Title

Response of aquatic insects along gradients of agricultural development and flood magnitude in northern Japanese streams

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Abstract

Agricultural activities have increased environmental homogenisation in stream ecosystems. These alterations reduce the availability of flow refugia during flooding and increase the effects of flood disturbances on aquatic insects. Thus, we examined the effects of the agricultural development (percentage of pasture cover within the catchment) and flood magnitude (ratio of shear stress at high flow to that at low flow) on the resistance indices measured by relative changes in taxon richness or abundance between pre- and post-flood (all insects, five orders and 31 dominant taxa) at 27 sites in the Kitamihorobetsu River, northern Japan. The resistance index of taxon richness decreased with increasing agricultural development, whereas that of the abundance of all insects decreased synergistically with increasing agricultural development and flood magnitude. Among 31 dominant taxa, the resistance indices of 20 taxa, generally belonging to Ephemeroptera, Plecoptera and Trichoptera, exhibited stronger negative relationships with agricultural development than with flood magnitude. By contrast, three Diptera taxa exhibited week negative relationships with agricultural development. These results showed that the interactive effect between agricultural development and flood magnitude was taxon dependent, but agricultural development could be detrimental to the resistance of most of the studied taxa, especially Ephemeroptera, Plecoptera and Trichoptera taxa. Additionally, agricultural developments in our study watersheds was relatively low (< 18% pasture cover), and nevertheless, apparent interacting effects with

natural disturbance was detected. This implies that limited agricultural development along the river line can lower the resistance of instream insects to natural disturbances.

Keywords

natural disturbance, anthropogenic disturbance, snowmelt flood, resistance, population persistence

43 **Introduction**

44 Human activities have extensively altered instream and near-stream terrestrial habitats, and
45 most streams or watersheds have been exposed to anthropogenic disturbances, such as land use and dams
46 (Allan 2004; Nilsson et al. 2005). These anthropogenic disturbances are superimposed on the natural
47 disturbance regimes (e.g. flooding and drying) of stream ecosystems, and both natural and man-made
48 disturbances and their interactions contribute to determining the assemblages of aquatic organisms
49 (Stanley et al. 2010). Additionally, multiple disturbances often affect organisms more synergistically than
50 do additively (Crain et al. 2008).Thus, separating the influences of natural and anthropogenic
51 perturbations in streams is impossible.

52 Flooding is a major natural disturbance that increases the temporal heterogeneity of stream
53 ecosystems (Resh et al. 1988; Death 2010). Aquatic insects are susceptible to flood disturbances, whereas
54 their abundances rapidly recover after the disturbances (Mackay 1992). A major determinant of the
55 response of aquatic insects to flood disturbances is habitat heterogeneity (Townsend and Hildrew 1994),
56 which provides flow refugia (i.e., hydraulic dead zones) where aquatic insects can escape and survive
57 during intensive floods (Lancaster and Hildrew 1993). Many studies have reported that the stabilities of
58 populations and communities of aquatic insects can be sustained by various flow refugia, such as stable
59 stones, woody debris and floodplain gravel bars (e.g. Palmer et al. 1996; Rempel et al. 1999; Matthaei et
60 al. 2000).

61 However, spatial habitat heterogeneity has rapidly decreased due to human activities.
62 Specifically, agricultural land use has caused biotic and abiotic homogenisation in various ecosystems
63 (e.g. Roschewitz et al. 2005; Maloney et al. 2011; Rodrigues et al. 2013). In streams, the deposition of
64 fine sediments fills the interstitial spaces between stones and homogenises benthic habitats (e.g.
65 Kaufmann et al. 2009; Larsen et al. 2009). Additionally, channel straightening restricts the floodplain area
66 and diminishes the channel morphology (e.g. Nakano and Nakamura 2008; Nakamura et al. 2014). Thus,
67 floods in human-altered streams may have a greater detrimental effect on aquatic insects than those in
68 natural streams (Dunbar et al. 2010a, b).
69 Several studies have investigated the interactive effects of agricultural activities on the
70 response of benthic invertebrates to a flood disturbance and have reported contrasting results. Negishi et
71 al. (2002) reported a significant decrease in the species richness and density of benthic invertebrates in a
72 channelised stream, and Parkyn and Collier (2004) reported a significant decrease in crayfish density in
73 agricultural streams. By contrast, several previous studies did not find significant differences in species
74 richness and density between agricultural and natural streams (e.g. Collier and Quinn 2003; Melo et al.
75 2003; Mesa 2010). Thus, the interactive effects of agricultural activities on the response of benthic
76 invertebrates to flood disturbances may alter with species and their composition. Additionally, these
77 previous studies were limited by the simple categorisation of streams as either agricultural or natural and
78 the conditions as either before or after a flood. In actual streams, however, agricultural land use varies

along a gradient (King et al. 2005), and the flood magnitude differs at different positions in the stream network (Leopold et al. 1964; Lepori and Hjerdt 2006).

