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EFFECTS OF THE RED-PINE FOREST MANAGEMENT FOR MUSHROOM CULTIVATION ON THE GROUND, BELOW- AND ABOVE-GROUND INVERTEBRATES IN SUZU, CENTRAL JAPAN

Linawati¹⁾, S. Tanabe²⁾, A. Ohwaki¹⁾, D. Akaishi¹⁾, R. E. Putra¹⁾, I.
Trisnawati¹⁾, I. Kinasih¹⁾, C. Kikuchi¹⁾, T. Kasagi¹⁾,
S. Nagashima¹⁾ and K. Nakamura^{1,2)}

1) *Laboratory of Ecology, Graduate School of Science and Technology, Kanazawa University, Kakuma, Kanazawa, 920-1192, Japan*

2) *Division of Biodiversity, Institute of Nature and Environmental Technology, Kanazawa University, Kakuma, Kanazawa, 920-1192, Japan*

The effects of red-pine forest management for matsutake mushroom production on invertebrate communities were examined using four sampling methods: window and pitfall traps, and sampling of litter and soil. Samples were collected from the "managed site" and from the surrounding "control site" without management. The total number of individuals collected was significantly lower for pitfall trap and higher for litter sampling in the control site than in the managed site. Management significantly reduced the diversity of higher taxa in litter samples in the managed site. DCA analysis revealed the difference in faunal composition of higher taxa between the two sites.

KEY WORDS: satoyama management, matsutake mushroom, red pine forest, invertebrate fauna, pitfall trap, window trap, soil and litter sampling.

Линавати¹⁾, С. Танабе²⁾, А. Оваки¹⁾, Д. Акаиси¹⁾, Р. Е. Путра¹⁾, И. Триснавати¹⁾, И. Кинасих¹⁾, К. Кикуси¹⁾, Т. Касаги¹⁾, С. Нагасима¹⁾, К. Накамура^{1,2)}. Влияние разведения грибов в сосновом лесу на почвенных и наземных беспозвоночных в Сузу, Центральная Япония // Дальневосточный энтомолог. 2006. N 166. С. 1-15.

Изучено влияние выращивания грибов матсутаке в сосновом лесу на сообщества почвенных беспозвоночных с использованием 4 методов сбора (оконные ловушки, почвенные стаканчики, пробы опада и почвы). Отбор проб производился как на участке с плантациями грибов, так и на расположенном поблизости контрольном участке леса. Отмечено, что количество экземпляров членистоногих, собранных почвенными ловушками на контрольном участке, существенно меньше, чем на участке с плантациями матсутаке, а в пробах опада, наоборот, существенно выше. Показано, что выращивание грибов приводит к уменьшению разнообразия таксонов высокого ранга в опаде. Отмечены различия в составе фауны изученных участков на уровне отрядов.

1) *Лаборатория экологии, Высшая школа естественных наук и технологии Университет Канадзавы, Канадзава, Япония.*

2) *Отделение биоразнообразия, Институт природы и технологий охраны окружающей среды, Университет Канадзавы, Канадзава, Япония.*

INTRODUCTION

"Satoyama" is the traditional rural landscape in Japan, consisting of a mosaic of paddy fields, farmlands, ponds, stream and forests and so on. In Japan, much attention has recently been paid to satoyama, because (1) it stretches between urban areas and natural areas in mountainous regions, making up 40% of national land; (2) it provides essential services, such as food, water, clean air, cultural and aesthetic services (Washitani, 2001; Takeuchi et al., 2003); (3) it is a key to biodiversity conservation in Japan (The National Biodiversity Strategy of Japan, 2002). However, the satoyama is being threatened (termed, the satoyama problem) chiefly because maintenance is neglected due to changes in lifestyle, and decreasing and ageing populations with a background of long slumps in agriculture and forestry.

Around 70 % of Ishikawa Prefecture (Japan: Honshu) is satoyama, where forests are one of the most important elements. Formerly, satoyama forests in Noto Peninsula (Fig.1) were predominantly red pine (*Pinus densiflora* Sieb. et Zucc.), which local people strictly maintained by cutting all vegetation other than the pine trees and by raking the forest beds in order to harvest matsutake mushrooms (*Tricholoma matsutake* (Ito et Imai) Sing.). Since this ectomycorrhizal symbiont of pine trees requires a clean forest floor and infertile soil conditions to thrive, management of pine forests is essential to cultivate matsutake mushrooms effectively. Young (about 20-30 years old) and well-managed pine forests are known to support the highest production (Kato, 2001; Ogawa, 1978).

