1 **Title:** Indirect effects of excessive deer browsing through understory vegetation on

2 stream insect assemblages

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16
17 **Number of text pages:** 23
18 **Number of tables:** 4
19 **Number of figures:** 6
20 **Number of Electronic Supplementary Materials:** 1

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22

23   **Abstract**

24

25   Over the past decade, the abundance of sika deer has rapidly increased around Japan.

26   Previous studies have showed overabundance of deer causes drastic reduction of forest

27   understory vegetation, leading excessive soil erosion. However, no study has

28   investigated the effects of excessive deer browsing on aquatic insect assemblages via

29   sediment runoff. These effects are important to understand whether the terrestrial

30   alteration by deer influences aquatic ecosystems. In a primary deciduous forest

31   catchment in Ashiu, Kyoto, a deer exclusion fence has been in place since 2006. We

32   compared forest floor cover, overland flow, stream environment, and aquatic insect

33   assemblages in first-order streams and catchments inside and outside of the deer-

34   exclosure from May-2008 to April-2009. The floor inside the deer-exclosure catchment

35   was covered by lush understory vegetation, whereas outside was almost bare. The

36   overland flow runoff rate at midslope and the dominancy of fine sediment deposition in

37   the streambed were higher outside than inside. Among aquatic insects, burrowers,

38   which are tolerant against fine sediment deposition, were significantly more abundant

39   outside than inside, whereas clingers exhibited the opposite patterns. Collector-

40   gatherers, which feed on fine detritus, were significantly more abundant outside than

41   inside. Meanwhile, filterers were more abundant inside. The Simpson's diversity index

42   of the aquatic insect assemblages was higher inside than outside. These results suggest

43   that the demise of understory vegetation due to excessive deer browsing has indirectly

44   caused changes in the aquatic insect assemblages of this catchment via increased

45   sediment runoff and subsequent sandy sedimentation of the streambed.

46

Introduction

Deer populations are increasing in many countries due to various factors such as the

extinction of predators, moderation of the winter climate, decreased hunter populations,

and strengthening of game laws (Côté et al. 2004). Increased deer populations can cause

reductions in preferred plants, increases in deer-resistant plants, and declines in plant

diversity (e.g., Fuller and Gill 2001; Gill and Beardall 2001; Rooney 2001; Horsley et

al. 2003; Casabon and Pothier 2008). Population of sika deer (*Cervus nippon*

Temminck) has increased in many places of Japan since 1980s (Miura and Tokida

2008). Excessive sika deer browsing directly affects plant communities by denuding

forest floor vegetation (Takatsuki and Gorai 1994), stripping tree bark and causing tree

death (Akashi and Nakashizuka 1999), damaging shrubby bamboo stands (Yokoyama

and Shibata 1998), seed predation (Asada and Ochiai 1996), and inhibiting tree

regeneration (Nomiya et al. 2003).

Excessive deer browsing can also lead to the devastation of natural vegetation and

the alteration of soils. For example, denuded understory vegetation causes runoff of soil

and litter (Furusawa et al. 2003) as well as changes in the physical properties of forest

soil (Miyashita et al. 2008; Yanagi et al. 2008). Understory vegetation protects soil from

becoming encrusted by the impact of raindrops; thus, understory vegetation sustains the

70   high infiltration capacity of forest soil (Onda and Yukawa 1994; Gomi et al. 2008).

71   Consequently, the denudation of the understory accelerates the discharge of infiltration

72   excess (Hortonian) overland flow, in turn causing soil erosion (Horton 1945; Sidle et al.

73   2007; Gomi et al. 2008). Several previous studies have demonstrated that such soil

74   erosion occurs in areas where understory vegetation has been denuded by excessive

75   deer browsing (Miyashita et al. 2008; Wakahara et al. 2008).

76   Small catchments, which contain first-order streams, are located at the top,

77   precipitous edges of rivers, and are the most active geomorphic development areas in

78   river basins because of erosion and landslides. Therefore, active sediment supply

79   originating from terrestrial slopes in these catchments greatly influences the

80   environmental and ecological systems of first-order streams. Sediment runoff alters not

81   only turbidity but also stream substrates, both of which may affect stream communities

82   (e.g., Rabení and Minshall 1977; Minshall 1988). In headwater systems, riparian forests

83   also influence aquatic insect communities in streams by controlling solar radiation and

84   temperature (Richardson and Danehy 2007); providing litter and cladoptosis, which are

85   sources of food and case materials; and creating multiple habitats through the

86   production of woody debris (Richardson and Danehy 2007). Aquatic insects represent

87   various life form types and functional feeding groups, as they have adapted to diverse

88   stream microhabitats and food resources (Takemon 2005; Merritt et al. 2008). These

89   insects play important roles in sustaining river ecosystems, functioning as decomposers,

90   primary consumers, prey for fish and other predators, and agents transporting organic

91   matter from stream to terrestrial ecosystems (Covich et al. 1999). Because aquatic insect

92   communities are vulnerable to various environmental changes, the status of these

93   organisms is often used as an index of river health (e.g., Robinson and Minshall 1986;

94   Zweig and Rabeni 2001; Rainbow 2002; Heino et al. 2003; Matthaei et al. 2006;

95   Yoshimura 2007).

96   As noted above, excessive deer browsing accelerates soil erosion in small forested

97   catchments. In this study, we examined whether such consequences of deer browsing

98   affect aquatic insect communities. To test this question, we compared forest floor cover,

99   overland flow, stream environment, and aquatic insect assemblages inside and outside

100   of a deer exclosure in a cool–temperate primary forest in Japan. We then discuss the

101   effects of excessive deer browsing on aquatic insect assemblages in first-order streams.

102

103   **Materials and methods**

104

105   Study site

106

107   This study was conducted in the first-order streams of the Yura River at the Ashiu

108   Forest Research Station, Field Science Education and Research Center, Kyoto

109   University (35°20'N, 135°45'E; Fig. 1). Average annual precipitation and temperature

110   were 2,298 mm and 11.9°C, respectively, from 1976 to 2005 at the Ashiu Research

111   Station. Maximum snow depth in winter exceeds over 2 m around the study site, and the

112   ground is covered with snow from mid-December to early April. The geological

113   components of the area are sandstone, mudstone, and shale of the Tanba Belt of the

114   Mesozoic. Most of the soil is brown forest soil.

115   Excessive deer browsing has become a serious problem at the study site since the late

116   1990s (Tanaka et al. 2008) and has caused drastic decreases in the abundance and

117   diversity of understory plants (Kato and Okuyama 2004). Resent minimum-maximum

118   population density of deer in the study site, estimated by block count during two days in

119   December, were; 2.30-4.21 (2006), 0.00-5.30 (2007), 1.15-5.75 (2008), 0.00-5.75

120   (2009), 4.60-13.80 indv. / km^2 (2010) (A. Takayanagi, unpublished data). A catchment

121   in the natural deciduous forest (area: 1.15 ha) has been fenced to exclude deer since

122   2006 (Fig. 1). The 2.5-m-high fence is constructed of poles and nets. No deer had

123   invaded inside the fence during the study period according to monthly fence

124   maintenance and visual survey of deer browsing scar along the fence (A. Takayanagi,

125   unpublished data). Understory vegetation in the exclosure catchment had recovered well

126   by 2008, whereas vegetation outside the exclosure has remained almost denuded.