Our objective is to examine the influences of agricultural development and flood magnitude on the stability (i.e., resistance) of assemblages (total abundance and taxon richness) and populations of aquatic insects (abundances of each taxon) during a snowmelt flooding season. In our study region, which is located in northern Japan, snowmelt floods represent large seasonal disturbances for aquatic insects, and flow refugia formed by complex channel morphology allow the aquatic insects to persist (Sueyoshi et al. 2014). The floodplain areas of the study basin (Kitamihorobetsu basin) were transformed into pastures approximately one hundred years ago. Currently, approximately 15% of the catchment is used as pastureland, which may be relatively low as compared to previous studies testing the effects of agricultural development on stream ecosystems (e.g. King et al. 2005; Maloney and Weller 2011), but the pasturelands are developed along the river line. As we previously reported, the deposition of fine sediments and environmental homogenisation increased in proportion to pasture cover in these catchments (Sueyoshi et al. 2016), and these processes may exacerbate the negative effects of flood disturbances on aquatic insects. Thus, we predicted that the resistance of aquatic insects would decline with increasing pasture cover in the catchments.

Materials and Methods

Study site and sampling design

The study sites were located in the Kitamihorobetsu River, Hokkaido Island, Japan. The catchment area of the Kitamihorobetsu River is 416 km^2 and is covered by forests (78%), natural grasslands (6%), pasture (15%) and other types of land use (1%). Many small patches of pastures are distributed along the mainstream and tributaries of the Kitamihorobetsu River (see details in Sueyoshi et al. 2016). The study was conducted from March through May 2011, and snowmelt flooding occurred from early April to late May, a period of approximately two months (Fig. 1). The flow fluctuation of snowmelt floods has been consistent in recent years. We selected 27 reaches from 1^{st}- through 3^{rd}-order streams in the Kitamihorobetsu River Basin.

To demonstrate the influence of a snowmelt flood on aquatic insects, we sampled insects twice: on March 26-28 (pre-flood) and May 21-23 (post-flood) in 2011. We shortened the sampling periods before and after the flood (three days for each) because the flow discharge of a snowmelt flood changes on a daily basis. To shorten the sampling periods, we selected study reaches where easy access was ensured, although the reaches were located more than 500 m apart and were characterised by different agricultural developments and flood magnitudes (see in a Supplementary figure). The length of a reach was set as approximately twenty times the width of the stream channel to include representative habitats such as riffles and pools. Additionally, we selected the reaches to avoid man-made obstructions, such as weirs and culverts.

115 We established six transects at even intervals in each reach and two random sampling points in
116 each transect. One quadrat sample was collected at each of the sampling points by using Surber net
117 (0.0625 m^2, mesh size 0.5 mm), and twelve insect samples were collected from each reach for a total of
118 648 samples (324 pre-flood and 324 post-flood samples). Twelve quadrat samples were pooled for data
119 analysis to represent the total abundance and species richness in each reach. All samples were preserved
120 in 70% EtOH with substrate particles in the field and were sorted and counted in the laboratory. All
121 individuals were identified to the genus level except for certain taxa whose identification was difficult
122 because of a lack of taxonomic information (Kawai and Tanida 2005). These taxa were identified to the
123 subfamily or family level.
124
125 ***Agricultural development***
126 All of the agricultural lands along the Kitamihorobetsu River are pastures (mostly used for
127 grass harvesting without cattle grazing) situated close to the riverbanks without riparian buffers; therefore,
128 they supply fine sediments directly into streams during various hydrological events. All of the study sites
129 are located above the main urban areas, and the influence of urbanisation on the study sites is limited.
130 Pasture cover in our study catchments was relatively little (less than 18%). However, previous studies
131 demonstrated the positive relationship of sand cover on streambed to % of pasture cover in Hokkaido
132 streams having equal range of pasture cover (Nakamura and Yamada 2005; Sueyoshi et al. 2016).

133 Furthermore, Sueyoshi et al. (2016) reported that pasture cover showed a significant positive relationship
134 with the homogenisation of instream environments (i.e. coefficients of variation in flow characteristics)
135 probably caused by channelization. Therefore, we used the percentage of pasture cover within a
136 catchment area (%pasture) as an indicator of fine sediment deposition and habitat homogenisation. We
137 used available vegetation/land use maps (scale of 1:50,000, Ministry of the Environment of Japan 1998)
138 and a geographic information system (GIS, ArcGIS 10.0; ESRI, Redlands, CA, USA) to determine the
139 percentage of pasture cover within the catchment area above each study site.
140
141 ***Environmental characteristics***
142 To describe the local environmental characteristics of the study sites, we measured the flow
143 velocity (Model 2000 Portable Flowmeter, Marsh McBirney Inc., Frederich, MD., USE), water depth and
144 ratio of substrate particles in each quadrat before insect sampling during the pre-flood period. Ratio of
145 substrate particles in each quadrat were visually classified into four size categories based on the
146 intermediate axis: 1, silt and sand (< 2 mm); 2, gravel (2–64 mm); 3, cobble (64–256 mm); 4, boulder (>
147 256 mm). We also measured water width at each transect, and bed slope at each reach (Impulse 200,
148 Laser Technology Inc., Centennial, CO, USA), Additionally, we calculated the coefficient of variation
149 (C.V.) for the flow velocity, water depth and water width, as well as Shannon's diversity for substrate
150 particles, to represent the environmental heterogeneity within each reach. The raw data of environmental

151 characteristics of each reach are summarised in Supplementary material.