The Noto region with well-managed red pine forests was previously famous for matsutake production, however, since the 1960's, the pine forests have been abandoned due to the satoyama problem. This has promoted the recovery of ground vegetation, invasion of evergreen shrubs and natural succession to deciduous oak forests (Nakagoshi & Hong, 2001). As a result, matsutake production has decreased to a negligible level.

The abundance and structure of invertebrate communities are undoubtedly influenced by various ecological factors (Hutcherson et al., 1999). For invertebrates in pine forests, management activities for matsutake cultivation, such as pruning, selective cutting and removal of litter and ground vegetation, are likely to positively or negatively affect the abundance, diversity and faunal composition of the communities. Responses to such activities may differ among invertebrate groups, reflecting their variety of trophic status, habitat preference, food resources, behavioral traits and life history.

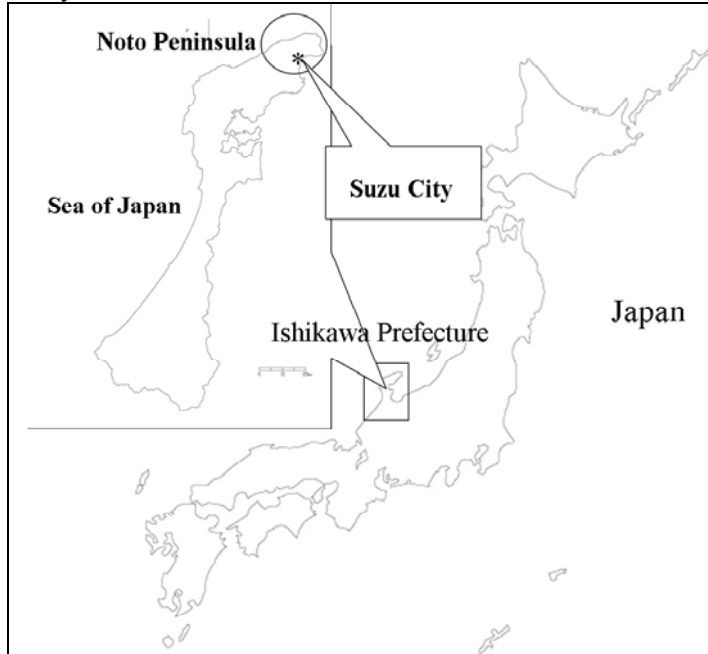


Fig. 1. Map of Suzu City, showing the location of the study sites.

In Suzu, located in Noto Peninsula (Fig. 1), a matsutake revival project was launched in the late 1990's, in which several patches of pure pine stands have been established by cutting all vegetation except red pine trees and by raking forest beds (henceforth referred to as the “managed site”), surrounded by a “control site” without maintenance, *i.e.* dense forest with red pine trees and other vegetation.

In this study, we examined the effects of red-pine forest maintenance by sampling invertebrate communities using four different methods, including pitfall and window traps, and sampling litter and soil from forest beds. The use of different methods covering various types of habitats and functional groups is desirable to give a more complete picture of the effects of management on invertebrate communities (Lassau et al., 2005). Focusing on higher taxa of invertebrates, this study aims to provide basic information on how invertebrate communities are affected by changes resulting from the management of red pine forests in terms of abundance, diversity and faunal composition.

STUDY SITES

The study was carried out in a red pine forest in Kyonen, Wakayama Town, Suzu City, Ishikawa Prefecture, Japan (37.26° N, 137.15° E). Suzu City is located in the eastern finger of Noto Peninsula, extending to the Sea of Japan (Fig. 1). The peninsula is hilly with narrow stretches of coastal plains. In the upper half of the peninsula, the topography is generally gentle with the highest peak being Mt. Horyu (468.8 m elevation). In Suzu, the average annual temperature is 12.8° C and rainfall 2051 mm.

The study sites were located at an altitude of 100 m, 4 km NW of the central of Suzu City. The sites were near the top of the northwest facing slope (20°). The maintained pine forest (managed site) was 0.35 ha (70 m x 50 m), and had been maintained four times before this study: March 2001 and September 2002, 2003 and 2004. The pine trees are approximately 40 years old with an average height of 14 m and a density of 21 trees/100 m². For the control site, an area with approximately the same size as the managed site (0.35 ha) was selected in the upper part of the study site. The two sites were separated with a small path.

Abundant trees in the control site included *Quercus serrata* Thunb. Ex Murray), *Carpinus tschonoskii* Maxim, *Prunus verecunda* (Koidz.) Koehne, *Acer amoenum* var. *matsumurae* (Koidz.) Ogata, *Eurya japonica* Thunb., *Styrax japonica* Sieb. et Zucc., *Clerodendrum trichotomum* Thunb., *Aucuba japonica* var. *borealis* Miyake et Kudo and so on. The average litter thickness was 4 cm and 5 cm in A₀ and A zones, respectively, in the control site, while in the managed site, the forest floor was almost clean due to annual management.