127   Outside the deer exclosure in a neighboring valley, we selected a control catchment

128   (area: 1.66 ha) (Fig. 1). The plant community structures at the exclosure and control

129   catchments had been very similar at the start of deer exclusion (Sakaguchi et al. 2008),

130   and water temperature and quality in the streams at each catchment were almost same

131   (Table 1 and Fukushima and Tokuchi 2008). To clarify the indirect effects of excessive

132   deer browsing on aquatic insect assemblages as much as possible, the selected two

133   catchments were adjoining and have topographically similar streams in the same way of

134   the antecedent control experiments (e.g., Allan 1982; Christopher and Minshall 1986;

135   Matthaei et al. 2006). We compared forest floor cover, overland flow, environmental

136   stream characteristics, light conditions, periphyton abundance, and aquatic insect

137   assemblages between the exclosure and control catchments (EC and CC, respectively).

138   The first-order streams in each catchment contain permanent water. Both catchments

139   are covered by primary cool–temperate deciduous forests dominated by *Aesculus*

140   *turbinate* Blume, *Quercus crispula* Blume, *Fagus crenata* Blume, *Clethra barbinervis*

141   Sieb. et Zucc., *Acer palmatum* subsp. *matsumurae* (Koidz) Ogata, *Pterocarya rhoifolia*

142   Sieb. et Zucc., and *Cryptomeria japonica* var. *radicans* Nakai.

143

144   Forest floor cover and overland flow

145

146   One belt transect (1 m wide) from the valley floor to 30 m up the upper slope was

147   established on the left bank of each catchment. The belt transect, which was oriented to

148   include representative vegetation of each catchment, was divided into fifteen 1 × 2 m

149   plots, and coverage of understory vegetation in every plot was recorded by visual

150   observation. Then, abundance and number of understory plant species in the belt

151   transect was also recorded. The survey was conducted in June and August 2008.

152   To evaluate the quantity of litter in each catchment, we collected litter in four

153   randomly selected quadrats along the downhill slopes of each catchment in August and

154   November 2009. Collected litter was dried at 60°C for 24 h and then weighed.

155   Runoff plots (0.5 × 2.0 m) were established at the midslopes of each catchment.

156   Plastic borders were inserted about 5 cm into the soil along all sides of the plots, and a

157   trough was inserted several centimeters into the soil (parallel to the slope direction) to

158   collect storm runoff. Runoff from these plots was routed to a rain gauge (Davis

159   Instruments, Rain Collector II) to estimate discharge per 5 min (Fig. 1). Precipitation

160   was measured by a rain gauge (Davis Instruments, Rain Collector II) situated in an open

161   area (Fig. 1). Overland flow and precipitation were monitored from June to November

162   2009. We defined rainfall event as rainfalls whose total precipitations were more than

163   10 mm and there is no rain during at least 3 h before and after the rainfall. In addition,

164   we classified rainfall event into three types (1) intermissive, (2) continual and (3) one-

165 peak rainfall events. If a rainfall event has over 15-min-intermission of rainfall more

166 than four times, we regard the rainfall event as intermissive rainfall event. If a rainfall

167 event continues with no intermission above noted, and has more than one peak, the

168 rainfall event is regarded as continual rainfall event. If the rainfall has only one peak,

169 the rainfall is regarded as one-peak rainfall event.

170

171 Aquatic insects

172

173 Four quadrats were set with a surber net (25×25 cm, 0.5-mm-mesh sieve) in the

174 streams in each catchment. Each sampling point was located over at least a 50-cm-wide

175 stretch of the streams, at locations where some very coarse gravel was distributed.

176 Sediments with benthic animals in each quadrat were collected into the surber net, and

177 as many animals as possible were collected after being placed into white vats.

178 Collections were conducted every month from May to November 2008 and in April

179 2009. Collected animals were preserved immediately in 70% ethanol. Aquatic insects

180 were separated out and classified using a stereomicroscope (Nikon SMZ800) following

181 Kawai and Tanida (2005) and Merritt et al. (2008). Because all identified taxa were not

182 classified to species, the number of species was underestimated. Identified aquatic

183 insects were sorted by life form type (swimmers, crawlers, clingers, or burrowers) and

184 functional feeding group (shredders, filterers, collector–gatherers, predators, or grazers)

185 based on Takemon (2005) and Merritt et al. (2008).

186   In general, aquatic insect distribution is ultimately structured by physical-chemical

187 tolerance of individuals in the population (Cummins et al. 2008), and fecundity of

188 aquatic insects is precisely determined by temperature (Vannote and Sweeny 1980;

189   Rader and Ward 1990). Individuals of aquatic insects are distributed following their

190   optimal temperature regime along a thermal gradient related to altitude. Therefore, we

191   regarded aquatic insect assemblages in the EC and CC before the start of deer exclusion

192   in 2006 as very similar structures because of their physical (Table 1 and Fig. 1),

193   chemical (Fukushima and Tokuchi 2008) and thermal similarities (Table 1).

194

195   Environmental characteristics of the streams

196

197   The water depth in each quadrat was calculated by averaging the depths at six points in

198   each quadrat. Current velocity at the center of each quadrat was calculated by averaging

199   three averages of repeated 5-s measurements using a current meter (Kenek, VE10).

200   We used visual estimation and grain size test to evaluate streambed characteristics.

201   To evaluate the stream substrate, photographs were taken from 50 cm above the

202   streambed in each quadrat. The proportion of fine sediment in each quadrat was

203   calculated using Adobe Photoshop Elements, version 5.0. Randomly shoveled three

204   1000 ml stream substrates were sieved into eleven grain sizes: 63, 31.5, 16, 8, 4, 2, 1,

205   0.5, 0.25, 0.125, and 0.063 mm, and dried at 105°C for 24 h and weighed. These

206   surveys were conducted in August, September, and October 2008 except grain size test,

207   which was conducted in December 2010. We monitored the water temperature in the

208   terminal point of each catchment from April 2010 to November 2010 per 5 min using

209   thermometer (Trutrack, SE-TR/WT500).

210

211   Light conditions

212

213   Hemispherical photographs were taken around the quadrats in each catchment in August

214   2008 and April 2009 to determine the light conditions above each streambed. The first

215   photographs were taken in the terminal area of each catchment, and the last five were

216   taken about 6 m from the previous point. Photographs were taken with a digital camera

217   (Nikon E995) equipped with a fish-eye lens (Nikon FC-E8) that was fixed horizontally

218   at 1 m above the streambed. Relative solar radiation from May to October 2008 was

219   calculated as a measure of light conditions in the growing season using photographs

220   taken in August. Values from November 2008 to April 2009 were calculated as light

221   conditions in the fall using photographs taken in April. Solar radiation was estimated

222   from photographs using Gap Light Analyzer version 2.0. Magnetic north was set at a

223   declination of 7.20° west. The radiation component was set as the default value.

224

225   Periphyton

226

227   Four submerged rocks were randomly collected from around the quadrats in each

228   catchment in August, September, and October 2008. Periphyton was collected by

229   brushing 4 cm^2 of the upper surface of each rock and filtering the water through glass

230   microfiber filters (Whatman GF/F). These samples were ground in 90% acetone and

231   then centrifugally separated (Hitachi CF16RXII) after being dried and frozen. The

232   absorbance of the periphyton samples was measured at 750, 664, 647, and 630 nm

233   (Hitachi U-1800). The amount of chlorophyll a was calculated by substituting the

234   measured values into the formula of Jeffrey and Humphrey (1975).

235

236   Statistical analyses

237

238   *T* tests were used to determine the differences between the EC and CC in the coverage

239   of understory vegetation, amount of litter, water temperature, water depth, current

240   velocity, proportion of fine sediment, relative solar radiation, and periphyton

241   abundance. The values of coverage of understory vegetation and proportion of fine

242   sediment were arcsine-transformed to normalize distributions and standardize variance

243   structures.

244   To test for differences in aquatic insect variables between the EC and CC, a two-way

245   analysis of variance (ANOVA) was performed using streams ($n = 2$) and sampling

246   month ($n = 8$) as factors. For ANOVAs with significant effects, multiple mean

247   comparisons were made using Tukey's test. Abundance data were log-transformed to

248   normalize distributions and standardize variance structures following Yamamura (1999)

249   prior to statistical analyses.

