

Comparison of stream benthic invertebrate assemblages among forest types in the temperate region of Japan

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Received: 16 January 2006 / Accepted: 2 October 2006 / Published online: 11 November 2006
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Abstract We compared benthic invertebrate assemblages among headwater streams in several forest types in Japan. Forests were divided into three clusters based on vegetation composition: old-growth broad-leaved forest, planted coniferous forest, and mixed forest. The numbers of individuals and families and the diversity (Shannon-Wiener) of benthic invertebrate assemblages did not differ significantly among the three forest clusters. However, principal components analysis of family abundance showed differences in the benthic invertebrate assemblages among the three forest clusters. No environmental factors were correlated with these differences. Benthic invertebrate assemblages differed depending on forest composition. The abundances of Taeniopterygidae and Athericidae in old-growth broad-leaved forest were significantly greater than in planted coniferous forest. The abundances of Heptageniidae, Baetiidae, Stenopsychidae, Uenoidae, Chironomidae, and Potamidae in planted coniferous forest were significantly greater than in old-growth broad-leaved forest. If the remaining old-growth broad-leaved forest were to be converted to coniferous plantation, species that inhabit old-growth forest may become extinct.

Keywords Benthic invertebrate assemblage · Forest type · Impact · Old-growth forest · Planted coniferous forest

Introduction

The naturally forested landscapes of western Japan consist of various types of deciduous trees, evergreen broad-leaved trees, and coniferous trees. These forests have been exploited since ancient times: lowland forests were converted to rice paddies, farmland, and residential areas; highland forests were converted to coppice for fuel wood production and to conifer plantations. As a result, the area of natural

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forests has decreased, and there is currently a small percentage of forested area remaining in western Japan. The reduction in natural forest habitat may lead to the decrease and extinction of terrestrial insects that rely on these forests.

Differences in forest type affect in-stream ecology. The presence of streamside forest affects stream water quality, and the effect differs depending on the forest type (Friberg 1997; Friberg et al. 1997). Deciduous broad-leaved vegetation may provide more abundant and higher quality food for shredders than coniferous vegetation (Eggert and Burton 1994). Riparian red alder forest provides nutrient-rich litter to the stream ecosystem (Volk et al. 2003) and supports a greater biomass of aquatic invertebrates than does riparian conifer forest (Piccolo and Wipfli 2002). The density of benthic invertebrates is high in beech forest and low in coniferous forest in Denmark (Friberg 1997). Leaf litter that falls into the stream may play several roles for benthic invertebrate assemblages depending on the litter species (Cummins et al. 1989).

The species composition of a basin forest is also an important factor in considering the stream habitat of benthic invertebrates. In-stream chemistry is affected by the quality and quantity of vegetation in the basin, and in turn, may indirectly affect the growth of benthic invertebrates (Krueger and Waters 1983; Johnson et al. 1997). Hemlock forests in northeastern Pennsylvania support more benthic invertebrate taxa than do mixed hardwood forests (Snyder 2002). The composition of benthic invertebrates also appears to differ depending on the basin forest type.

Planted monocultures of conifer forest currently cover 60% of the land in western Japan. The scale of natural forest has decreased; the largest of these areas are mostly located at high altitudes and consist of only a few hundred hectares. In North America and Europe, natural forest is coniferous forest and often preserved on a large scale. Benthic invertebrate assemblages in headwaters in Japan may differ from those in North America and Europe because the natural forest types differ. The composition of the basin and riparian forest would be one of the most important variables affecting benthic invertebrate assemblages. However, the differences in benthic invertebrate assemblages resulting from different forest types have not been thoroughly investigated in Japanese headwaters except of recent study by Yoshimura and Maeto (2006).