SAMPLING METHODS

Four plots in the control and managed sites, respectively, were randomly selected for sampling invertebrates with four different methods.

Pitfall traps: to collect ground invertebrates, five pitfall traps (plastic containers of 9 cm in diameter and 11 cm in height) were set in a 3 x 3 cross arrangement with 2 m distance between the traps in each plot. The traps were partially filled with 50% ethylene glycol as a preservative. The lids of the containers were set above the traps to prevent the traps from flooding.

Soil and litter sampling: to collect below-ground invertebrates, a 25 cm x 25 cm quadrant was used as the sampling unit in each plot. First, the litter was removed and then the soil (10 cm depth) was taken from the quadrant. Soil and litter were brought to the laboratory, and first, macro-fauna were hand-sorted and then meso- and micro-fauna were extracted using a Tullgren funnel for 2-3 days.

Window traps: to collect above-ground (actually flying) invertebrates, IBOY standard traps (Nakashizuka & Stork, 2002) consisting of a yellow collecting bucket and transparent intersect panels were used. The buckets were filled with 2L of 50% ethylene glycol as a preservative. One trap was set in each plot at the height of 1.5 from the ground using ropes.

Soil and litter samples were taken on one day (September 4, 2005) while the pitfall and window traps were set on the same day and after being exposed for 8 days, the samples captured in the traps were collected.

The invertebrate samples were identified to class level (Oligochaeta, Hirudinoidea, Chilopoda and Diplopoda) and to order level (other taxa). Hymenopteran samples were divided into two groups: ants (Formicidae) and other Hymenoptera. Larvae of Coleoptera, Lepidoptera and Diptera were treated as higher taxa in this study.

DATA ANALYSIS

U-test was used to examine differences in the abundance and diversity of invertebrate communities between the managed and control sites. Taxa with less than eight collected individuals less than eight were excluded from the analysis. In addition, it was expected that the power of this analysis would be low because there were only four replicate plots in each site, which could generate substantial variation in the abundance, diversity and distribution of higher taxa among plots. Consequently, results based on $P < 0.1$ as well as $P < 0.05$ were reported here to reduce the risk of Type II error. Detrended correspondence analysis (DCA) using CANOCO version 4.5 (ter Braak & Šmilauer 2002) was carried out to analyze the variation in the faunal composition of invertebrate communities stemming from the treatments (and control), and different types of sampling methods. Before DCA analysis, the number of individuals collected for each of the higher taxa included in the analysis was square-root transformed.

RESULTS

Abundance and diversity of communities and distribution of higher taxa

General features: 26 higher taxa and 6095 invertebrates were collected across managed and control sites and four sampling methods in this study. The total number of higher taxa was slightly higher in the control site (24) than in the managed site (21). Three times more invertebrate specimens were collected in the control site (4579) compared with the managed site (1516) (Table 1). Significant difference ($P < 0.05$) in the mean abundance of invertebrates between the control and sites collected by pitfall traps and litter sampling was observed (Fig. 2). Those collected by pitfall traps were significantly more abundant in the managed site than in the control site ($P < 0.05$), while those collected by litter sampling were significantly more abundant in the control site ($P < 0.05$) (Fig. 2).

Pitfall traps: 744 invertebrate specimens of 21 higher taxa were collected by pitfall traps in both sites. No significant difference ($P < 0.05$) was found in the number of higher taxa between the managed and sites but the number of individuals was significantly higher in the managed site than in the control site ($P < 0.05$) (Table 1). Abundant taxa in the control site were Formicidae (25 %), Aranea (22 %), Diptera (13 %) and Collembola (11 %) and these higher taxa comprised 71 % of invertebrates collected in the control site (Fig. 3). In the managed site, Formicidae dominated the invertebrate sample and represented 61 % of specimens (Fig. 3). For the distribution pattern of each taxon, Formicidae were distributed more abundantly in the managed site than in the control site (Table 1), whereas Aranea significantly preferred the control site to the managed site (Table 1).