250

251   **Results**

252

253   Forest floor cover and overland flow

254

255   Vegetation cover on the hillslope was higher in the exclosure catchment (EC) than in

256   the control catchment (CC) (Table 1 and Fig. 2), where understory vegetation was

257   almost denuded and the soil was exposed in a large area (Fig. 2). The number of

258   understory plant species was higher in the EC (82 species) than in the CC (31 species).

259   Preferred plant species for deer were more abundant in the EC than in the CC whereas

260   unpreferred species were commonly distributed both in the catchments (S1 in the

261   Electronic Supplementary Material, ESM). The abundances of some unpreferred plant

262   species such as *Dennstaedtia scabra* (Wall. ex. Hook.) Moore and *Shortia uniflora* var.

263   *kantoensis* Yamazaki were higher in the CC than in the EC (S1 in the ESM). There were

264   16 intermissive, 12 continual and 8 one-peak rainfall events during the monitoring

265   period. Total runoff of overland flow during the representative rainfall event was lower

266   in the EC compared to the CC for all three types of rainfall events (Fig. 3). In particular,

267   the overland flow hydrographs at the CC were sharply peaked during intermissive and

268   one-peak rainfall events. Runoff rate of overland flow during entire of the motoring

269   period (i.e., runoff / precipitation) was 4.10% and 1.55% in the CC and EC respectively.

270   Thus, overland flow discharge was about 2.65 times greater in the CC than in the EC.

271

272   Environmental characteristics of the streams

273

274   Water depth, current velocity, and relative solar radiation were relatively similar

275   between the EC and CC (Table 1). However, the proportion of fine sediment in the

276   streambed was significantly higher in the CC than in the EC (Table 1), and the grain

277   size of particles was biased to small in the CC in comparison with that the EC (Fig. 4).

278   The effective grain size (D_{50}) was larger in the EC than in the CC (10.3 mm vs. 6.0 mm,

279   respectively).

280   Although we did not detect a significant difference in periphyton abundance between

281   the two catchments, the average quantity of periphyton was higher in the EC than in the

282   CC (Table 1).

283

284   Aquatic insects

285

286   A total of nine orders, 52 families, 75 genera, 111 species, and 3,311 individuals of

287   aquatic insects were collected during our surber-net samplings.

288   The number of species was higher in the EC than in the CC in May, June, November

289   and April (Fig. 5). The Simpson's diversity index was relatively higher in the EC than

290   in the CC in all sampling months (Fig. 5). In terms of aquatic insects classified by life

291   form type, the abundance of burrowers was significantly lower in the EC than in the

292   CC, whereas the abundance of clingers was significantly higher in the EC (Table 2 and

293   Fig. 6). In terms of insects classified by functional feeding group, the abundance of

294   collector–gatherers was significantly lower in the EC than in the CC, whereas the

295   abundance of filterers was significantly higher in the EC (Table 2 and Fig. 6). The

296   abundance of shredders was significantly different among sampling months in the EC

297   and CC (Table 2 and Fig. 6). Overall samples of all months in the EC contained more

298   species of Ephemeroptera and Trichoptera than those in the CC (Table 3). The

299   proportion of the five most dominant species was lower in the EC (38.7%) than in the

300   CC (43.9%) (Table 4).

301

302   **Discussion**

303

304   Although the plant community structure at the EC and CC was very similar at the start

305   of deer exclusion in the EC (Sakaguchi et al. 2008), diverse and abundant understory

306   vegetation has recovered in the EC, whereas the forest floor has remained nearly bare

307   outside the exclosure, including the CC (Table 1, Fig. 2). The unpreferred plant species

308   for deer were commonly distributed both in the EC and CC, and the abundances of such

309 plant species were relatively higher in the CC than in the EC (S1 in the ESM). These

310 results suggest that the great differences in coverage and species richness of understory

311 vegetation between the EC and CC were caused by excessive deer browsing.

312   Forest floor cover, such as understory vegetation and litter, protects the soil

313 infiltration capacity against raindrop impact (Onda and Yukawa 1994; Gomi et al. 2008)

314 and prevents overland flow from discharging (Sidle et al. 2007; Gomi et al. 2008). In

315 this study, lush understory vegetation in the EC buffered the runoff of overland flow,

316 whereas overland flow hydrographs in the CC exhibited large peaks after intermissive

317 or one-peak rainfall events (Fig. 3). The total runoff of overland flow during all three

318 types of rainfall events was lower in the EC than in the CC (Fig. 3). Because understory

319 vegetation is a good predictor of soil erosion potential (e.g., Lyon and Sagers 1998;

320 Wear et al. 1998; Heartsill-Scalley and Aide 2003), these results suggest that lush

321 understory vegetation prevents sediment runoff and soil erosion by recharging soil

322 infiltration capacity and consequently reducing overland flow. Although current

323 velocity did not differ significantly between the EC and CC, the proportion of fine

324 sediment was significantly lower in the EC (Table 1), and the grain size of particles was

325 biased to small in the CC in comparison with that the EC (Fig. 4). These findings

326 suggest that soil erosion on the denuded slope caused increased sedimentation of fine

327 particles such as sand. In terms of the turbidity index, the abundance of periphyton was

328 higher in the EC than in the CC (Table 1). Increases in light intensity are well known to

329 cause increases in the quantity of periphyton (e.g., Hill and Harvey 1990; Wootton and

330 Power 1993). The higher growth rate of periphyton in the EC can be attributed to less

331 inflow of turbid water containing suspended sediment and to increases in light intensity

332 in the stream water (Yamada and Nakamura 2002), because of no difference in light

333   condition (Table 1). These results suggest that the diffused fine sediment and lower

334   abundance of periphyton in the CC resulted from active sediment runoff via soil erosion

335   caused by excessive deer browsing of understory vegetation.

336   Differences in fluvial environments caused by presence or absence of deer browsing

337   are expected to alter aquatic insect assemblages. Deposited sediment is considered a

338   good quantifiable stressor for examining the functional responses of aquatic insects

339   (Waters 1995). Several studies have demonstrated the effects of fine particles that fill

340   the interstices of substrates or cover surfaces of aquatic insect habitats (e.g., Chutter

341   1969; Rabení and Minshall 1977; Minshall 1988; Wood and Armitage 1997; Zweig and

342   Rabení 2001; Rabení et al. 2005).

343   In this study, the Simpson's diversity index was greater in the EC than in the CC

344   among all sampling months (Fig. 5). Overall samplings contained more species in the

345   EC than in the CC (Table 3). The insect assemblage in the CC was characterized by the

346   dominance of sediment-burrowing ephemeropterans (e.g., *Ephemera japonica*

347   McLachlan and *Paraleptophlebia japonica* Matsumura) and dipterans (chironomid

348   midges of Orthocladiinae) (Table 4). In contrast, the assemblage in the EC was

349   dominated by crawling plecopterans (e.g., *Nemoura* spp. and *Togoperla* sp.). All of the

350   dominant sediment-burrowing taxa in the CC were collector–gatherers. Several studies

351   have reported decreases in species richness caused by increases in fine sediment

352   deposition (Zweig and Rabení 2001; Rabení et al. 2005). Our results also suggest that

353   fine sediment deposition of the streambed causes reductions in the diversity of aquatic

354   insect assemblages.

