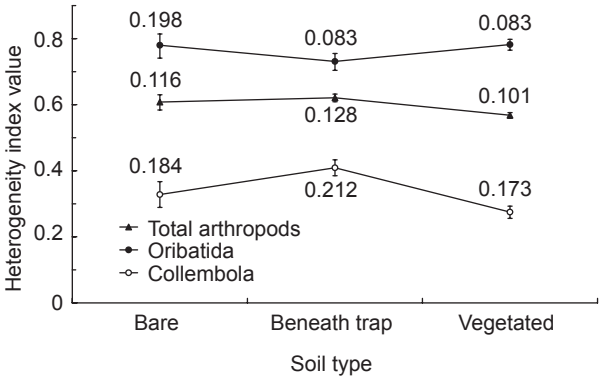

Fig. 3. Heterogeneity index values and confidence intervals of all arthropods (-▲-), oribatid mites (-●-), and springtails (-○-), assessed for soil samples from bare trails, beneath litter traps, and in vegetated areas. The evenness value is given at the top of each group for each soil type.

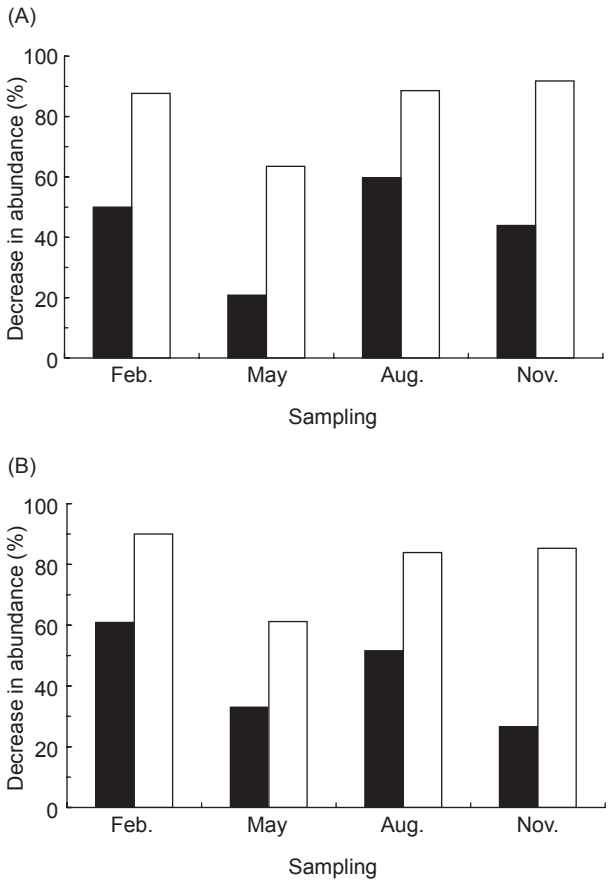

Fig. 4. Reductions in the relative abundances of (A) Acari, and (B) springtails, between soil samples from vegetated areas and from beneath litter traps (■); and that between soil samples from vegetated areas and from bare soils (□), in the 4 sampling sessions.

May samples to 59.7% in Aug. samples (Fig. 4A). Similar declines were observed for springtails, which ranged from 61.2% in May samples to 90% in Feb. samples, and from 26.6% in Nov. samples to 60.9% in Feb. samples, respectively (Fig. 4B). At the family level, a significantly lower density in soils from bare trails was observed in 5 families of springtails and 7 families of oribatid mites, respectively, than either soils beneath the litter traps, or soils of vegetated areas, or both (Pillai's *trace* = 0.41, $F_{(44, 520)} = 3.2$, $p < 0.001$; Tables 1, 2).