In Japan, deforestation and plantation occurs on a small scale, and the area that is not planted converts to secondary broad-leaved forest. Thus, most forest basins in Japan are composed of various forest types. Deforestation causes increased sediment loads (MacDonald et al. 2003) and decreased detritus (Price et al. 2003) in streams, resulting in changes in the benthic invertebrate community (Friberg et al. 1997; Fuchs et al. 2003; Price et al. 2003; Hernandez et al. 2005). Because secondary broad-leaved forest forms after deforestation, the benthic invertebrate assemblage in these forest basins may differ from those in old-growth and planted coniferous forests. Thus, we compared the benthic invertebrate assemblages in broad-leaved old-growth forest, planted coniferous forest, and secondary broad-leaved forest in the headwater streams of a basin in Japan. We discuss the possible effects of forest conversion on the alteration of benthic invertebrate assemblages.

Materials and methods

Study site

The study focused on the Shimanto River basin in Shikoku, the fourth largest island of the Japanese archipelago (Fig. 1). The basin was covered by lowland and hilly

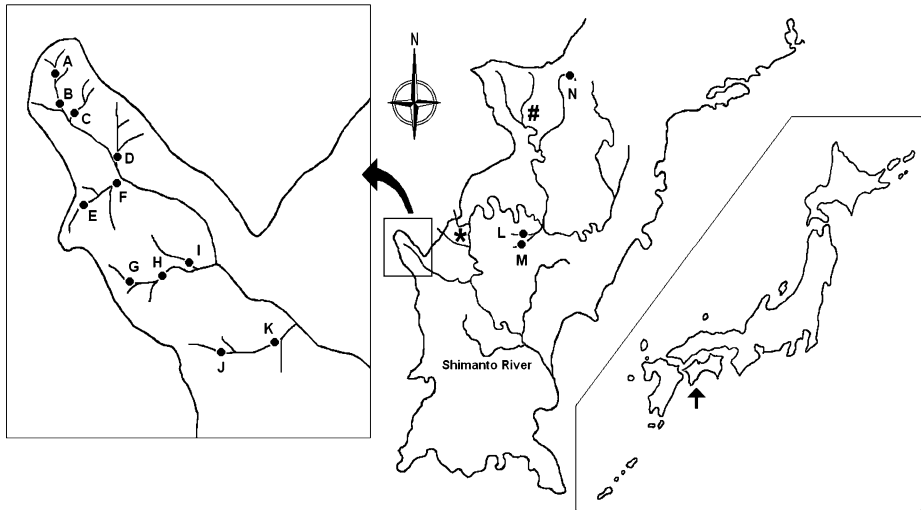


Fig. 1 Study site in the Shimanto basin, Kochi Prefecture, Japan. •, sampling sites A–N; #, Yusuhara; *, Ekawasaki

forests up to 1400 m a.s.l. and was principally composed of conifer plantations (about 60% of the total forested area), secondary forest (about 40%), and remnants of old-growth forest that had no historical record of having been cleared (< 1%).

The old-growth forests were dominated by evergreen conifers (e.g., *Abies firma*, *Tsuga sieboldii*, and *Chamaecyparis obtusa*) and diverse evergreen broad-leaved trees (e.g., *Quercus* spp., *Castanopsis cuspidata*, *Machilis japonica*, and *Cleyera japonica*). At around 800 m a.s.l., evergreen broad-leaved trees were gradually replaced by deciduous trees (e.g., *Lindera erythrocarpa*, *Mallotus japonicus*, *Carpinus* spp., *Fagus* spp., *Betula grossa*, and *Acer* spp.). The lowland secondary broad-leaved forests consisted of coppices dominated by evergreen broad-leaved trees (e.g., *Castanopsis cuspidata* and *Quercus glauca*), whereas those at higher altitudes consisted of deciduous broad-leaved trees (e.g., *Quercus serrata* and *Carpinus* spp.). The conifer plantations consisted of monocultures of Japanese cedar (*Cryptomeria japonica*) or Japanese cypress (*Cryptomeria obtusa*), which were cut at 30–80 year intervals. Managed plantations were thinned, and their forest floors were covered by abundant shrub species. The annual mean temperature and precipitation from 1995–2004 were 13.4°C and 2733 mm, respectively, at Yusuhara (415 m a.s.l.) and 15.6°C and 2375 mm, respectively, at Ekawasaki (60 m a.s.l.; Fig. 1).