355   In terms of the life form types of aquatic insects, the abundance of burrowers was

356   significantly higher in the CC than in the EC (Table 2 and Fig. 6). In contrast, the

357   abundance of clingers was significantly lower in the CC than in the EC, suggesting that

358   gravelly substrates were less common in the CC due to sedimentation. In general, a

359   relative tolerance to the deposition of fine sediment (< 2 mm in diameter) is strongest

360   in burrowers, followed by climbers, sprawlers (crawlers), swimmers, and clingers

361   (Rabení et al. 2005). The high abundance of burrowers and the low abundance of

362   clingers in the CC corresponded to the dominance of sandy sedimental environments

363   (Table 1 and Fig. 4). In contrast, the high abundances of clingers and the low abundance

364   of burrowers in the EC corresponded to the presence of gravelly sedimental

365   environments (Table 1 and Fig. 4).

366   In terms of the functional feeding groups of aquatic insects, the abundance of

367   collector–gatherers was significantly higher in the CC than in the EC, whereas that of

368   filterers was significantly smaller in the CC (Table 2 and Fig. 6). In general, a relative

369   tolerance to the deposition of fine sediment is strongest in shredders, followed by

370   collector–gatherers, predators, grazers, and filterers (Rabení et al. 2005). Our results

371   suggest that the high abundance of collector–gatherers and the low abundance of

372   filterers in the CC corresponded to increased fine particles deposition supplied from

373   terrestrial slopes and increased overland flow.

374   In conclusion, our comparisons of aquatic insect assemblages and stream

375   environments at sites inside and outside of a deer exclosure indicate that excessive deer

376   browsing of understory vegetation causes increased overland flow and sandy

377   sedimentation of the streambed, consequently altering aquatic insect assemblages. This

378   indirect effect of deer on aquatic insects shows unexpectedly extensive effects of deer as

379   an ecosystem engineer. Deer can alter not only a terrestrial ecosystem which they

380   belong to, but also stream assemblages outside their original ecosystem.

381

Acknowledgements

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Table 1 Comparisons of average values of eleven environmental characteristics between the exclosure and control catchments. Differences between the catchments in coverage of understory vegetaion, quantitiy of litter, water temperature, water depth, current velocity, proportion of fine sediment, relative solar radiation and periphyton abundance were tested using *t* test. Values are means ± standard deviation.

	Exclosure catchment	Control catchment
Catchment area (ha)	1.15	1.66
Deer invasion	Deer excluded	Invasion frequent
Forest type	Deciduous forest	Deciduous forest
Coverage of understory vegetation (%)	45.40 ± 29.36**	18.20 ± 12.60**
Quantity of litter (g): August	79.75 ± 24.55	47.54 ± 23.51
: November	74.25 ± 35.28	124.25 ± 25.90
Water temperature (°C)	14.70 ± 4.04	14.66 ± 4.05
Water depth (cm)	2.35 ± 1.76**	3.25 ± 1.65**
Current velocity (cm s^{-1})	4.34 ± 2.72	4.82 ± 2.75
Proportion of fine sediment (%)	18.10 ± 7.86**	36.99 ± 9.37**
Relative solar radiation (%): August	19.31 ± 6.88*	12.58 ± 2.2*
: November	38.01 ± 6.82	40.70 ± 7.67
Periphyton abundance (mg chl.*a* 4cm^{-2})	32.09 ± 19.76	7.45 ± 2.52

The same letters indicate significant differences (*$P<0.05$, **$P<0.01$).

Table 2 Results of ANOVAs testing for effects of site and month on abundances of each aquatic insect group.

	Site		Month		Site × month	
	F	*P*	*F*	*P*	*F*	*P*
Burrowers	14.481	**<0.001**	1.864	0.097	1.456	0.206
Clingers	8.869	**0.005**	0.585	0.765	0.843	0.558
Crawlers	3.522	0.068	1.413	0.222	2.128	0.058
Swimmers	0.015	0.902	1.779	0.113	1.264	0.288
Collector-gatherers	12.033	**0.001**	2.026	0.071	1.615	0.154
Filterers	6.288	**0.016**	0.668	0.698	0.809	0.584
Grazers	0.014	0.906	0.841	0.559	1.849	0.099
Predators	2.494	0.121	1.603	0.157	1.192	0.325
Shredders	3.265	0.077	3.535	**0.004**	1.556	0.172

Bold characters indicate significant differences ($P < 0.05$)

Table 3 Richness and abundance of aquatic insect of overall samples in all months in each order in each catchment.

Order	Exclosure catchment		Control catchment	
	Taxa	Indv.	Taxa	Indv.
Ephemeroptera	17	339	12	610
Odonata	7	13	8	39
Plecoptera	14	462	11	464
Coleoptera	5	77	6	49
Diptera	25	239	25	549
Trichoptera	19	206	14	231
Others	5	16	2	17
Total	92	1,352	75	1,959

Table 4 Dominant species of aquatic insect assemblages of overall samples in all months in each catchment. E, P and D in order row correspond to Ephemeroptera, Plecoptera and Diptera respectively.

Rank	Site	Order	Life form type	Feeding group	Indv.	Proportion
	Exclosure catchment					
1	*Ephemera japonica*	E	Burrower	Collector-gatherer	129	9.5%
2	*Nemoura* spp.	P	Crawler	Shredder	123	9.1%
3	*Togoperla* sp.	P	Crawler	Predator	110	8.1%
4	*Caroperla* sp.	P	Crawler	Predator	82	6.0%
5	*Paraleptophlebia japonica*	E	Burrower	Collector-gatherer	81	6.0%
					Total	38.7%
	Control catchment					
1	*Ephemera japonica*	E	Burrower	Collector-gatherer	298	15.2%
2	*Caroperla* sp.	P	Crawler	Predator	156	8.0%
3	*Paraleptophlebia japonica*	E	Burrower	Collector-gatherer	149	7.6%
4	*Nemoura* spp.	P	Crawler	Shredder	138	7.0%
5	Orthocladiinae spp.	D	Burrower	Collector-gatherer	120	6.1%
					Total	43.9%

529

530   **Figure Legends**

531   **Fig. 1** The study site in the Ashiu Forest, Kyoto Prefecture, Japan.

532   **Fig. 2** Landscapes at (**a**) the exclosure catchment (EC) and (**b**) the control catchment

533   (CC) on 28 June 2008.

534   **Fig. 3** Representative overland flow hydrographs (mm / 5 min) at the exclosure and

535   control catchments.

536   **Fig. 4** Grain size distribution of stream substrate at the exclosure and control

537   catchments. Error bars indicate $\pm$ standard deviation.

538   **Fig. 5** Number of species and Simpson's diversity index in each sampling month at the

539   exclosure and control catchments. Error bars indicate $\pm$ standard deviation.

540   **Fig. 6** Abundances of four life form types and five functional feeding groups of aquatic

541   insects in each sampling month at the exclosure and control catchments. Error bars