152

153 ***Flood disturbance magnitude***

154 To evaluate the flood magnitude, we used an index modified from the relative flood magnitude.

155 The relative flood magnitude (peak discharge/mean discharge at low flow) is often used as an index that

156 reflects the flood disturbance intensity for aquatic insects (McMullen and Lytle 2012). In this study, we

157 tested the response of aquatic insects to flooding based on the relative change in abundance or taxon

158 richness before and after the flood (see the "Data analysis" section). Therefore, the relative flood

159 magnitude would be more appropriate than other absolute indices such as a maximum flow discharge.

160 However, it is difficult to measure discharge at high flows. Shear stress, which indicates the force on the

161 channel bed, is a more direct index for estimating the disturbance intensity for aquatic insects (Schwendel

162 et al. 2010). We calculated the relative shear stress (ratio of shear stress at high flows to shear stress at

163 low flows) at the sampling points instead of the relative flood magnitude. Shear stress at the sampling

164 points was estimated using an approximation of the following equation:

$$\tau = \rho g R S$$

165 where ρ is the density of water (1.0 g mL^{-1}), g is the acceleration due to gravity (980 cm s^{-2}), R is the

166 average water depth at the sampling points, and S is the bed slope. Because the variables ρ, g and S

167 changed only slightly during the study period, the relative disturbance magnitude was calculated using the

168 average water depth at high flows/the average water depth at low flows. During a flood, we could not
169 enter the central part of the large river; therefore, we set one fixed point on each of the six transects within
170 a reach and measured the increase in the water level at the fixed points (six in total per reach).
171 Measurements at the fixed points were conducted twice at low flows (pre- and post-flood) and twice at
172 high flows. The average water depth of each reach during low flows was calculated using data from
173 twelve quadrats at each site during the pre- and post-flood period. The average water depth at high flows
174 was calculated by adding the average increase in the water level measured at the six fixed points to the
175 average water depth during low flows.
176
177 ***Data analysis***
178 Initially, to verify whether %pasture is useful as an indicator of environmental homogenisation
179 and fine sediment deposition, we examined the relationships between agricultural land use (%pasture) and
180 each environmental variable (sand cover, H' diversity of substrates, C.V. of flow velocity, water depth and
181 water width) based on Spearman's correlation tests. A significant level was adjusted by Bonferroni
182 correction. Then, to determine the relationships between the agricultural development, flood magnitude
183 and their interactions with the stability of the assemblages and populations, we used a generalised linear
184 mixed model (GLMM). To represent stability, we used the resistance index, which is calculated by the
185 post-flood abundance or taxon richness/pre-flood abundance or taxon richness. This index indicates the

186 relative change between the pre- and post-flood values and ignores the absolute changes (i.e. for
187 abundance, both 1/2 and 100/200 become 0.5 even though the former lost only one individual and the
188 latter lost 100 individuals). To take absolute number of individuals into account, pre-flood value was set
189 as an 'offset' variable in the GLMM. Thus, the response variable was the post-flood value with a Poisson
190 error structure, and the pre-flood value was included in the model as log (pre-flood value) with other
191 explanatory variables. The explanatory variables examined included %pasture, relative shear stress and
192 their combined effect. Prior to the GLMM analysis, the correlation between %pasture and relative shear
193 stress was tested using a Pearson correlation to avoid multicollinearity, and the relationship was not
194 significant ($r = 0.31$, $P > 0.1$; in a Supplementary figure). Stream identity was also treated as a random
195 effect intercept. We built the models in all cases and evaluated the models based on the Akaike
196 information criterion (AIC). We compared models with all combination of explanatory variables
197 including a model without explanatory variables (i.e. Null model). AIC was calculated for all models, and
198 the model with the lowest AIC value indicated the best fitness (best model). Then explanatory variables
199 included in a best model are "influential" to explain the response variable. We also calculated the
200 standardised coefficients for each explanatory variable in the best model.
201 First, we used the GLMMs to test the influences of explanatory variables on abundance and
202 taxon richness of total aquatic insects. Then, to examine the more detailed responses of the aquatic insect
203 taxa, we used the GLMMs to determine the abundance of five orders (Ephemeroptera, Plecoptera,