Fourteen sampling sites were selected within a 50 × 50 km area of the Shimanto river basin. The surface soil at these sites was categorised as Shimanto Terrane and consisted of alternating sandstone and mudstone beds. The vegetation at each sampling basin was determined using a 1/20,000 vegetation map (National Forest Map for the 1996 Management Plan) and field surveys. The vegetation was divided into eight categories based on forest age (> 100 years old, 50–100 years old, 25–50 years old, < 25 years old) and type of trees (broad-leaved forest, coniferous forest). Each sampling basin was divided into 100 × 100-m grids, and the number of grids of each vegetation category was counted (Table 1). When two categories were found in one grid, each was assigned 0.5 grids.

Sampling of benthic invertebrates and measurement of environmental factors

Benthic invertebrates were quantitatively sampled five times at each site in winter. A 30×30 cm quadrat was established on the substrate in shallows 20–25 cm in depth with a flow rate of 0.15–0.2 m/s within a 25 m length of each sampling site. A D-frame net with 1 mm mesh was placed downstream of the quadrat. Large stones in the quadrat were removed and placed directly into a white tray. Then, the substrate surface in the quadrat was disturbed to allow insects to drift into the D-frame net. All larvae on the stones and in the D-frame net were removed and preserved in 80% ethanol. The preserved benthic invertebrates were later identified under a $50\times$ microscope (SMZ-U; Nikon). I identified specimens to the family level because this is thought sufficient for broad-scale monitoring (Hewlett 2000).

At each site where benthic invertebrates were collected, I measured the electrical conductivity (EC) using a portable compact twin conductivity meter (B-173; Horiba), the pH using a portable compact twin pH meter (B-212; Horiba), and the dissolved oxygen (DO) using a portable DO meter (DO-5509; Lutron; Table 1). The wetted stream width (SW) was measured using a portable meter (Yardage Pro; Bushnell; Table 1).

Statistical analysis

The similarity in forest composition among the sites was assessed using the Ward method and the proportion of each of the eight vegetation-type categories. Sites were clustered by Euclidean distance.

The Shannon-Wiener diversity index represents species richness and the abundance of each species. The γ -level diversity indicates within- and among-quadrat diversity at each site. Thus, the Shannon-Wiener diversity index was used to calculate the γ -diversity at each site (each site contained five quadrats). Abundance data were pooled for each site. The number of individuals, number of families, and γ -diversity of each site were compared among the forest clusters using a Kruskal-Wallis test. Correlations among the three diversity indices and the stand variables were tested using Kendall's coefficient of rank correlation (τ).

The similarity in the composition of benthic invertebrate families among the sites was assessed using the Ward method and abundance data. Sites were clustered by Euclidean distance.

The benthic invertebrate assemblages were analysed using principal components analysis (PCA) of the family abundances. I included only families that were observed at two or more sites. The values of the PCA axes were compared among forest clusters using a Kruskal-Wallis test. Kendall's τ was used to examine correlations among the PCA axes and several stand variables.

To determine which families tended to inhabit each forest type, the abundances of families in the five samples of each site were compared among sites using a Kruskal-Wallis test.

All the statistical analyses were performed using SYSTAT version 10 (SPSS Inc., 2000).