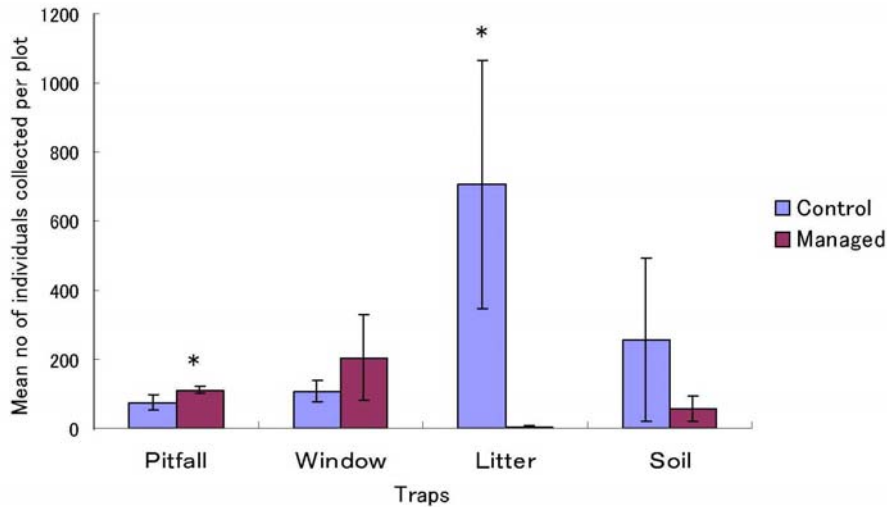


Fig. 2. Comparison of the mean number of individuals per plot between the control and managed sites collected with four sampling methods. (*) - Significant at 95% level.

Window traps: 13 higher taxa and 1253 invertebrates were collected by window traps. There were no differences in the numbers of higher taxa and individuals between the managed and control sites (Table 1). Diptera (31 %), other Hymenoptera (18 %), Homoptera (13 %) and Aranea (13 %) were abundant in the control site, comprising 75 % of the total catch (Fig. 3). In the managed site, other Hymenoptera were an important taxa, representing half of invertebrate specimens collected, followed by Diptera (23 %) and Homoptera (13 %) (Fig. 3). The numbers of homopteran and mecopteran specimens were significantly higher ($P < 0.05$ and $P < 0.1$, respectively) in the managed site than the control site (Table 1), whereas Coleoptera and Aranea were more abundant in the control site than in the managed site ($P < 0.05$ and $P < 0.1$, respectively). Although not significant ($P < 0.1$), the number of other Hymenoptera was five times larger in the control site than in the managed site (Table 1).

Litter sampling: 19 higher taxa and 2840 invertebrates were collected by litter sampling. Large and significant differences between the control and managed sites were detected in the numbers of higher taxa and individuals (Table 1). In the managed site, very few specimens were collected and the number of higher taxa was less than half of that in the control site (Table 1). Collembola (59 %) and Acari (34 %) were the predominant invertebrate samples in the control site, and accounted for up to 93 % of the total catch (Fig. 3). In contrast, only one collembolan specimen and no Acari were collected in the managed site, where Formicidae (44 %) were the most abundant taxon (Fig. 3).

Soil sampling: 17 higher taxa and 1258 invertebrates were collected by soil sampling. No significant differences between the managed and control sites were found in the numbers of higher taxa and individuals. Compared to the managed site,