204 Trichoptera, Coleoptera and Diptera) and 31 dominant taxa (eight taxa within Ephemeroptera, seven taxa
205 within Plecoptera, six taxa within Trichoptera, one taxa within Coleoptera and nine taxa within Diptera).
206 We selected the taxa that appeared in more than one-half of the reaches pre-flood (fourteen reaches). The
207 other taxa were excluded from the analysis because of a small sample size and the poor accuracy of the
208 models. Reaches with no pre-flood individuals for target taxa were excluded from the analyses because
209 the resistance index could not be calculated in these reaches. All the statistical analyses were conducted
210 using the R environment for statistical computing (R Core Team 2015) and package 'glmmML' (Broström
211 2017) and 'MuMIn' (Burnham and Anderson, 2002).
212
213 **Results**
214 The correlations between the agricultural development (%pasture) and local environments
215 suggested that environmental heterogeneities (the C.V. values of flow velocity and water width) showed
216 significant negative correlations with agricultural development (Spearman's rho = -0.69 and -0.54,
217 adjusted $P < 0.01$). Additionally, sand cover on riverbeds exhibited a significant positive correlation with
218 agricultural development (Spearman's rho = 0.71, adjusted $P < 0.01$). These relationships indicated
219 that %pasture was a useful index to represent habitat homogenisation and fine sediment deposition.
220 The results of the GLMMs are summarised in Table 1. Only %pasture was influential in the
221 best model of taxon richness (Table 1, Fig. 2a, b). This result indicated that the resistance index for taxon

222 richness decreased with increasing %pasture regardless of the relative shear stress. By contrast, %pasture,
223 relative shear stress and their interaction were influential in the best model of total abundance (Table 1,
224 Fig. 2c). The resistance index of total abundance decreased synergistically with %pasture and relative
225 shear stress. The average observed resistance index was relatively high for taxon richness (0.69) and low
226 for total abundance (0.29).

227 The relative shear stress, %pasture and their interaction were influential in the best models for
228 Ephemeroptera, Plecoptera, Trichoptera and Diptera (Table 1). The former three orders exhibited similar
229 responses in which the resistance indices rapidly decreased with increasing %pasture compared to the
230 relative shear stress (Fig. 3a, b, c). Diptera exhibited a different response compared to the three
231 above-noted orders because the resistance index rapidly decreased with increasing relative shear stress
232 (Fig. 3d). By contrast, Coleoptera was influenced to a comparable extent by %pasture and relative shear
233 stress (Table 1; Fig. 3e). The resistance indices of Coleoptera decreased linearly with increasing %pasture
234 and relative shear stress. All average observed resistance indices were lower than 0.5, and Plecoptera and
235 Coleoptera exhibited low values (both 0.14).

236 Among the 31 dominant taxa, the relative shear stress, %pasture and their interaction were
237 selected in the lowest AIC models for ten taxa (four taxa in Ephemeroptera, three in Trichoptera and three
238 in Diptera) (Table 1). Standardised coefficients indicated that %pasture showed more negative
239 relationships with ephemeropteran and trichopteran taxa (e.g., *Epeorus* spp. and *Hydropsyche* spp.) than

was the relative shear stress. By contrast, the dipteran taxa (e.g. Tanypodinae spp. and Diamesinae spp.) showed more negative relationships with the relative shear stress than with %pasture. The standardised coefficient of interaction showed a positive value for nine taxa (Table 1), which indicated that the negative relationships between %pasture and the resistance index was weak under conditions of high flood magnitude (see in Fig. 3a, b, c).

Both the relative shear stress and %pasture, without their interaction, were selected in the lowest models for eleven taxa (three taxa in Ephemeroptera; three in Plecoptera; two in Trichoptera; Elmini spp. in Elmidae, Coleoptera; and two in Diptera) (Table 1). These taxa showed similar responses in which the resistance indices decreased linearly with increasing %pasture and relative shear stress. However, the observed resistance indices were relatively high in ephemeropteran taxa (0.66 for *Paraleptophlebia japonica*, 0.71 for *Baetis* spp. and 0.56 for *Ameletus* sp.) compared to those of taxa from other orders (< 0.5 for all taxa) (Table 1).

Only the relative shear stress showed a negative relationship with the resistance indices of *Prosimulium* spp. and Chironominae spp. in Diptera (Table 1). The resistance indices of these taxa decreased with increasing relative shear stress regardless of %pasture. Additionally, *Stenopsyche marmorata* (Stenopsychidae) in Trichoptera was influenced by %pasture alone. Neither the relative shear stress nor %pasture influenced seven taxa (*Ephemera strigata* in Ephemeridae, Ephemeroptera, four in Plecoptera and two in Diptera) (Table 1). Ephemeropteran and dipteran taxa exhibited relatively high

258 average observed resistances (> 0.5) compared to that of the plecopteran taxa (< 0.15).

Discussion

Our prediction that the persistence of population (abundances for each taxa) and assemblage (total abundance and taxon richness) of aquatic insects would decrease with increasing agricultural development and flood magnitude was supported by the results, which showed that both disturbances were influential for the resistance indices of total abundance, five order groups and 21 dominant taxa. Surprisingly, agricultural developments in our study catchments was relatively low (less than 18% pasture cover) compared to other previous studies which observed the influences of agricultural development on instream biomes (e.g. King et al. 2005; Maloney and Weller 2011). Nevertheless, most of the studied taxa exhibited stronger negative relationships with agricultural development than with flood magnitude. This result suggested that limited agricultural developments along the river line caused habitat homogenisation and fine sediment deposition, dampening the resistance of aquatic insects to flood disturbances. The interactive effects of both disturbances varied among taxa. Eleven dominant taxa showed influential relationships with both disturbances without interaction, which indicated that the combined effects of land use and flood disturbance accumulate additively. By contrast, in nine taxa that were influenced by the interactive effects of both disturbances with positive standardised coefficients, a weakly negative relationship with agricultural development was observed, under high flood conditions. This observation is likely because the high flood magnitude washed out most individuals (more than 75% of pre-flood total abundances in our study reaches) and masked the importance of flow refugia within a reach. These