Results

The forest composition at the 14 sites was divided into three clusters by similarity analysis (Fig. 2). The first cluster consisted of sites A, B, K, and J, of which >70% of

Table 1 The value of EC, pH, DO, stream width, altitude, basin area of sampling sites and the percentage of each kind of trees in each basin of the sites

Site	EC ($\mu\text{s}/\text{cm}$)	pH	DO (mg/L)	Stream width (m)	Altitude (m)	Basin area (ha)	Broad-leaved forests ^a				Coniferous forests ^a				
							Older than 100 (age)	50–100 (age)	25–50 (age)	Younger than 25 (age)	Older than 100 (age)	50–100 (age)	25–50 (age)	Younger than 25 (age)	
A	53	7.1	11.0	6	620	142.8	91.7	0	0	0	8.3	0	0	0	0
B	55	6.9	11.8	9	500	301.4	82.0	0	0	0	4.9	0	13.1	0	0
C	53	6.7	11.3	5	500	76.0	0	30.9	0	0	0	0	11.9	0	57.2
D	44	6.3	11.3	6	360	186.0	0	28.8	0	0	3.2	0	29.8	0	38.2
E	50	7.1	11.5	3	540	92.3	0	0	0	25.8	0	0	0	74.2	0
F	51	6.9	11.4	5	440	202.5	0	0	0	24.3	0	0	0	75.7	0
G	62	7.5	11.1	5	570	90.5	11.6	0	0	0	0	0	0	88.4	0
H	57	7.1	11.2	7	380	290.0	6.7	0	0	4.5	0	0	0	88.8	0
I	51	6.8	11.3	4	300	102.0	9.3	0	0	26.5	0	0	0	64.2	0
J	27	6.2	13.1	5	570	99.5	87.6	0	0	0	0	0	0	0	12.4
K	35	6.4	13.2	7	300	213.4	72.1	15.3	0	0	6.8	0	0	0	5.8
L	82	7.2	11.9	6	260	347.5	0	0.9	0	0	0	0	43.2	30.9	25.0
M	89	7.0	11.4	3	400	63.5	0	0	0	0	0	0	88.2	11.8	0
N	55	6.5	13.0	5	600	138.5	50.9	0	0	0	0	0	1.1	43.7	4.3

^a percentage of eight kinds of trees in each basin

the area was composed of >100 year-old old-growth forest (OGF cluster). The second cluster consisted of sites E, F, G, H, and I, of which >60% of the area was composed of 25–50 year-old planted conifer forest (PCF cluster). The third cluster consisted of sites C, D, L, M, and N, whose compositions varied (NOP cluster): sites C and D consisted of secondary broad-leaved forest (30% of the area of these sites); sites L and N consisted of 50–100 year-old planted conifer forest (> 40% of the area); and site M consisted of old-growth conifer forest.

The EC, pH, DO, stream width, altitude, and basin area of the sites did not differ significantly among the three forest clusters (Table 2).

In total, 6238 individuals from 47 families of benthic invertebrates were collected at the 14 sites. The number of families collected at each site gradually increased with the increase in the number of individuals collected ($\tau = 0.506$, $n = 14$, $P < 0.05$; Kendall test, Fig. 3). However, the number of individuals, number of families, and γ -diversity at each site did not differ significantly among the three forest clusters. These indices showed no correlation with the EC, pH, DO, stream width, altitude, or basin area of the sites (Table 3). The number of individuals was negatively correlated with the percentage of 50–100 year-old broad-leaved forest and positively correlated with the percentage of 25–50 year-old broad-leaved forest. The number

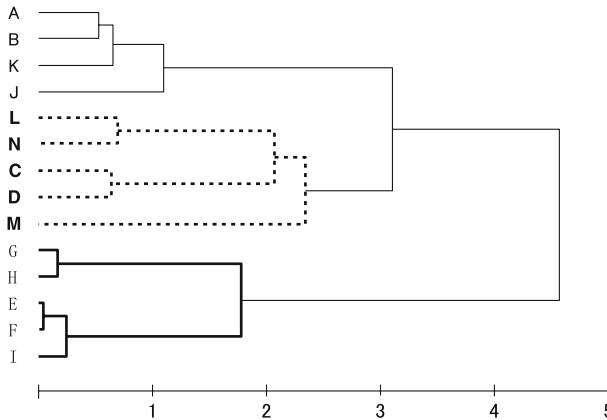


Fig. 2 Cluster analysis of the similarity among forest vegetation compositions assessed using the Ward method, using Euclidean distance