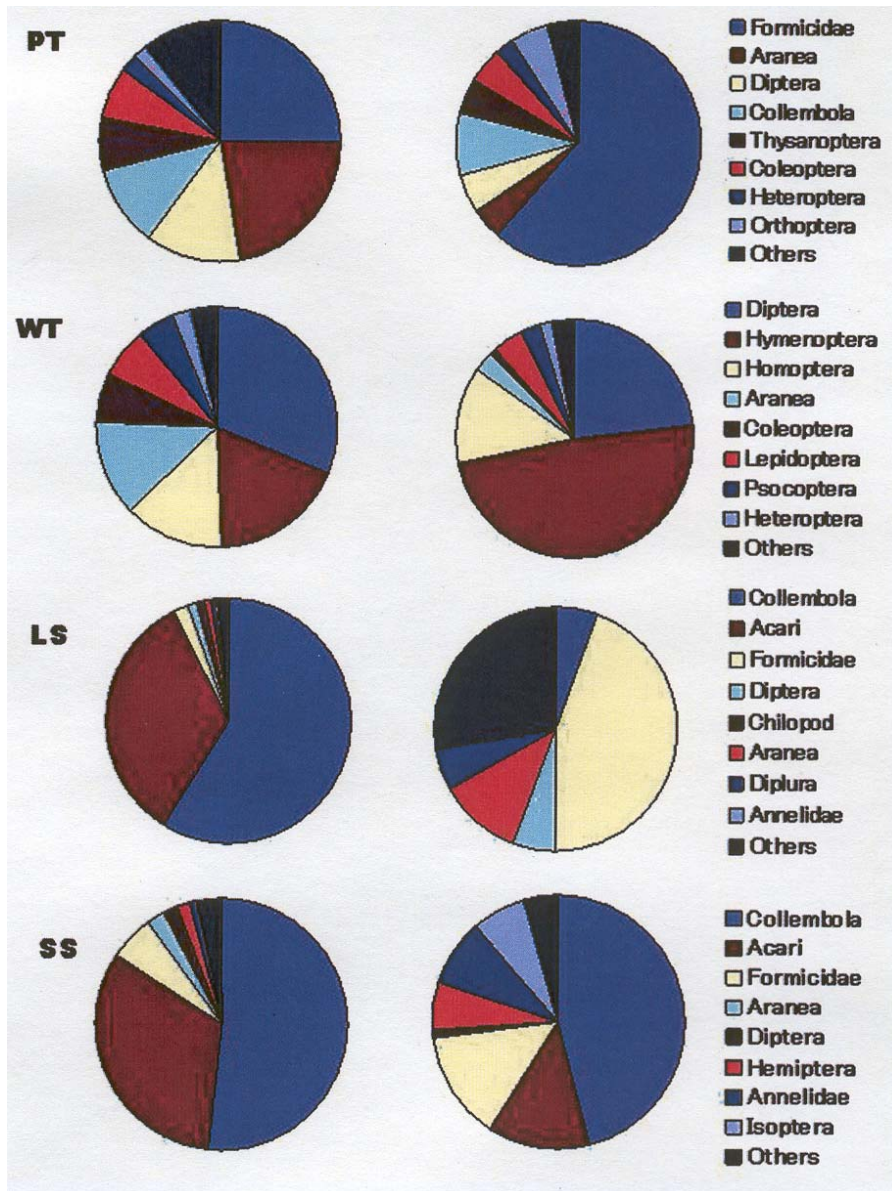


Fig. 3. Comparison of invertebrate faunal composition between the control and managed sites collected with four sampling methods. PT - pitfall traps, WT - window traps, LS - litter sampling, SS - soil sampling. Only the eight most abundant taxa are presented and other taxa are pooled as "others".

Comparisons of mean abundance and standard deviation (in parenthesis)

| Taxa | Sampling | | | | | |
|-----------------------|--------------|-----------|--------|--------------|-------------|--------|
| | Pitfall trap | | | Window trap | | |
| | C | M | U-test | C | M | U-test |
| Collembola | 8.0 (3.6) | 9 (11.5) | NS | 2 (2.5) | 2 (1.8) | NS |
| Coleoptera | 5.3 (2.1) | 5.3 (4.8) | NS | 7.25 (3.3) | 2.25 (1.3) | ** |
| Diplura | 0,0 | 0,0 | - | 0,0 | 0,0 | - |
| Diptera | 9.8 (5.6) | 5.8 (3.7) | NS | 33.5 (21.6) | 47.5 (10.1) | NS |
| Formicidae | 19.0 (7.8) | 68 (8.2) | ** | 0,0 | 0,0 | - |
| Other hymenoptera | 1.8 (2.2) | 1 (1.4) | NS | 19.5 (2.7) | 100 (103.1) | NS |
| Heteroptera | 1.8 (2.4) | 2.8 (1.7) | NS | 2.5 (3.8) | 3.3 (2.8) | NS |
| Homoptera | 1.8 (2.4) | 0,0 | - | 14.3 (4.8) | 26.8 (11.4) | * |
| Isoptera | 0,0 | 0,0 | - | 0,0 | 0,0 | - |
| Lepidoptera | 0.8 (1.5) | 1.3 (1.5) | NS | 7 (4.1) | 8.5 (2.9) | NS |
| Mecoptera | 0,0 | 0.3 (0.5) | NS | 0,0 | 2.3 (0.5) | ** |
| Neuroptera | 0,0 | 0,0 | - | 0,0 | 0.3 (0.5) | NS |
| Orthoptera | 1.3 (1) | 5.5 (4.4) | NS | 0.25 (0.5) | 1.25 (1.0) | NS |
| Psocoptera | 0.5 (1) | 0.5 (0.6) | NS | 5.5 (4.04) | 5.8 (2.4) | NS |
| Thysanura | 5.5 (3.3) | 5.3 (2.9) | NS | 1.75 (2.9) | 0.5 (0.6) | NS |
| Larvae (Coleoptera) | 0.8 (1.5) | 0,0 | NS | 0,0 | 0,0 | - |
| Larvae (Lepidoptera) | 0,0 | 0,0 | - | 0,0 | 0,0 | - |
| Larvae (Diptera) | 0,0 | 0,0 | - | 0,0 | 0,0 | - |
| Isopoda | 0.8 (1.5) | 0.3 (0.5) | NS | 0,0 | 0,0 | - |
| Amphipoda | 0.3 (0.5) | 0,0 | NS | 0,0 | 0,0 | - |
| Aranea | 17 (6.5) | 4.5 (2.4) | ** | 13.8 (3.3) | 5.8 (4.9) | * |
| Acarina | 0.8 (1.5) | 0.3 (0.5) | NS | 0,0 | 0,0 | - |
| Opiliones | 0.3 (0.5) | 0,0 | NS | 0,0 | 0,0 | - |
| Chilopoda | 0.5 (1.0) | 0,0 | NS | 0,0 | 0,0 | - |
| Diplopoda | 0,0 | 0,0 | - | 0,0 | 0,0 | - |
| Pseudoscorpionidae | 0,0 | 0,0 | - | 0,0 | 0,0 | - |
| Hirudinoidea | 0,0 | 0.5 (0.6) | NS | 0,0 | 0,0 | - |
| Oligochaeta | 0.3 (0.5) | 0.8 (0.5) | NS | 0,0 | 0,0 | - |
| Gastropoda | 0,0 | 0,0 | - | 0,0 | 0,0 | - |
| Total no. of taxa | 19,0 | 16,0 | | 11,0 | 13,0 | |
| Mean No. of taxa (SD) | 11 (1.3) | 11 (1.3) | NS | 8.5 (2.4) | 11 (0.8) | NS |
| Mean no. of ind. (SD) | 75.3 (20.9) | 111 (9.9) | ** | 107.3 (31.4) | 206 (123.8) | NS |