277 interactions between land use and flood magnitude would result in synergistic or antagonistic effects that
278 are far greater than additive effects and would greatly alter the prediction of temporal changes in
279 communities and populations (Crain et al. 2008). Thus, it is essential to understand the various
280 interactions between multiple stressors to prevent aquatic organisms from further degradation.
281
282 ***Taxon-specific response to flooding and agricultural land use***
283 First, the resistance indices of eleven dominant taxa belonging to all orders decreased linearly
284 with increasing agricultural development and flood magnitude. However, the observed resistance indices
285 exhibited different tendencies between the ephemeropteran taxa and those of other orders. Notably, these
286 indices were higher in the ephemeropteran taxa. Three taxa within Ephemeroptera (*Paraleptophlebia*
287 *japonica* in Leptophlebiidae, *Baetis* spp. in Baetidae and *Ameletus* spp. in Ameletidae) exhibited a
288 "swimmer" life form with high mobility and efficiently used limited refugia and exhibited rapid
289 colonisation after floods (Hose et al. 2007; Sueyoshi et al. 2014). Therefore, these mayfly populations can
290 be maintained by using the few refugia remaining in streams with high agricultural development or high
291 flood magnitude.
292 The resistance indices of six taxa in Ephemeroptera (*Epeorus* spp. and *Cinygmula* spp. in
293 Heptageniidae, *Cincticostella* spp. and *Drunella* spp. in Ephemerellidae) and Trichoptera (*Hydropsyche*
294 spp. in Hydropsychidae and *Neophylax ussuriensis* in Uenoidae) decreased rapidly with increasing

295 agricultural development compared to the flood magnitude. This result indicates that the populations of
296 taxa with high resistance to flood disturbances cannot be maintained in intensive agricultural streams. For
297 example, *Epeorus* spp. and *Cinygmula* spp. have dorsoventrally flattened bodies adapted to fast flows,
298 and *Hydropsyche* spp. are net-spinning caddisflies that build nests between stones. Additionally, the
299 species *Stenopsyche marmorata* (Stenopsychidae), within Trichoptera, exhibited a negative relationship
300 with agricultural development alone. This species is a net-spinning caddisfly similar to *Hydropsyche* spp.
301 The nets of *S. marmorata* exhibit a high coherent strength (Takao et al. 2006; Nunokawa et al. 2008),
302 which allows this species to remain on the substrate during large floods. These taxa may exhibit
303 resistance under suitable flow conditions and in the presence of coarse substrata; however, such
304 environments disappear in strongly impacted agricultural streams due to the deposition of fine sediments
305 (Jones et al. 2012).
306 The resistance indices of two dipteran taxa (Diamesinae spp. and Orthocladiinae spp.)
307 decreased rapidly with increasing flood magnitude compared to agricultural development. These two taxa
308 belong to Chironomidae, which generally inhabit shallow deposited substrates and are generally abundant
309 among drifting individuals during floods (Brittain and Eikeland 1988). Additionally, two taxa in Diptera
310 (*Prosimulium* spp. and Chironominae spp.) decreased only with increasing flood magnitude due to their
311 low resistance ability to flood disturbances. As noted above, chironomids are easily washed out by a flood.
312 Similarly, simuliids such as *Prosimulium* spp. actively drift with increasing flow discharge (Robinson et

313 al. 2004).Therefore, flood magnitude influenced these species more than others.

314 Seven dominant taxa from Ephemeroptera, Plecoptera and Trichoptera showed no negative
315 relationships with either type of disturbance. These taxa were classified into two groups with different
316 ecological characteristics. The first group, including *E. strigata* (Ephemeridae), *Limnephila* spp.
317 (Tipulidae) and Ceratopogonidae spp., contains burrowers that inhabit deep, fine streambed sediments.
318 The hyporheic zone beneath the streambed is considered a refugium, especially for hyporheic species (see
319 the review by Dole-Olivier 2011). The high observed resistance indices of these three taxa imply the use
320 of hyporheic refugia in our study sites. The second group, which includes four dominant taxa in
321 Plecoptera, showed extremely low observed resistance indices of approximately zero, even at sites with
322 low agricultural intensities and flood magnitudes. The resistance indices were also influenced by
323 emergence during the floods. In fact, in the studied streams, adult flies of Capniidae were often observed
324 during snows in March, and the emergence period of *Mesyatsia* spp. (Taeniopterygidae) occurs in March
325 (Zhiltzova 2006). Life cycles synchronised with seasonal floods represent an evolutionary adaptation to
326 flood disturbances (Lytle 2002). Therefore, these taxa would adapt to seasonal floods and maintain their
327 populations by emerging early, before snowmelt.