Table 2 Mean and range of six environmental factors

Environmental factors	Forest clusters			H^a
	OGF	NOP	PCF	
EC ($\mu\text{s}/\text{cm}$)	42.5 (27–55)	64.6 (44–89)	54.2 (50–62)	2.48
pH	6.65 (6.2–7.1)	6.74 (6.3–7.2)	7.08 (6.8–7.5)	2.71
DO (mg/L)	12.28 (11.0–13.2)	11.78 (11.3–13.0)	11.30 (11.1–11.5)	2.43
Stream width (m)	6.5 (5–9)	4.8 (3–6)	4.8 (3–7)	3.00
Altitude (m)	498.0 (300–620)	424.0 (260–600)	446.0 (300–570)	0.92
Basin area (ha)	189.3 (99.5–213.4)	162.3 (63.5–347.5)	155.5 (90.5–290.0)	1.01

^a Differences tested by Kruskal-Wallis test

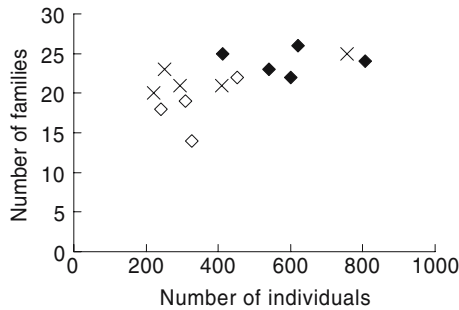


Fig. 3 Relationship between the number of individuals and number of families of benthic invertebrates. ◇, OGF; ×, NOP; ◆, PCF

of families was positively correlated with the percentage of 25–50 year-old broad-leaved and coniferous forest (Table 3).

The similarity analysis divided the benthic invertebrate family compositions of the 14 sites into four groups (Fig. 4). The first group consisted of sites A, B, K, and J, which were all in the OGF cluster. The second group consisted of sites L and N, which were in the NOP cluster. The third group consisted of sites E, F, H, and I, which were all in the PCF cluster. The fourth group consisted of sites C, D, G, and M, which were in the NOP and PCF clusters. Thus, the benthic invertebrate assemblages appeared to differ depending on the forest composition.

The first three axes of the PCA ordination of the benthic invertebrate family compositions explained 46.9% of the variation in families (Fig. 5). In terms of benthic invertebrate family composition, sites A, B, J, and K, in the OGF cluster, were clustered at the left, whereas, sites E, F, H, and I, in the PCF cluster, were located at the right of the ordination diagram (Fig. 5). Site M, which consisted of old-growth conifer forest, was located near the OGF sites. Sites C and D, which were deforested and replanted before their conversion to secondary forest, were located near the PCF sites. Sites L and N, whose forest compositions were different from those of sites C, D, and M, were located at the upper left of the ordination diagram. Only axis 1 differed significantly among the three forest clusters (Table 3). No axes correlated with the EC, pH, DO, stream width, altitude, or basin area of the sites. Axis 1 was negatively correlated with the percentage of >100 year-old broad-leaved forest and positively correlated with 25–50 year-old broad-leaved and coniferous forest. Axis 2 was positively correlated with the percentage of 50–100 year-old coniferous forest. Axis 3 was negatively correlated with the percentage of 50–100 year-old broad-leaved forest (Table 3).

The abundance for 17 families of benthic invertebrates differed significantly among the three forest clusters (Table 4). Athericidae were found only in the OGF, and the abundance of Taeniopterygidae was highest in the OGF and lowest in the PCF. In contrast, the abundances of Heptageniidae and Uenoidae were highest in the PCF. The abundances of Baetiidae, Stenopsychidae, Chironomidae, and Potamidae were highest in the PCF and lowest in the OGF. The abundances of Ephemerellidae, Psephenidae, Tipulidae, and Gammaridae were highest in the NOP.