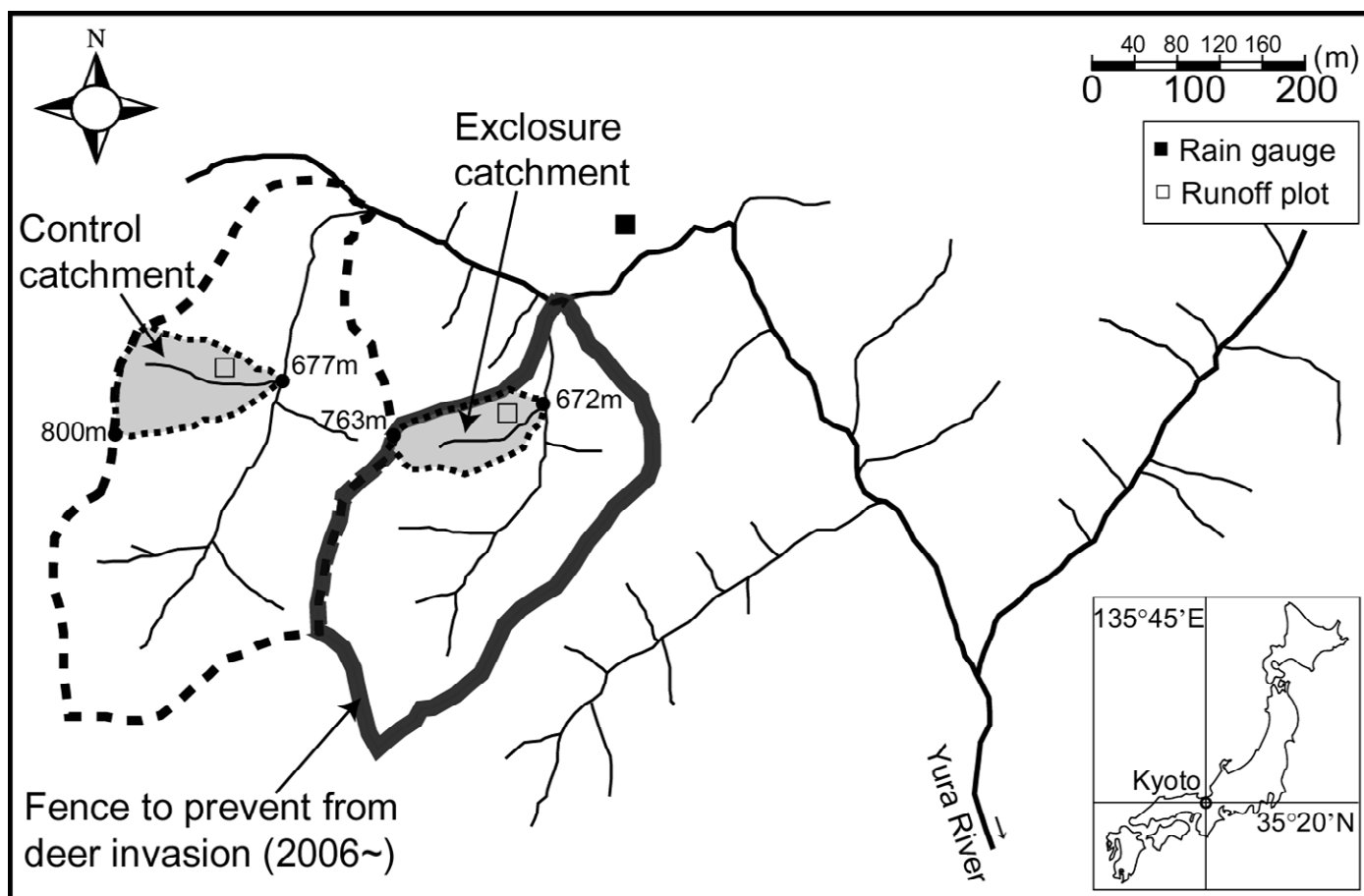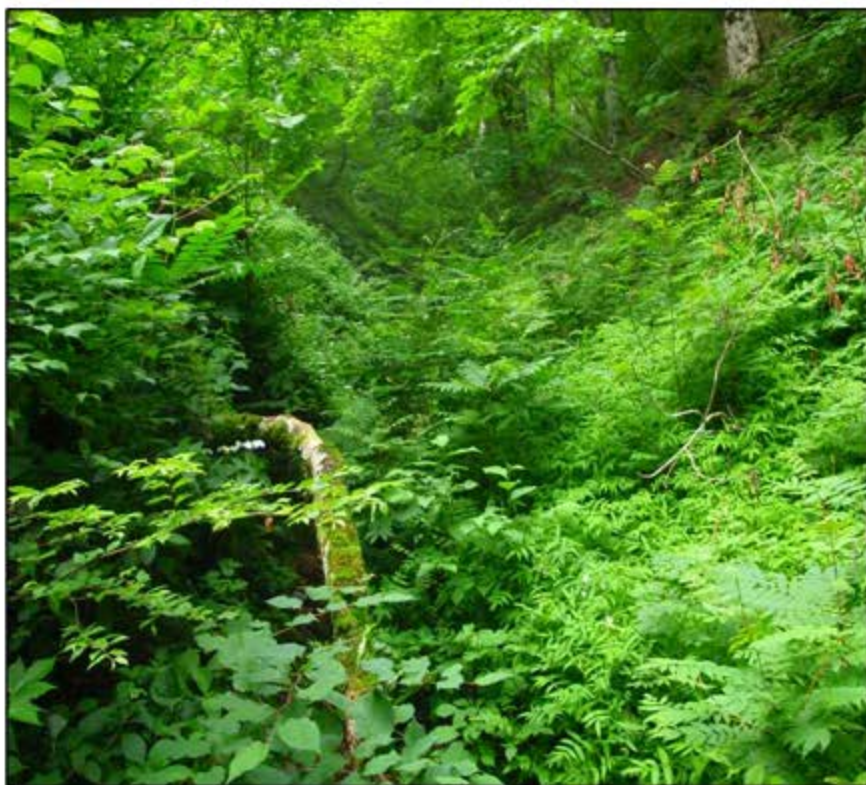542   indicate $\pm$ standard deviation.