328 In conclusion, the response to both disturbances differed among taxa based on their ecological
329 traits. Taxa showing the high resistance to flood magnitude itself such as dorsoventrally flattened mayflies
330 and net-spinning caddisflies, have probably adapted to regional natural disturbance regime and

maintained their populations. However, agricultural development lowers the resistance to natural disturbance via habitat homogenisation and fine sediment deposition. Thus, in regions having high flood magnitude, land managers should pay attention to interacting effects between anthropogenic and natural disturbances on aquatic biomes, even if the man-made disturbance seems to be relatively low. Enhancing and maintaining the habitat heterogeneity (e.g. Nakano and Nakamura 2008) and/or building the riparian buffer strip along the river for filtering fine sediment (e.g. Nakamura and Yamada 2005) may be useful management strategies to conserve aquatic organisms in natural disturbance regime.

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Data availability

Environmental data are included in a supplementary table. Biological data analysed during the current study available from the corresponding author on reasonable request.

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466

Table legend

Table 1. Results of GLMMs for all aquatic insects and taxonomic groups. The values in columns 2-4 indicate standardised coefficients. The observed resistance index in column 5 was calculated from the observed post-flood abundance or taxon richness / the observed pre-flood abundance or taxon richness. "Null" indicates that Null model (without explanatory variables) was chosen by the lowest AIC value. Taxa were ordered by observed resistance values. E: Ephemeroptera, P: Plecoptera, T: Torichoptera, C:Coleoptera, D: Diptera.

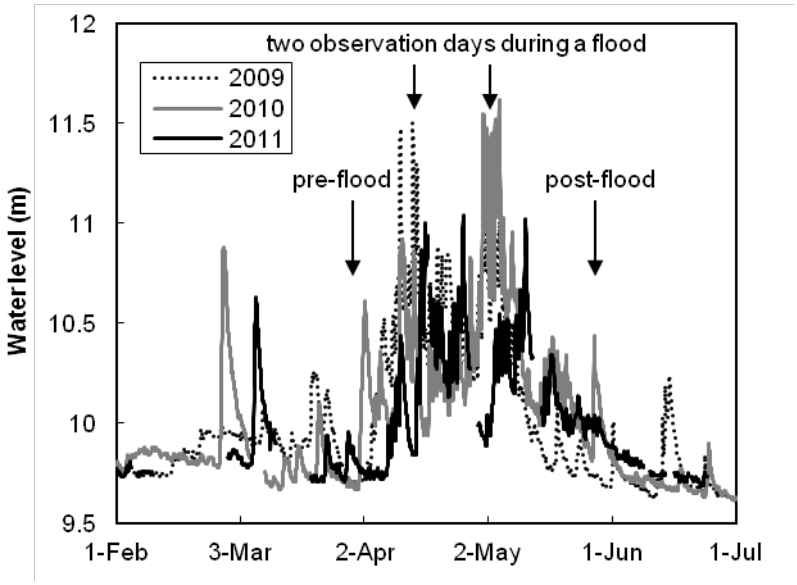
		Coefficients			Observed resistance index
Response variable		Relative shear stress	%pasture	Interaction	average (s.d.)
Taxon richness			-0.18		0.69 (0.14)
Abundance		-0.3	-0.3	-0.02	0.29 (0.16)
Ephemeroptera (E)		-0.1	-0.45	0.13	0.36 (0.23)
Plecoptera (P)		-0.06	-0.91	0.15	0.14 (0.17)
Trichoptera (T)		-0.1	-0.55	0.16	0.38 (0.31)
Coleoptera (C)		-0.42	-0.67		0.14 (0.22)
Diptera (D)		-0.33	-0.17	-0.07	0.29 (0.16)
Limnephila spp.	D	Null			0.90 (1.28)
Baetis spp.	E	-0.09	-0.17		0.71 (0.57)
Ephemera strigata	E	Null			0.68 (0.69)
Paraleptophlebia japonica	E	-0.3	-0.39		0.67 (0.44)
Stenopsyche marmorata	T		-0.95		0.63 (0.69)
Ameletus sp.	E	-0.27	-0.61		0.56 (0.63)
Ceratopogonidae spp.	D	Null			0.51 (0.68)
Tanypodinae spp.	D	-0.34	-0.21	0.09	0.51 (0.46)
Antocha spp.	D	-0.14	-0.15		0.47 (0.29)

