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The effects of mixed broad-leaved trees on the collembolan community in larch plantations of central Japan

Motohiro Hasegawa[a,*], Aino T. Ota[b], Daisuke Kabeya[a], Toru Okamoto[a], Tomoyuki Saitoh[a], Yoshihiko Nishiyama[c]

[a] *Forestry and Forest Products Research Institute, Tsukuba, Ibaraki 305-8687, Japan*
[b] *Yokohama National University, Yokohama, Kanagawa 240-8501, Japan*
[c] *Kiso Experimental Forest, Forestry and Forest Products Research Institute, Kiso, Nagano 397-0001, Japan*

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ABSTRACT

The effects of broad-leaved trees on the collembolan community in larch plantations were investigated at the foot of Mt. Yatsugatake (1200–1400 m a.s.l.) in Japan. The study sites comprised five pure larch plantation plots (larch dominated more than 95% of the area at breast height) and five mixed forest plots (larch dominated between 50% and 80% of the area at breast height). We compared the collembolan community structures between stand types and related them to the plant community composition and soil properties at each plot. Density and species richness of Collembola were not significantly different between pure larch and mixed plots. Using partial redundancy analysis (pRDA), the variance of collembolan species data in the litter layer was explained by the biomass of grass on the forest floor, and the variance in the soil layer was explained by the biomass of total forest floor plants. These results suggest that the biomass or the composition of forest floor plants influence the collembolan community more than the crown trees in this area.

1. Introduction

In Japan, *Larix kaempferi*, a deciduous conifer species, is planted in dry inland areas typified by light snow cover and cold winters (Nagaike et al., 2003). Most of these plantations were established after the 1940s to replace primary and secondary broad-leaved deciduous forests that had been substantially overharvested, but the contributions of *L. kaempferi* plantations to regional biodiversity are still unknown (Nagaike, 2002). To achieve ecologically sustainable forest management in this region, studies have been undertaken to determine the status of biodiversity in forests and the effects of forest management practices in the area, i.e., the basic information necessary for ecologically sustainable management (Nagaike, 2002; Ohsawa, 2004, 2007). The study area is covered by Japanese larch plantations, which were established for timber production, and thinning has been conducted twice within a 45-year period in this area to enhance the growth of dominant trees. After the planting of larch seedlings, trees species (e.g., birch, oak, and pine) started to regenerate from the stumps or seeds, and grow alongside the larch. During the mowing and thinning stage, mixed trees were cut or left, depending on prevailing silvicultural management policy. As a result, a mosaic of larch plantations with various mixtures of broad-leaved trees has developed over the study area.

Plant species identity, vegetation composition, physiology, chemistry, and phenology all influence soil invertebrate community composition (Sylvain and Wall, 2011). The effects of litter species richness on soil fauna have been tested using mixed litter bag experiments (Kaneko and Salamanca, 1999; Takeda, 1987), which have revealed idiosyncratic relationships between plant species and soil animals (St. John et al., 2006; Wardle et al., 2006). The effects of mixing tree species on Collembola have been investigated in a European spruce plantation mixed with beech (Salamon and Alphei, 2009; Salamon et al., 2008; Scheu et al., 2003), and these studies have suggested relatively moderate effects on the collembolan community. Total density and species richness did not change significantly, but species composition was affected (Salamon and Alphei, 2009; Scheu et al., 2003). To determine the effects of mixing tree species on Collembola, its community structure should be evaluated using the response of different functional groups or through multivariate analysis.

Salamon et al. (2008) suggest that forest age and stand type are likely to impact Collembola communities via changes in the amount and quality of food resources, including both living plants and herb litter materials. The effects of herbs on Collembola have been emphasized in grassland and meadow studies (Dombos, 2001;

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* Corresponding author. Tel.: +81 298 29 8251; fax: +81 298 73 1543.
E-mail addresses: motohiro@ffpri.affrc.go.jp (M. Hasegawa), mt.indigo@gmail.com (A.T. Ota), kabeta@ffpri.affrc.go.jp (D. Kabeya), okamotot@ffpri.affrc.go.jp (T. Okamoto), tsaitoh@ffpri.affrc.go.jp (T. Saitoh), nishiyam@ffpri.affrc.go.jp (Y. Nishiyama).

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Greenslade, 1997; Salamon et al., 2004), and the effects of the undergrowth in forest sites were also recently studied (Eisenhauer et al., 2011). The findings have revealed that studies should not only consider the effects of crown trees but also those of undergrowth on collembolan communities.

In this study, we investigated the effects of a mixture of broad-leaved trees on Collembola in terms of their density, diversity, and species composition. The relationship of the collembolan community with the stand type, forest floor plants, and soil abiotic factors are discussed.