Abbreviations. (*) - $P < 0.1$; (**) - $P < 0.05$; NS - not significant

Table 1

of invertebrates between control (C) and managed (M) sites

| methods | | | | | |
|-----------------|------------|--------|---------------|-------------|--------|
| Litter sampling | | | Soil sampling | | |
| C | M | U-test | C | M | U-test |
| 415.8 (283.6) | 0.25 (0.5) | * | 132.8 (132.3) | 26.5 (28) | NS |
| 0.5 (0.6) | 0,0 | NS | 1 (0.8) | 0.5 (0.6) | NS |
| 3.5 (2.1) | 0.3(2.1) | ** | 4.5 (7.1) | 3.5 (4) | NS |
| 1.8(1.3) | 0,0 | NS | 5 (9.4) | 0.8 (0.5) | NS |
| 12.8 (9) | 2 (1.8) | ** | 15.3 (17.9) | 8 (5.4) | NS |
| 0,0 | 0,0 | - | 0,0 | 0,0 | - |
| 1,0 | 0,0 | - | 0,0 | 0,0 | - |
| 0,0 | 0,0 | - | 0,0 | 0,0 | - |
| 0.8 (1.5) | 1.0 (2) | NS | 0,0 | 4 (4.6) | NS |
| 0.3 (0.5) | 0,0 | NS | 0.3 (0.5) | 0.3 (0.5) | NS |
| 0,0 | 0,0 | - | 0,0 | 0,0 | - |
| 0,0 | 0,0 | - | 0,0 | 0,0 | - |
| 0,0 | 0,0 | - | 0,0 | 0,0 | - |
| 0,0 | 0,0 | - | 0,0 | 0,0 | - |
| 0,0 | 0,0 | - | 0,0 | 0,0 | - |
| 2.5 (1.0) | 0,0 | ** | 3.3 (2.6) | 0.3 (0.5) | ** |
| 2.5 (1.3) | 0,0 | ** | 0,0 | 0.5 (0.6) | NS |
| 9.25 (9.9) | 0.25 (0.5) | ** | 0.3 (0.5) | 0.3 (0.5) | NS |
| 0.5 (1.0) | 0,0 | NS | 0.3 (0.5) | 0.5 (1) | NS |
| 0,0 | 0,0 | - | 0,0 | 0,0 | - |
| 6.3 (3.4) | 0.5 (0.6) | ** | 5.3 (6.2) | 0,0 | ** |
| 237 (86.7) | 0,0 | ** | 83.3 (67.8) | 7.5 (7) | * |
| 0,0 | 0,0 | - | 0,0 | 0,0 | - |
| 6.8 (3.4) | 0,0 | ** | 3.3 (2.6) | 0,0 | ** |
| 1.5 (0.6) | 0,0 | NS | 0,0 | 0.3 (0.5) | NS |
| 1.3 (1.5) | 0,0 | - | 0.5 (0.6) | 0,0 | NS |
| 0,0 | 0,0 | - | 0,0 | 0,0 | - |
| 2 (1.8) | 0.3 (0.5) | NS | 2 (2.8) | 5 (4.2) | NS |
| 0.5 (1.0) | 0,0 | - | 0,0 | 0,0 | - |
| 18,0 | 7,0 | | 14,0 | 14,0 | |
| 13.8 (1.9) | 4.5 (3.5) | ** | 9.3 (2.2) | 7.8 (1.5) | NS |
| 705.5 (359.3) | 4.5 (3.5) | ** | 256.8 (237.1) | 57.8 (36.5) | NS |