Table 3 Mean and range of three indices and three axes of PCA ordination of benthic invertebrate assemblage, and their statistic results by Kendall's correlation coefficient by ranks (τ)

	Indices			Axes		
	Number of individuals	Number of families	Diversity index	Axis 1	Axis 2	Axis 3
Forest clusters						
OGF	332.3 (242 to 452)	18.3 (14 to 22)	3.622 (3.33 to 3.88)	-5.278 (-4.45 to -5.86)	-3.434 (-8.78 to 0.36)	-0.425 (-1.85 to 1.06)
NOP	386 (220 to 757)	22 (20 to 25)	3.576 (2.86 to 3.98)	-1.917 (-7.40 to 0.91)	3.471 (-2.98 to 12.41)	-0.77 (-4.17 to 10.18)
PCF	595.8 (412 to 807)	24 (22 to 26)	3.788 (3.30 to 4.45)	6.14 (-1.22 to 11.18)	-0.724 (-2.90 to 3.05)	1.11 (-6.27 to 7.08)
H ^a	5.466	4.166	0.36	8.143 ^c	2.991	1.731
EC ($\mu\text{s} / \text{cm}$)	-0.022	0.023	-0.201	-0.045	0.112	-0.134
PH	0.236	0.195	-0.258	0.146	-0.146	0.034
DO (mg / L)	-0.101	-0.276	0.034	-0.236	0.101	0.169
Stream width (m)	-0.224	-0.109	0.106	-0.128	0.082	-0.221
Altitude (m)	0.313	0.069	-0.112	-0.358	-0.223	0.358
Basin area (ha)	-0.055	0.124	0.275	0.055	0.253	-0.121
Broad-leaved forests						
Older than 100 (age)	0.072 ^b	-0.283 ^b	0.096 ^b	-0.529 ^e	-0.120	0.168
50–100 (age)	-0.433 ^b	-0.221 ^b	-0.093 ^b	0.093	0.062	-0.402 ^b
25–50 (age)	0.464 ^b	0.474 ^b	0.278 ^b	0.649 ^c	0.124	0.155
Younger than 25 (age)	-0.309 ^b	-0.285 ^b	-0.124 ^b	-0.309	-0.371	0.093
Older than 100 (age)	-0.063 ^b	0.043 ^b	-0.105 ^b	-0.314	0.021	0.147
50–100 (age)	-0.071 ^b	0.029 ^b	0.099 ^b	-0.212	0.495 ^b	-0.155
25–50 (age)	0.351 ^b	0.461 ^b	0.050 ^b	0.526 ^c	0.050	0.025
Younger than 25 (age)	-0.304 ^b	-0.243 ^b	0.066 ^b	-0.119	0.251	-0.357

^a Differences tested by Kruskal-Wallis test, ^b $P < 0.05$, ^c $P < 0.01$

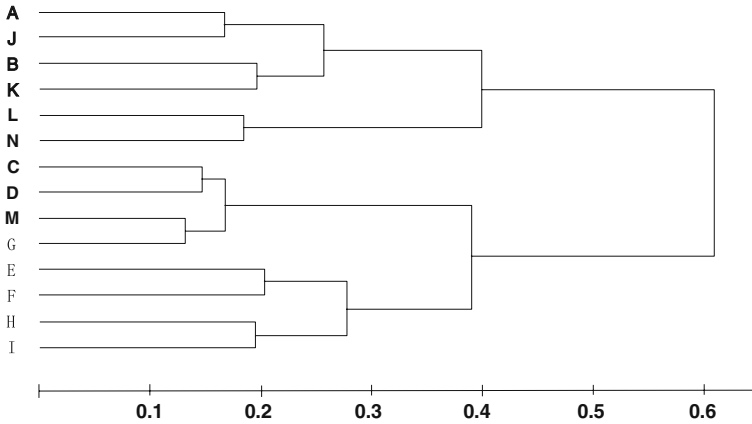
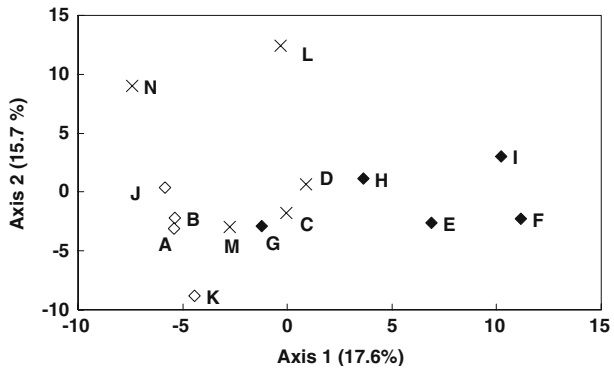