2. Materials and methods

The study area was located on the south and west slopes of Yatsugatake mountain range, in Yamanashi and Nagano, central Japan (approximately 36°50–56′N, 140°34–35′E, 1200–1400 m a.s.l.; mean annual air temperature 7.1 °C; mean annual precipitation 1454 mm). Larch (*L. kaempferi*) was planted at the study area after a previous land cover of grass fields or sparse pine forests. Landscape at 1200–1400 m a.s.l. on the slope of Yatsugatake mountain range was totally at most covered by the larch plantation. The forest of this area was mostly national or prefectural forest and classified into fine compartment (with several ha of area). The management plan for the compartment was often determined as this small unit, therefore the compartment in the vicinity could have different forest structures. Ten study plots were located within a 15 × 20 km area (Fig. 1). The forest age was 40–50 years at the time of sampling (Table 1). The total basal area of each plot ranged from 22.9 to 41.2 m^2 ha^{-1}. Size of a plot was 30 m × 30 m. Each plot was divided in 9 sub-plots: where they 10 m × 10 m. Thinning had been conducted several times until 40 years after planting, but in some plots, all of the trees except larch had been completely removed (Table 1). In other plots, *Betula platyphylla*, *Quercus mongolica*, and other tree species had invaded and were left in place during the thinning procedure. As a result, the percentage of larch based on basal area in each plot ranged from 100% to 46.4% (Table 1). We classified these plots as five pure larch plots (>95% larch) and five mixed plots (between 50% and 80% larch). Ideally, in order to consider the effects of the forest category to the soil fauna, these two categories of plots should be set pair-wisely and replicated the pair of plots in the study area. However, because of the limited availability of the study plots, we only fulfilled these design in the part of the plots (Fig. 1). Therefore, we scattered these two categories of plots in the study area as evenly as possible shown in Fig. 1. The average distances (±standard errors) among pure larch plots, among mixed plots and between different categories of plots were 5553 (±977), 5389 (±677) and 5895 (±1195) m respectively. To extract the spatial autocorrelation structure to the collembolan community composition, we use the principal coordinates of neighbor matrices (PCNM) as explained in a statistical analysis.

In October 2006 and May 2007, samples from the litter layer and soil (0–5 cm) were collected with a corer (125 mL, 5 cm depth, 25 cm^2 area) from each subplot. Most Collembola occur in the litter layer and the upper mineral soil layer, within the top 5 cm of the profile. In total, 180 samples (10 plots × 9 subplots × 2 dates) for each substrate (litter and soil) were collected. Collembola were extracted using a Macfadyen high gradient extractor at a constant temperature of 35 °C for 7 days. The water content of the litter layer was calculated as (wet weight of litter – dry weight of litter)/dry weight of litter).

Soil samples were taken from five quadrats in each plot in August 2007 to determine physical and chemical parameters. Cores of 100 mL of the top 5 cm of soil were collected for chemical analysis. For soil pH and EC analysis, 5 g of fresh soil was mixed with 25 mL of deionized water. A glass electrode (HM14P; DKK-Toa Corp., Tokyo, Japan) was used to measure pH and a conductivity cell electrode (SC82; Yokogawa Electric Corp., Tokyo, Japan) was used to measure soil electrical conductivity (EC). Total carbon and nitrogen concentrations in soil samples were measured with an NC analyzer (Sumigraph NC-900; SCAS Ltd., Tokyo, Japan). The air-dried litter layer was classified as broad-leaved, needles (larch), and bamboo grass (*Sasa nipponica*), and the weight of each category was estimated.

At each plot, the diameter at breast height (DBH) above 5 cm was measured for all trees in each plot. We set five 0.5 m^2 circles randomly in each plot, and cut out the aboveground forest floor vegetation in each circle. The forest floor plant cuttings were classified into trees, grass, herbs, and *Sasa*, weighed for each category and dried to constant mass at 70 °C for three days. The number of plant species in each circle was counted.

2.1. Statistical analysis

2.1.1. Detection of spatial autocorrelation, RDA, variation partitioning and GLMM

To extract the spatial autocorrelation structure, we used principal coordinates of neighbor matrices (PCNM) developed by Borcard and Legendre (2002) because it is flexible for expressing various spatial scales and can be used in redundancy analysis (RDA). This method creates a set of explanatory variables (PCNMs: eigenvectors) that represent the structure at all spatial scales from the distance matrix among the plots. Ten PCNMs were calculated in our study, and we referred to them as PCNM-1 to PCNM-10. We used the library spacemakeR (Dray et al., 2006) in the statistical environment R (R Core Team, 2012), to calculate the PCNMs.

For the RDA, environmental variables were selected by a forward-selection procedure to detect meaningful factors and so reduce the large number of potential factors. Variables were incorporated stepwise into the model according to their increasing effect on the variance (contribution to the eigenvalues of the model), and their significance was tested by comparing them to Monte Carlo permutations (5000 times) of the null model (which does not have the variable to be incorporated). We set a standard selection criterion ($p < 0.05$) to retain parameters for use in the final models. All of the RDA and forward selections were performed with CANOCO for Windows, version 4.5 (ter Braak and Smilauer, 2002).

Initially, we conducted RDA using only the PCNMs as explanatory variables, and the significant variables were selected as relevant spatial autocorrelations in the species composition by a forward-selection procedure. We wanted to determine the effect of the environment variables after partialling out the effect of spatial autocorrelation. Therefore, we executed a partial RDA using the selected PCNMs as covariables and other environmental variables as explanatory variables.

We investigated the effects of forest category of plots (pure larch and mixed forest plots, as the fixed effect) to the environmental variables and collembolan community structures. Because the sampling protocol in this study formed nested structure (i.e., the samplings were conducted in 5 subplots within each plot for 2 seasons), the effect of the plot difference and that of seasonal difference were also considered as the random effects. Hence, generalized linear mixed models (GLMMs) (*nlme* library and *glmmLM* library on R version 2.13.0; (R Core Team, 2012) were used for the analyses. For comparison of the litter weight, soil chemical and physical properties, and the biomass of forest floor plants between pure larch and mixed forest plots we used a GLMM with the assumption of a Gaussian distribution. We also used a GLMM for the density of Collembola with the assumption of a negative binomial distribution and for the species richness with the assumption of a Poisson distribution due to discrete variables. Significance tests were based on the *t*-statics for each parameter. Spearman rank correlation