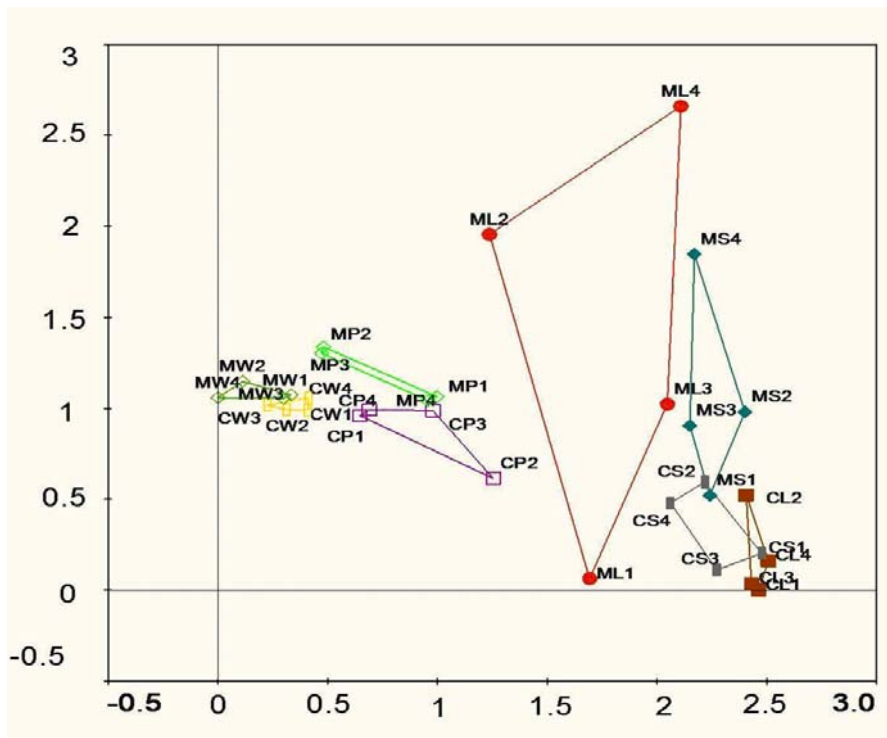


Fig. 4. DCA ordination, showing the distribution of invertebrates in the control sites (C) and managed sites (M) collected with four sampling methods. P - pitfall traps, W - window traps, L - litter sampling and S - soil sampling.

however, approximately five times more specimens were collected in the control site (Table 1). In both sites, Collembola and Acari were dominant, accounting for 84 % and 59 % of the total catch in the control and managed sites, respectively (Fig. 3). In addition, Formicidae (14 %) were also abundant in the managed site (Fig. 3). Aranea, Chilopoda and larva of Coleoptera were significantly more abundant ($P < 0.05$), while Acari were significantly more abundant ($P < 0.01$) in the control site than in the managed site (Table 1). The number of Collembola was also five times larger in the control site than in the managed site (Table 1) although not significant ($P > 0.1$).

Faunal composition

DCA ordination revealed a clear separation of invertebrate communities, reflecting the different sampling methods, along the first axis in both the control and managed sites. For each sampling method, samples from the control and managed sites were separated from each other along the second axis (Fig. 4). The first and second axes

explained 85.1% of the variability in the faunal composition of invertebrate samples. Conspicuous difference in the degree of inter-plot heterogeneity in the faunal composition was observed. In litter and soil samples, inter-plot heterogeneity in the faunal composition was larger in the managed site than in the control site. In pitfall and window samples, however, inter-plot heterogeneity in the control and managed sites was nearly the same (Fig. 4).

DISCUSSION

Ground and below-ground invertebrate

As a whole, below-ground invertebrates living in litter and soil were more affected by the management practices compared with ground and above-ground invertebrates. A large number of insects inhabiting the soil environment also use the litter as their habitats, especially the fermentation and humification layers (Szujecki, 1987).

For Acari and Collembola, the major component of soil ecosystems, it is known that most of them live in the litter and feed on fungi or decaying materials (Coleman, 2004). The practice of litter removal in managed red pine forests directly reduces the habitat space and food availability of below-ground invertebrates, which can be a main cause of the decrease in the abundance of Acari and Collembola in the site under management. In addition, the management practices could indirectly affect below-ground invertebrates in negative ways by altering the physical conditions of their surrounding environments. Selective cutting and removal of litter and ground vegetation can reduce the level of soil moisture by exposing the ground to more light. Collembola have been proven to be sensitive to changes in the moisture and relative humidity of their habitats and enter a deeper layer of soil when conditions are not favorable (Coy, 1994). Lensing et al. (2005) revealed that the activity of Collembola was about 60% lower when they were exposed to dry conditions. In most dipteran flies and some groups of Coleoptera and Lepidoptera, larvae are generally associated with moist habitats such as damp soil, mud or decomposing organic matter; similarly, Diplura are found mainly in damp soil (Nauman et al., 1991).