Fig. 4 Cluster analysis of the similarity between benthic invertebrate family compositions assessed using the Ward method, using Euclidean distance

Fig. 5 Principal components analysis ordination diagram of benthic invertebrate family compositions. \diamond , OGF; \times , NOP; \blacklozenge , PCF



Discussion

Cluster analyses showed that differences in the benthic invertebrate assemblages were related to differences in forest composition, although the number of individuals, number of families, and diversity did not differ significantly among the three forest clusters. The PCA of benthic invertebrate families also showed that the assemblages differed among the three forest clusters. No environmental factors, except for forest composition, were correlated with the PCA axes. The sites investigated were all found on the same type of surface soil. Thus, we conclude that differences in the benthic invertebrate assemblages were caused by differences in forest composition.

When planted areas are deforested, sediment in streams in these areas increases (MacDonald et al. 2003), and benthic invertebrate communities differ between streams surrounded by clear cuts and those surrounded by old-growth forest (Friberg et al. 1997; Fuchs et al. 2003; Price et al. 2003; Hernandez et al. 2005). Thus, benthic invertebrate assemblages are altered by deforestation. When deforested areas are not afforested, grassland vegetation colonises. After 20–30 years, broad-leaved trees

Table 4 Mean abundance of benthic invertebrate in one site of each forest cluster and statistical difference among three clusters of forest composition

Families	Forest clusters			H^a
	OGF	NOP	PCF	
Perlidae	45.0	38.6	44.0	2.13
Perlodidae	0.5	9.8	5.6	2.85
Leuctridae	0.3	0.8	0.6	0.67
Nemouridae	26.8	26.0	6.2	5.56
Taeniopterygidae	13.0 ^c	10.8	0.0 ^e	11.72 ^g
Chloroperlidae	4.0	7.0	0.4	6.06 ^e
Siphonuridae	26.8	16.8	36.0	5.33
Heptageniidae	134.0 ^c	122.0 ^d	271.0 ^{cd}	18.31 ^h
Ephemeridae	3.0	6.2	10.2	5.86
Ephemerellidae	0.0 ^{bc}	9.4 ^b	1.6 ^c	12.03 ^g
Baetiidae	29.8 ^c	45.0 ^d	97.0 ^{cd}	14.03 ^h
Leptophlebiidae	14.8	10.4	13.2	1.20
Stenopsychidae	0.0 ^b	0.8	7.2 ^c	12.60 ^g
Rhyacophilidae	0.0 ^b	7.0 ^b	3.8	14.17 ^h
Uenoidae	1.5 ^c	0.4 ^d	24.4 ^{cd}	22.50 ^h
Hydropsychidae	1.8	7.8	7.8	5.05
Lepidostomatidae	5.0	4.2	2.2	2.96
Philopotamidae	3.8	1.2	2.6	1.23
Phryganopsychidae	0.8	0.0	0.8	4.76
Brachycentridae	0.8	0.2	0.4	0.87
Polycentropodidae	0.5	0.0	1.2	4.14
Glossosomatidae	0.0	0.0	1.2	7.52 ^e
Epiophlebiidae	2.5	3.4	5.4	3.24
Corydalidae	0.3	1.0	3.6	6.58 ^e
Psephenidae	0.5 ^b	5.8 ^b	4.8	11.39 ^g
Elmidae	0.0	3.2	0.6	3.18
Ptilodactylidae	0.0	1.0	0.0	7.52 ^e
Helodidae	0.0	0.6	0.0	3.65
Chronomidae	2.8 ^c	4.8	9.2 ^c	11.37 ^g
Athericidae	6.8 ^{bc}	0.0 ^b	0.0 ^e	25.30 ^h
Tipulidae	0.8 ^{bc}	9.0 ^b	6.4 ^c	11.37 ^g
Gammaridae	0.0 ^{bc}	24.4 ^b	16.6 ^c	18.72 ^h
Potamidae	2.3 ^c	4.6	7.6 ^c	8.67 ^f
Planariidae	4.3	2.4	2.4	0.45