Orthocladiinae spp.	D	-0.32	-0.35	-0.13	0.47 (0.28)
Lepidostoma spp.	T	-0.27	-1.84	1	0.45 (0.79)
Hydropsyche spp.	T	-0.19	-0.6	0.16	0.43 (0.38)
Skwala spp.	P	-0.35	-0.58		0.42 (0.38)
Rhyacophila spp.	T	-0.17	-0.24		0.40 (0.31)
Epeorus spp.	E	1.03	-2	1.11	0.38 (0.48)
Dicranota spp.	D	-0.26	-0.67		0.38 (0.45)
Apataniidae spp.	T	-0.59	-0.81		0.35 (0.57)
Neophylax ussuriensis	T	0.43	-1.23	0.49	0.35 (0.45)
Cincticostella spp.	E	0.06	-0.94	0.19	0.34 (0.40)
Drunella spp.	E	0.22	-0.49	0.3	0.34 (0.19)
Diamesinae spp.	D	-0.8	-0.19	0.18	0.22 (0.33)
Amphinemura spp.	P	-0.24	-1.06		0.22 (0.29)
Chironominae spp.	D	-0.22			0.18 (0.18)
Cinygmula spp.	E	0.2	-0.58	0.56	0.17 (0.18)
Chloroperlidae spp.	P	Null			0.15 (0.16)
Perlodidae spp.	P	-1.25	-3.36		0.14 (0.36)
Elimini spp.	C	-0.39	-0.63		0.14 (0.22)
Nemoura spp.	P	Null			0.10 (0.24)
Prosimulium spp.	D	-0.53			0.04 (0.05)
Mesyatsia sp.	P	Null			0 (0.01)
Capniidae spp.	P	Null			0 (0.01)

474

475

476 **Figures**



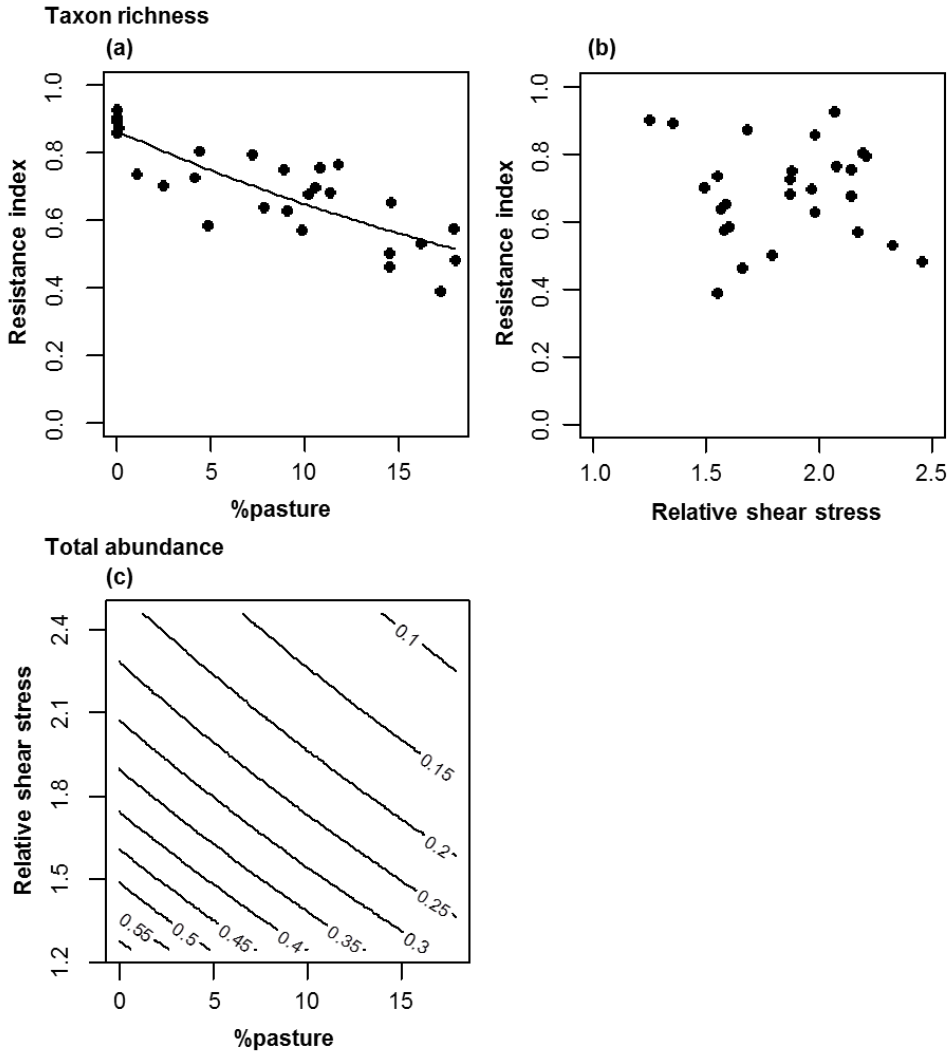
477

478 Fig. 1. Variation in the water level of the Kitamihorobetsu River during the study period. The water level

479 was monitored at a site downstream (4^{th}-order stream) by the Ministry of Land, Infrastructure and