Soil physicochemical properties and arthropods

Soils were most compacted on bare trails (32.14 ± 0.39 N/mm in resistance; MANOVA: Pillai's *trace* = 0.69, $F_{(2, 348)} = 30.1$, $p < 0.001$), then beneath litter traps (22.74 ± 0.54 N/mm), and were least compacted in vegetated areas (19.21 ± 0.51 N/mm; Table 3). In contrast, soil moisture and temperature tended to vary more over sampling sessions (Pillai's *trace* = 1.49, $F_{(3, 348)} = 56.8$, $p < 0.001$, factor × factor interaction $F_{(6, 348)} = 5.1$, $p < 0.001$). While soil moisture was higher in Feb. samples (2.23 ± 0.14 g/100 g dry soil) than in others (1.18-1.26 g; Tukey's HSD, $p < 0.001$), the lowest temperature was in Nov. (13.9 ± 0.4°C), followed in turn by Feb. and May, and the highest was in Aug. (22.8 ± 0.05°C; Tukey's HSD, $p < 0.001$). Nitrogen and carbon contents were higher in soils of vegetated areas than soils beneath litter traps and bare trails (Table 3).

Overall, numbers of taxa (multiple regression:

Table 3. Mean (± S.E.) values of physicochemical properties of soils from the 3 types of treatments in the Fushan Experimental Forest. The treatment and sampling effects were examined by MANOVA, followed by a post hoc Tukey's HSD test, and are indicated by a *p* value, for each characteristic. A superscript letter with an asterisk indicates a significantly higher mean value of the specific measure in the associated soil type than that in the corresponding soil type with the same letter

	Bare	Underneath the trap	Vegetated	*p*
Compaction (resistance in N/mm)	32.14 ± 0.39$^{a*, b*}$	22.74 ± 0.54$^{a, b*}$	19.21 ± 0.51b	< 0.001
Temperature (°C)	18.1 ± 0.36	18.20 ± 0.35	18.10 ± 0.35	ns
Moisture (g/100 g of dry soil)	1.54 ± 0.07	1.50 ± 0.08	1.37 ± 0.09	ns
pH	4.10 ± 0.01^{a*}	3.99 ± 0.01^{a}	3.94 ± 0.01a	< 0.001
Nitrogen (%)	0.65 ± 0.02^{b}	0.71 ± 0.02$^{a, b*}$	0.79 ± 0.02$^{a*, b*}$	< 0.005
Carbon (%)	7.75 ± 0.30^{a}	8.00 ± 0.25^{a}	10.15 ± 0.34^{a*}	< 0.001

ns, not significant.

N_T = 11.4 - 0.1 Cp + 0.1 T - 0.3 M - 2 P + 2.1 N - 0.04 C; r = 0.47, $F_{(6, 330)}$ = 15.98, p < 0.001) and arthropod densities (D_A = 711 - 9.5 C + 6.5 T - 4.6 M - 178.4 P + 247.4 N - 3.7 C; r = 0.51, $F_{(6, 335)}$ = 19.25, p < 0.001) were correlated to soil compactness (Cp; taxa: t = -5.1, p < 0.001; density: t = -4.9, p < 0.001), temperature (T; taxa: t = 3.3, p < 0.005; density: t = 2.9, p < 0.005), and pH values (P; taxa: t = -3.1, p < 0.005; density: t = -3.7, p < 0.001). In addition, the numbers of arthropod taxa were correlated to soil moisture (M; t = -2.6, p < 0.05), and arthropod densities were correlated to nitrogen content (N; t = 3.1, p < 0.005).

DISCUSSION

Composition and relative abundances of soil arthropods in the subtropical forest

It is generally thought that abundances of soil arthropods are considerably lower, from several multiples to an order of magnitude, in the tropics than in temperate areas (Petersen and Luxton 1982, Heneghan et al. 1998). Great variations, however, occurs from site to site and among areas. The mean abundance of soil arthropods documented in our study in a subtropical forest, ca. 27.5 ind. per soil core, translates into a density of 13,982 ind./m^2. This is lower than those reported in most boreal-temperate areas (e.g., central Japan, 140,000 ind./m^2, Hijii 1994; see also a review by Petersen and Luxton 1982), and even some tropical sites (e.g., Seastedt 1984, Gonzalez et al. 2001). Our study and other studies conducted in tropical Asia (e.g., Wiwatwitaya and Takeda 2005) contradict the general pattern that soil arthropods in tropical or subtropical forests may be dominated by social insects, e.g., ants and termites, instead of the springtails and mites seen in temperate regions (Takeda and Abe 2001).