Fig. 1

Fig. 2

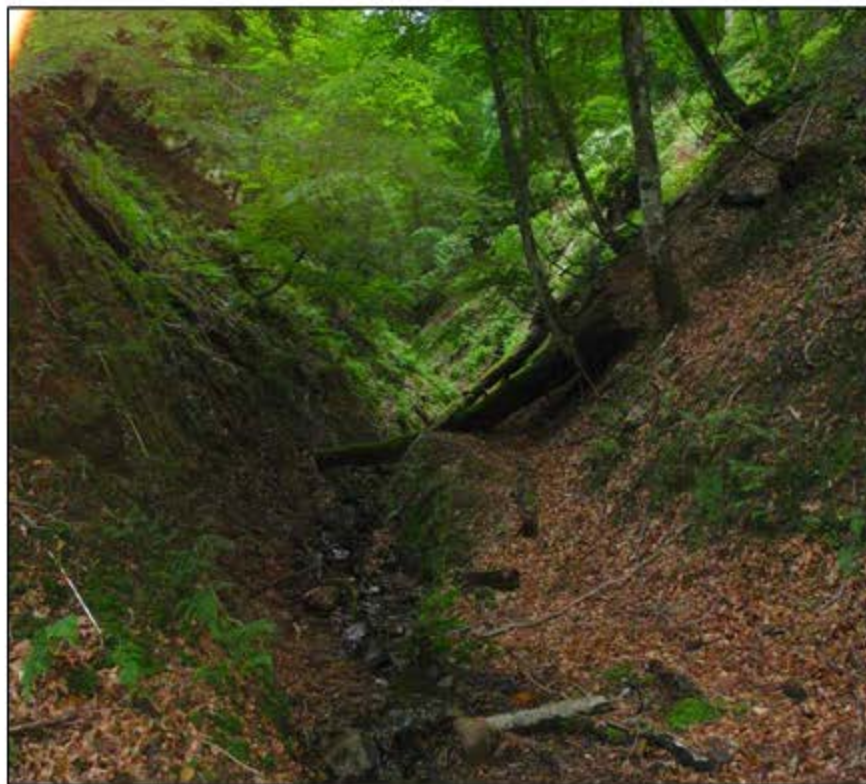## (a) Exclosure catchment (EC)
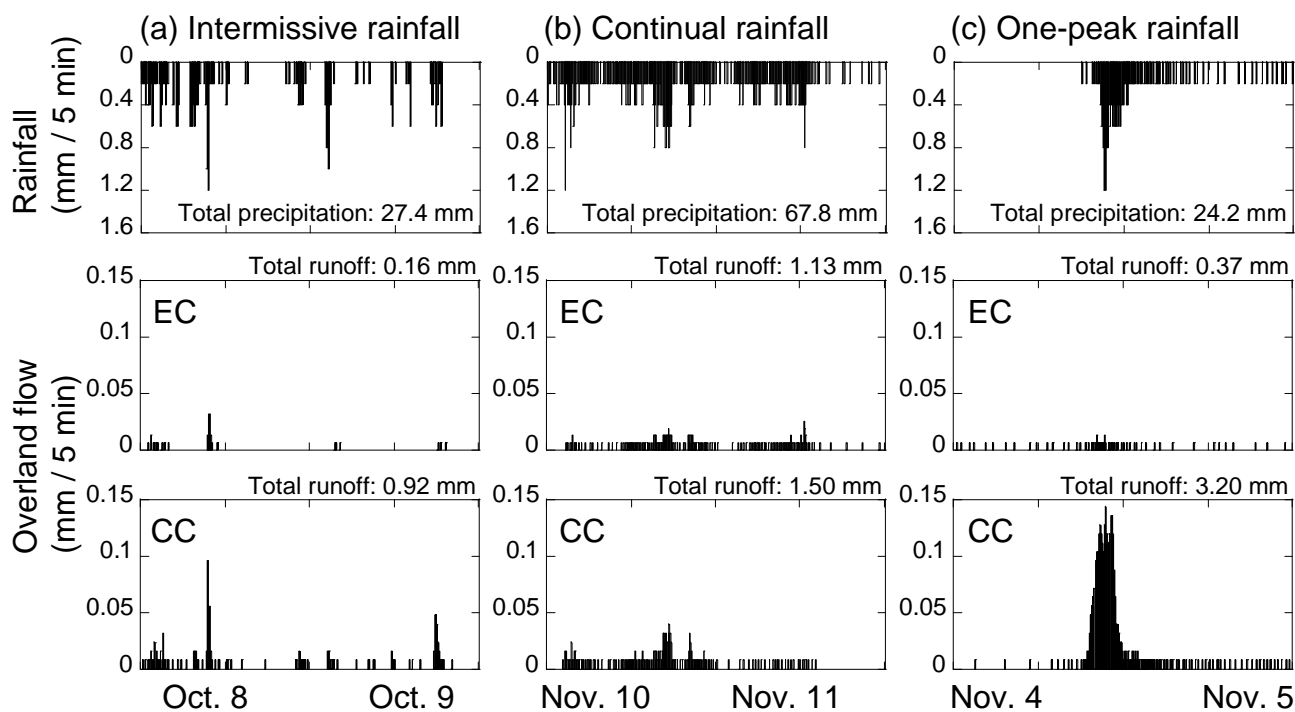

(b) Control catchment (CC)

Fig. 3

(a) Intermissive rainfall

(b) Continual rainfall

(c) One-peak rainfall

Rainfall (mm / 5 min)

Overland flow (mm / 5 min)