^a Differences tested by Kruskal-Wallis test.

Significant difference between OGF and NOP is indicated^b, between OGF and PCF is indicated^c, and between NOP and PCF is indicated^d

^e $P < 0.05$

^f $P < 0.01$

^g $P < 0.005$

^h $P < 0.001$

colonise, forming secondary forest. Fuchs et al. (2003) reported that the composition of the benthic macroinvertebrate community that developed 20–25 years after clear cutting differed from that of old-growth forest, even though the density and biomass did not differ. The NOP cluster consisted of various forest types, and its benthic invertebrate assemblage differed from that in OGF and PCF. In the NOP, sites C and D contained 30% secondary broad-leaved forest, and the PCA ordination placed the benthic invertebrate assemblages of these sites between those of ONF

and PCF. The forest condition of sites C and D would become similar to that of the OGF after >100 years, but would the benthic invertebrate assemblage? There are few old-growth forests left in western Japan. Adults of Ephemeroptera, Plecoptera, and Trichoptera have poor abilities to fly long distances. Thus, only when old-growth forest remains near secondary forest areas, such as at sites C and D, will benthic invertebrates from the old-growth forest be able to colonise the new habitat.

In contrast, what might happen when old-growth forest is converted to planted forest? We found a higher abundance of Taeniopterygidae and Athericidae in the OGF than in the PCF. There are few remaining old-growth forests in western Japan, and the conversion these forests to planted forest may cause the extinction of species that only inhabit old-growth forest.

The numbers of individuals and families were related to the percentage of forest between 25 and 100 years of age. These numbers decreased with the increase in the percentage of 50–100 year-old forest and increased with the increase in the percentage of 25–50 year-old broad-leaved forest. Cole et al. (2003) found that the total density of invertebrates decreased with forest age. In addition, the biomass of benthic invertebrates in a stream that flowed through a newly logged forest was higher than that in a stream that flowed through an old-growth forest or older, logged forests (Fuchs et al. 2003). Old-growth coniferous forest covered almost 90% of site M, and its benthic invertebrate assemblage was similar to that of the OGF cluster sites. Axis 1 of the PCA was positively correlated with the percentage of 25–50 year-old forest and negatively correlated with the percentage of >100 year-old broad-leaved forest. Thus, forest age may be a key factor determining the benthic invertebrate assemblage.

We found that differences in forest composition were correlated with differences in benthic invertebrate assemblages. Leaf litter, stream water quality, and light availability to the stream can differ depending on the forest vegetation. These environmental differences may cause differences in the assemblage of benthic invertebrates. Verification of the effect of forest age on the benthic invertebrate assemblage is required for further clarification of the relationship between the benthic invertebrate assemblage and forest conditions.

Acknowledgements We would like to thank Dr. Maeto for his assistance with sampling survey, Dr. Shigeo Kuramoto and Mr. Atsushi Sakai for their assistance with the riparian vegetation surveys. This work was partly funded by Reaearch grant #200004 of the Forestry and Forest Products Research.

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