Habitat simplification as the result of management may affect invertebrates through prey abundance. Coy (1994) found that increased temperature and habitat simplification after fire decreased the population of Chilopoda. As well as other Myriapoda, the distribution of Chilopoda tends to be limited to damp or moist environments and they are generally found in leaf litter or rotting timber (Coleman, 2004). Water loss may pose a serious problem for most of Myriapoda due to the lack of a waxy waterproofing layer on their cuticle (Coleman, 2004).

It is well documented that vegetation structure (height and density) is one of the crucial factors affecting the distribution and abundance of Aranea. Perner and Malt (2003) found that the frequency and time of disturbances (mowing and harvesting) resulted in a significant change in microclimatic conditions, particularly soil surface temperature, which affected the distribution and abundance of Aranea. Predacious in

nature, Aranea are dependent on prey abundance. Consequently, limited resources as the result of habitat simplification during the management and change in microclimatic conditions were presumably attributable to the low abundance of Aranea in the managed site.

The activity of ant workers (Formicidae) depends greatly on their habitat use and foraging activity (Bestelmeyer & Wiens, 1996). Formicidae collected by litter sampling were significantly more abundant in the control site. This result was consistent with previous studies showing higher diversity and abundance of Formicidae in more complex habitats and relatively undisturbed habitats (Bestelmeyer & Wiens, 1996; Lassau & Hochuli, 2004). However, those collected by pitfall traps showed significantly higher abundance in managed site possibly because of generalist or opportunist ants (Gibb & Hochuli, 2002). The contradictory results were also possibly due to the different trapping methods. Pitfall traps are likely to collect more Formicidae with different habitat use and functional groups during the trapping period, whereas soil sampling is likely to collect more true soil-inhabiting Formicidae at one collection time.

Above-ground invertebrates

Some groups of flying insects belonging to Diptera, Homoptera and Hymenoptera tended to show higher abundance in the managed site than in the control site. This pattern may be attributed to their preference for open habitats and their photophilous nature. Pruning, selective cutting and removal of ground vegetation undoubtedly resulted in more open areas in the managed site and allowed more light to penetrate to ground level.

Homoptera, Diptera and flying Hymenoptera tend to be more active at relatively higher temperature and show a preference for relatively open habitats and attraction to light (Kristofferson, Hanks et al., 2001; Pesquero et al., 1996). As a result, management activities could positively affect these flying insects indirectly by creating a more open and warmer environment in managed site. Mecoptera were also more abundant in the managed site. Most Mecoptera inhabit a moist environment (Byers, 2001); however, some species of the family Panorpididae are known to show a wide range of habitat preference across shrubs and the ground layer in densely-vegetated woodlands, often near water or wet seeps, and other habitats such as grasslands, cultivated fields and forest borders (Bartlett, 2005).

For adult Coleoptera, Koivula (2002) found a tendency for fewer common species to be found in the managed site. In this study, the abundance of Coleoptera collected by window traps was also lower in the managed site and confirmed his finding. It has been documented that highly complex habitats support greater numbers of species and individuals in coleopteran assemblages, possibly through increasing the availability of resources (Lassau et al., 2005). Therefore, management-induced simplification of habitats can be one cause of the reduced abundance of Coleoptera living above the ground in the managed site.

CONCLUDING REMARKS

This study clearly indicates that the effects of management activities for matsutake cultivation on diversity and abundance vary among invertebrate communities in red pine forests and can be negative, positive or negligible depending substantially on the habitats with which the invertebrate communities in question are closely associated. Strong negative effects of management were detected in the diversity and abundance of the invertebrate community associated with litter. Several groups of invertebrates, especially litter and soil dwellers, decreased in abundance under management.

Changes in faunal composition due to management were found in all four sampling methods employed in this study and were most conspicuous in litter sampling. We conclude that management practices to cultivate matsutake mushrooms negatively affect the structure of litter- and soil-dwelling invertebrate communities in red pine forests and can reduce function in the decomposition processes for which they are responsible. Inversely, some flying insects may benefit from management activities. However, these results are based on patterns in higher taxonomic groups, regardless of the diversity and abundance of species within higher taxa. Therefore, more detailed examination of the effects of management based on lower taxonomic levels would improve our conclusion and enhance our understanding of the effects. Temporal variation in the structure of invertebrate communities may occur through seasonal changes in both abiotic and biotic environments and thus seasonal replication can also improve the reliability and consistency of the results over time.

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