Total precipitation: 27.4 mm

Total precipitation: 67.8 mm

Total precipitation: 24.2 mm

Total runoff: 0.16 mm

Total runoff: 1.13 mm

Total runoff: 0.37 mm

EC

EC

EC

Total runoff: 0.92 mm

Total runoff: 1.50 mm

Total runoff: 3.20 mm

CC

CC

CC

Oct. 8   Oct. 9

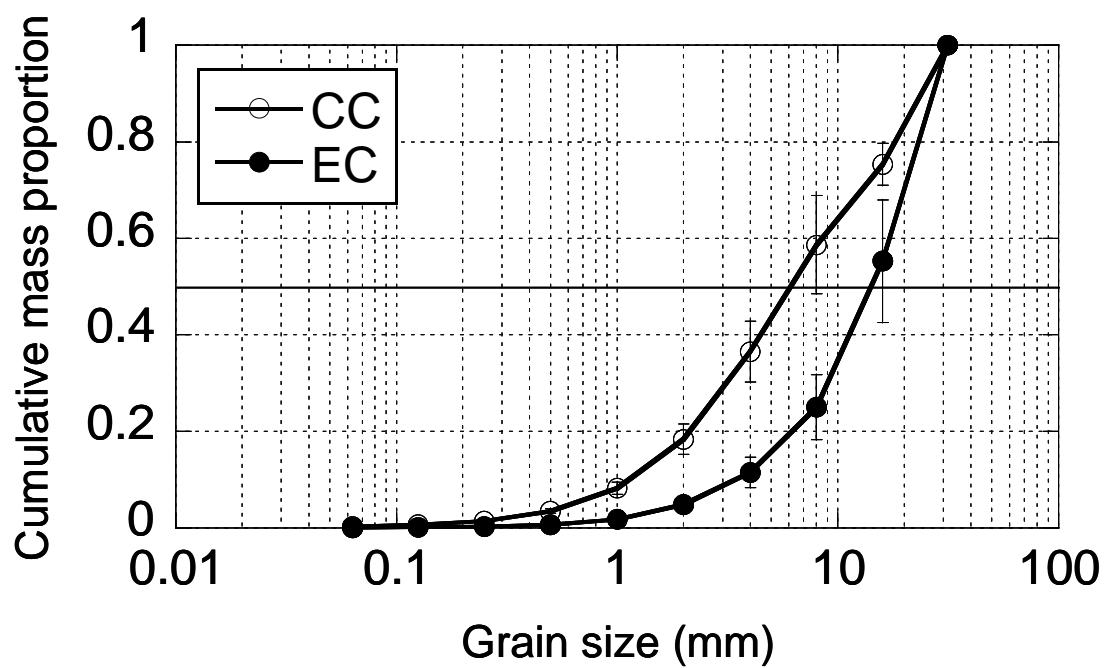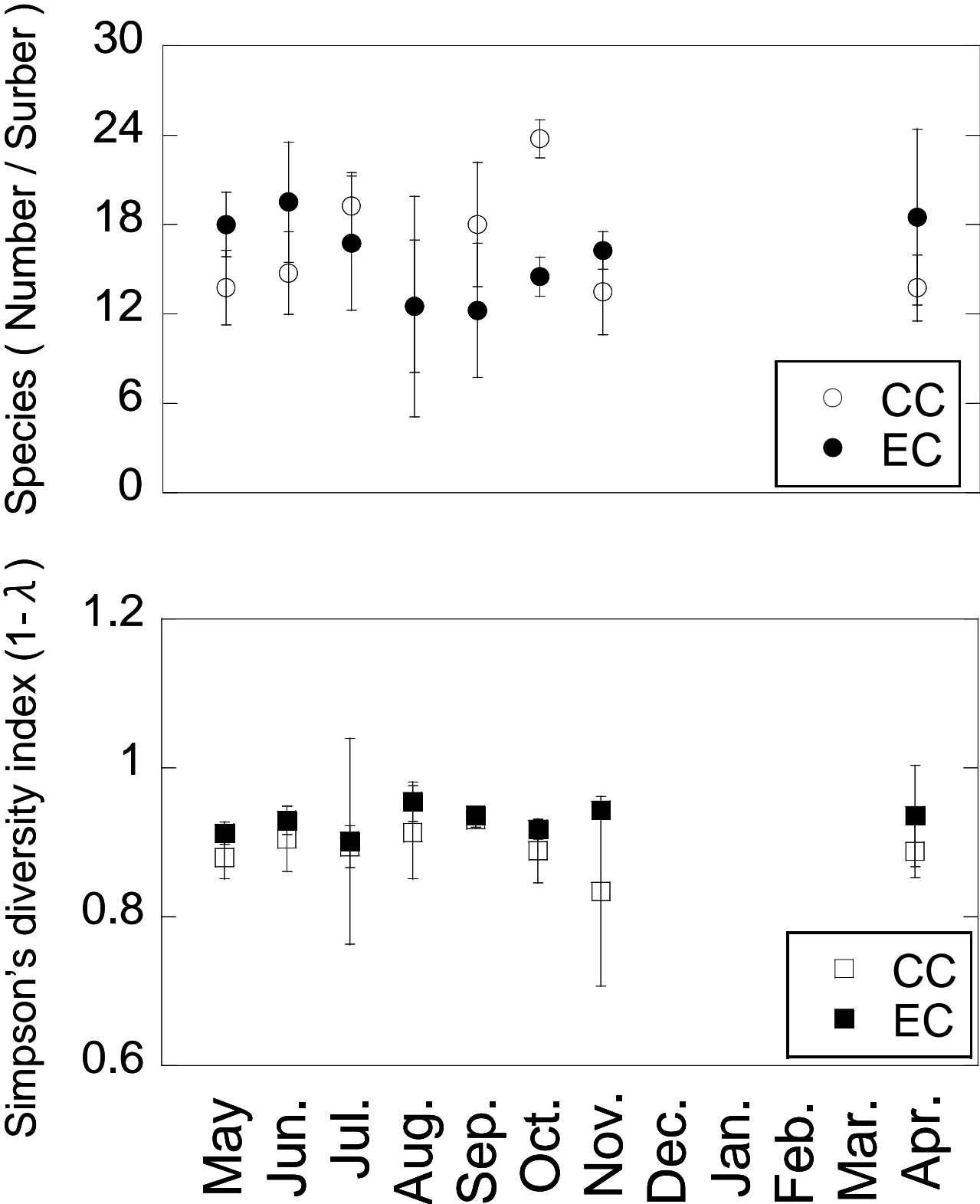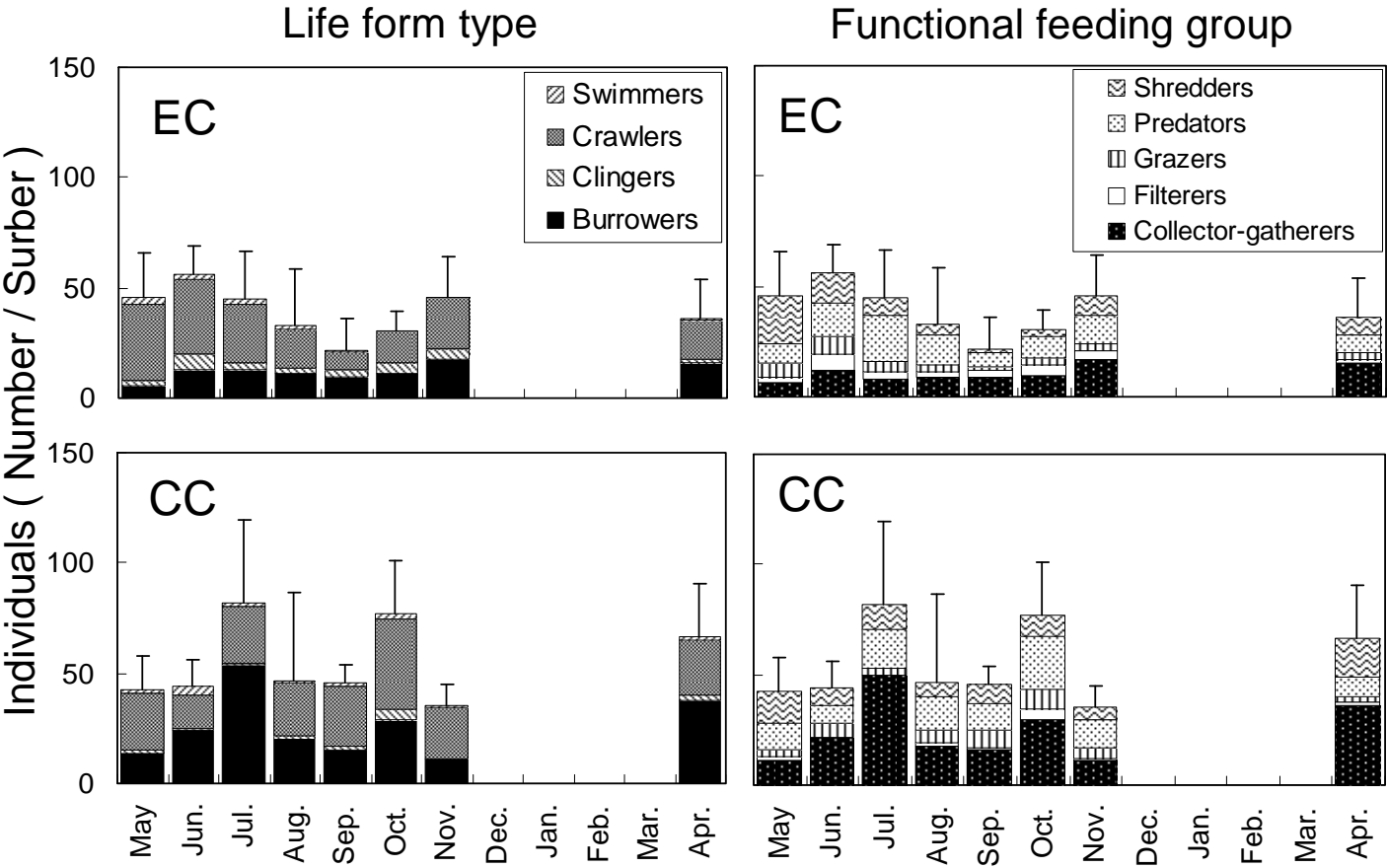Nov. 10   Nov. 11

Nov. 4   Nov. 5

Fig. 4

Fig. 5

Fig. 6

Title: Indirect effects of excessive deer browsing through understory vegetation on stream insect assemblages.

Authors: Masaru Sakai, Yosihiro Natuhara, Ayumi Imanishi, Kensuke Imai, Makoto Kato

ESM_S1 Coverage of understory plant species at the exclosure catchment and control catchment in the belt transect survey.