Unlike Wiwatwitaya and Takeda (2005) where mites dominated the composition in an evergreen dry forest in Thailand, the relative abundance of springtails (with a mean density of 8,946 ind./m^2) was higher than that of mites (5,220 ind./m^2) at our site. In temperate areas, while mites often dominate undisturbed forest soils, springtails are more important in arable soils and managed grasslands (Filser 2002). The Fushan forest is characterized by heavy rainfall, acidic soils, a large amount of litter accumulation, and slower decomposition rates than mean decomposition rates so far obtained in both tropical and temperate forests (Takeda and Abe 2001, Lin et al. 2002). Hijii (1994) reported similar soil features (strongly acidic soils and high litter accumulation) coupled with slow rates of decomposition in an alpine coniferous forest of temperate Japan, with a comparable ratio of springtail to mites (ca. 1.12).

The springtail density at our site fell into the range of abundances typical of tropical regions, being lower than several studies reporting on some African and neotropical sites (e.g., Culik and Filho 2003), but higher than many other tropical sites over various types of forests, from deciduous dry forests, lowland rainforests (Deharveng and Bedos 1993), to montane forests (Heneghan et al. 1998), and in both the New and Old Worlds (e.g., Badejo and Straalen 1993, Heneghan et al. 1998, Lasebikan 1975, reviewed in Wiwatwitaya and Takeda 2005). Springtails also appeared to be more diverse in our study than in others, at least at the family level, e.g., 8 families in our study vs. 6 in Thailand (Wiwatwitaya and Takeda 2005) and 5 in Nigeria (Badejo and Van Straalen 1993).

Effects of trampling and litter removal on soil arthropods

For arthropods as a whole, and at the family level for springtails and oribatids, the highest densities and numbers of taxa occurred in soils from vegetated areas, where no or little trampling had occurred and litter was allowed to accumulate naturally. In contrast, where trampling occurred and litter also accumulated, samples from bare soils contained the lowest numbers of arthropod taxa and densities. Soils beneath litter traps, where constant trampling was prevented but litter was not allowed to accumulate, were in between for both measures. Our data, as we predicted, indicate a clear negative effect of trampling on the composition of soil arthropods. This result was correlated with the fact that more-compacted soils occurred on bare trails and the least-compacted soils in more-vegetated areas, thus supporting our prediction.

While our sampling was set to the top soil layer of 5 cm, the result is consistent with findings of other studies in high Arctic tundra (e.g., Kevan et al. 1995) and temperate forest soils (e.g., Battigelli et al. 2004), that compaction reduces the abundances of soil arthropods. Litter removal revealed a similar, but weaker, effect than trampling. Battigelli et al. (2004) also concluded that the removal of organic matter reduces the density of the soil mesofauna. While Eaton et

al. (2004) found compaction had no effect on springtails and attributed this to their propensity to dwell in the litter layer instead of the soil, our study showed negative impacts of both compaction and litter removal. Stanton (1979) indicated that the majority of tropical soil species are non-colonizers, but that the tendency to colonize is inversely correlated to the litter present. Although our study cannot rule out the possibility of invasions or local movements by soil arthropods, Stanton's (1979) observations support our results on the effect of litter removal.