Family	Plant species	Life form[1]	Deer herbivory[2]	Coverage[3] EC	Coverage[3] CC
Lycopodiaceae	Lycopodium serratum	P	-	1	-
Aspleniaceae	Asplenium sarelii	P	+	-	1
Blechnaceae	Blechnum nipponicum	P	+	1	1
Dennstaedtiaceae	Dennstaedtia scabra	P	-	1	2
Dryopteridaceae	Arachniodes standishii	P	+	-	-
Dryopteridaceae	Polystichum tripteron	P	+	1	1
Plagiogyriaceae	Plagiogyria matsumureana	P	+	1	-
Thelypteridaceae	Stegnogramma pozoi	P	+	1	-
Woodsiaceae	Athyrium clivicola	E	+	1	1
Woodsiaceae	Athyrium vidalii	P	+	1	1
Cephalotaxaceae	Cephalotaxus harringtonia var. nana	S	+	-	-
Taxodiaceae	Cryptomeria japonica var. radicans	T	+	1	1
Cyperaceae	Carex dolichostachya	P	+	1	-
Cyperaceae	Carex japonica	P	+	1	-
Dioscoreaceae	Dioscorea japonica	V	+	-	-
Liliaceae	Disporum smilacinum	P	+	1	-
Liliaceae	Polygonatum sp.	P	+	1	-
Liliaceae	Smilax riparia var. ussuriensis	P	+	1	-
Orchidaceae	Calanthe reflexa	P	+	1	-
Juglandaceae	Pterocarya rhoifolia	T	+	1	1
Betulaceae	Betula grossa	T	+	1	1
Betulaceae	Carpinus japonica	T	+	1	-
Betulaceae	Carpinus laxiflora	T	+	1	1
Fagaceae	Castanea crenata	T	+	1	-
Fagaceae	Fagus crenata	T	+	1	1
Fagaceae	Fagus japonica	T	+	1	-
Fagaceae	Quercus crispula	T	+	1	1
Urticaceae	Elatostema umbellatum var. majus	P	+	1	-
Polygonaceae	Polygonum thunbergii	A	+	1	1
Polygonaceae	Fallopia japonica	P	+	2	-
Magnoliaceae	Magnolia salicifolia	T	+	2	1
Lauraceae	Lindera erythrocarpa	T	+	1	1
Lauraceae	Lindera umbellata var. umbellata	S	+	1	-
Theaceae	Eurya japonica	S	+	1	-
Hamamelidaceae	Hamamelis japonica var. obtusata	T	+	1	-
Saxifragaceae	Astilbe thunbergii	P	+	1	-
Hydrangeaceae	Hydrangea hirta	S	+	2	-
Hydrangeaceae	Hydrangea paniculata	S	+	2	1
Hydrangeaceae	Schizophragma hydrangeoides	L	+	1	1
Rosaceae	Pourthiaea villosa	S	+	1	-
Rosaceae	Padus grayana	T	+	1	-
Rosaceae	Prunus incisa ssp. kinkiensis	T	+	1	1
Rosaceae	Rubus crataegifolius	S	+	1	-
Rosaceae	Rubus illecebrosus	S	+	2	-
Rosaceae	Rubus palmatus var. palmatus	S	+	1	1
Oxalidaceae	Oxalis griffithii	P	+	1	1
Anacardiaceae	Rhus ambigua	L	+	1	1
Anacardiaceae	Rhus trichocarpa	T	+	1	1
Aceraceae	Acer amoenum var. matsumurae	T	+	1	1
Aceraceae	Acer micranthum	T	+	1	1
Aceraceae	Acer mono	T	+	1	-
Aceraceae	Acer rufinerve	T	+	1	1
Aquifoliaceae	Ilex crenata var. paludosa	S	+	1	1
Aquifoliaceae	Ilex pedunclosa	T	-	1	1
Celastraceae	Celastrus orbiculatus	L	+	1	1
Vitaceae	Ampelopsis glandulosa var. heterophylla	V	+	1	-
Violaceae	Viola grypoceras	P	+	1	-
Onagraceae	Circaea erubescens	P	+	1	-
Cornaceae	Aucuba japonica var. borealis	S	+	1	-
Cornaceae	Swida controversa	T	+	1	-
Araliaceae	Eleutherococcus sciadophylloides	S	+	1	-
Araliaceae	Aralia elata	S	+	1	-
Araliaceae	Evodiopanax innovans	T	+	1	1
Apiaceae	Hydrocotyle maritima	P	+	1	-
Diapensiaceae	Schizocodon soldanelloides var. magnus	P	-	-	-
Diapensiaceae	Shortia uniflora var. Kantoensis	P	-	-	2
Clethraceae	Clethra barvinervis	T	+	1	1
Ericaceae	Monotropastrum humile	P	+	1	-
Ericaceae	Elliottia paniculata	S	+	1	-
Ericaceae	Pieris japonica	S	-	1	-
Ericaceae	Vaccinium japonicum	S	+	1	1
Ericaceae	Vaccinium oldhamii	T	+	1	-
Styracaceae	Styrax japonica	T	+	1	1
Styracaceae	Styrax obassia	T	+	1	1
Symplocaceae	Symplocos coreana	S	-	1	-
Oleaceae	Fraxinus sieboldiana	T	+	1	-
Gentianaceae	Tripterospermum japonicum	L	+	1	1
Boraginaceae	Trigonotis brevipes	P	+	1	-
Ramiaceae	Plectranthus longitubs	P	+	1	-
Verbenaceae	Callicarpa japonica	S	+	1	1
Caprifoliaceae	Sambucus sieboldiana	S	+	1	-
Caprifoliaceae	Weigela hortensis	S	+	1	1
Campanulaceae	Peracarpa carnosa	P	+	1	-
Asteraceae	Carpesium abrotanoides	P	+	1	-
Asteraceae	Carpesium divaricatum	P	+	1	-
Asteraceae	Cirsium ashiuense	P	+	1	-

[1] Life form: E, epiphyte; L, liana; P, perennial; S, shrub; T, tree; V, vine.
[2] Deer herbivory: +, edible; -, inedible.
[3] Coverage: -, no cover; 1, 0-25%; 2, 25-50%; 3, 50-75%; 4, 75-100%.

Title: Indirect effects of excessive deer browsing through understory vegetation on stream insect assemblages.

Authors: Masaru Sakai, Yosihiro Natuhara, Ayumi Imanishi, Kensuke Imai, Makoto Kato

ESM_S2 List of families and genera of aquatic insects of overall samples in all months recorded at the exclosure catchment and control catchment.

Order	Family or genus	EC	CC	Order	Family or genus	EC	CC
Ephemeroptera	*Ameletus*	2	1	Diptera	*Ablabesmyia*	0	1
	Baetiella	1	2		*Antocha*	2	0
	Baetis	39	44		Athericidae	2	0
	Bleptus	3	0		Ceratopogonidae	10	48
	Cinygmula	7	3		*Conchapelopia*	27	13
	Dipteromimus	5	2		Diamesinae	22	64
	Ecdyonurus	64	108		*Dicranota*	6	9
	Epeorus	2	1		*Dixa*	3	5
	Ephemera	129	298		*Epoicocladius*	50	80
	Ephemerella	1	1		*Haxatoma*	2	0
	Heptagenia	2	0		*Limnophila*	21	14
	Paraleptophlebia	81	149		Limoniinae	2	1
	Procloeon	1	0		*Neobrillia*	4	2
	Rhithrogena	2	1		Orthocladiinae	18	120
Odonata	*Aeshna*	1	0		*Pedicia*	9	4
	Anotogaster	1	11		*Pentaneura*	2	3
	Davidius	4	8		*Pilaria*	0	1
	Epiophlebia	0	1		Simuliidae	0	1
	Gomphus	0	1		*Suragina*	3	1
	Lanthus	1	4		Tabanidae	21	58
	Mnais	1	5		Tanypodinae	6	6
	Planaeschna	3	8		*Tanytarsus*	11	116
	Polycanthagyna	2	0		*Tipula*	17	5
Plecoptera	*Amphinemura*	65	29		*Tvetenia*	1	0
	Caroperla	82	156	Trichoptera	*Agapetus*	8	6
	Haploperla	31	13		*Apatania*	0	1
	Isoperla	1	3		*Arctopsyche*	2	0
	Kiotina	1	0		*Brachycentrus*	3	0
	Leuctridae	22	18		*Diplectrona*	2	0
	Nemocapnia	1	0		*Dolophilodes*	30	22
	Nemoura	123	138		*Glossosoma*	1	0
	Niponiella	13	47		*Goera*	3	0
	Protonemura	10	0		*Hydropsyche*	79	25
	Pseudomegarcys	0	1		*Lepidosotma*	30	44
	Sweltsa	3	2		*Leptocerus*	0	2
	Togoperla	110	56		*Micrasema*	2	0
Megaloptera	*Parachauliodes*	12	9		*Perissoneura*	14	45
	Protohermes	1	0		*Plectrocnemia*	0	1
	Sialis	1	8		*Psilotreta*	3	63
Hemiptera	*Mesovelia*	1	0		*Rhyacophila*	25	21
Coleoptera	*Dryopomorphus*	2	0		*Setodes*	2	0
	Eubrianax	14	13		*Wormaldia*	2	1
	Hydrocyphon	0	1				
	Paralichas	59	32				
	Pseudamophihs	1	1				
	Sacodes	2	1				