Two major direct impacts of soil compaction are a reduction in soil porosity and an increase in the bulk density (USDA 1999), as also seen in our data. The effects of compaction and litter removal on soil animals, however, appear to differ among taxa, and this supports our prediction. Our results of *G*-tests on the randomness of the frequency distributions and relative abundances of the more-abundant arthropod taxa among soil types indicate a significant effect of compaction and litter removal on those dominant inhabitants, i.e., springtails and mites (Battigelli et al. 2004). Among the 4 major soil arthropods in the Fushan forest, many soil-dwelling beetles and ants are generally considered to be able to burrow and, thus, are better adapted to compacted soils. Non-burrowing soil arthropods such as springtails and mites, however, depend entirely on air-filled pores, and may be heavily affected by soil compaction (Hopkin, 2002, Larsen et al. 2004). The effects of compaction even differed and likely contributed to the difference in the community compositions and relative abundances at the family level between springtails and oribatids among soil types. Mechanisms such as life history and behavior may prove worthy of further explorations (Hopkin, 2002). This pattern, however, helps explain the often lower heterogeneity values in vegetated areas, as evaluated by the converted Simpson indices when both taxon richness and relative abundances of the arthropods are incorporated in the indices (Krebs 1999).

Soil compaction and litter removal may have different degrees of impact on different soil properties, which in turn may affect soil arthropod communities (Jordan et al. 2003). We detected correlations between both the numbers of arthropod taxa and their densities with soil pH values and temperature; and the former was also correlated with moisture and the arthropod densities to the nitrogen content of the soils. Temperature and moisture are considered to be directly related to the survival and distribution of soil animals (Mitchell 1978, Schaefer 1990). Although not really replicating the seasons, our sampling exhibited greater variations in soil temperature and moisture among sampling sessions, which in general conformed to the weather patterns in the Fushan area, namely a consistently moist and cold season from Nov./Dec. to Feb., and spring to fall often influenced by typhoons (Fushan Weather Station, TFRI).

The increase in pH is consistent with other studies in temperate areas (Godefroid and Koedam 2004); yet the biological processes contributing to this pattern and how this trend toward relatively and locally neutral soils would affect soil arthropod communities remain unclear. Carbon and nitrogen are critical energy and nutrient resources for decomposers, as well as soil micro-arthropods. The mean annual litter fall at our site, 4.95 ± 0.48 t/ha, is between that recorded in temperate and tropical forests (Takeda and Abe 2001). The heavy annual rainfall, however, may cause leaching effects. We found higher nitrogen concentrations in soils of the least-trampled and vegetated areas; carbon, however, appeared to vary over seasons, as was also observed by Kevan et al. (1995). This supports a generally lower than expected C:N ratio (< 20) for subtropical regions, as observed in the Fushan forest (Lin et al. 2002, YF Lee unpubl. data), and is consistent with an N immobilization effect under high water availability. Jordan et al. (2003) indicated greater nitrogen losses in more-compacted plots, whereas Godefroid and Koedam (2004) suggested pH increases and even eutrophication at a distance from the disturbed path. The relationship of trampling and litter removal to soil pH and other chemical properties, and their subsequent effects on soil arthropod compositions, are complex (Van Straalen and Verhoef 1997, Filser 2002), and warrant future more-detailed assessments.

Implications for forest soil conservation

In many protected forest areas around the world, such as national parks, trails of different forms may be established for management or recreational purposes, or to promote ecotourism as an approach or a goal of the sustainable use of biodiversity (Leung and Marion 1996). Yet, the potential impacts on soils and soil biota of few trails in protected areas have been evaluated (Godefroid and Koedam 2004). Our study indicates that with even limited human foot traffic in

a forest reserve, bare soils suffer from compaction that affects not only the composition but also the relative abundances of soil arthropods. This may further lead to impacts on soil respiration, microbial activities, C and N turnover, and plant growth (Filser 2002). The fact that certain families of mites and springtails respond differently to trampling and soil compaction suggests that these soil arthropods may serve as indicators of soil conditions. Planning of natural trails, particularly in protected areas, requires very careful consideration. Threshold levels of soil compaction that may cause a dramatic declines in diversity and abundances of soil arthropods need to be established through long-term research and monitoring. Trail designs that generate minimal impacts are desirable and should be prioritized for the purpose of conserving soil health, ecological processes, and ecosystem functions.

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