480 Transport of Japan.

481



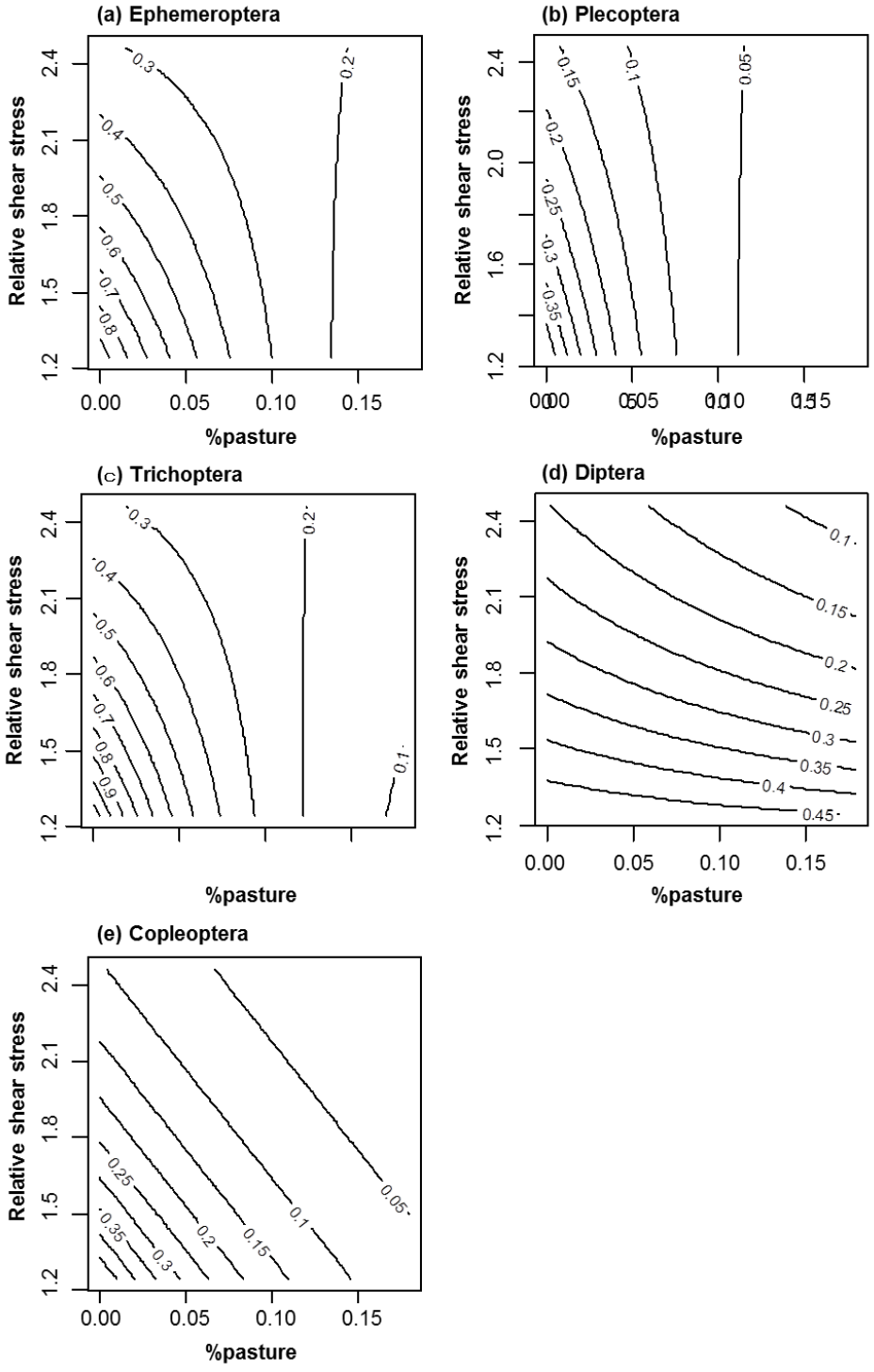
482

483 Fig. 2. Relationships between the resistance index and %pasture or relative shear stress for taxon richness

484 (a, b) and total abundance (c). Plots indicate the observed resistance indices, and solid lines and values

485 within the plot areas of (a, c) indicate the estimated resistance indices.

486



487

488 Fig. 3. Relationships between the resistance index and %pasture or relative shear stress for five order

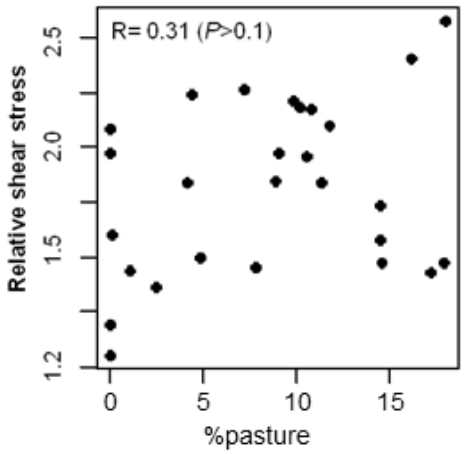
489 groups. Solid lines and values within the plot areas indicate the estimated resistance indices.

490

491 **Supplementary material**

492 Table 2. Environmental characteristics of study sites at pre-flood condition

Site	Pasture (%)	Relative shear stress	Slope (%)	Average flow velocity (cm s^{-1})	Average water depth (cm)	Average water width (m)	Average Sand cover (%)	C.V. of velocity	C.V. of depth	C.V. of width	H' diversity of substrates
Ki1	0	2.07	2.30	9.4	20.9	1.85	29.6	0.98	0.83	0.40	0.56
Ki2	0	1.98	2.51	17.9	13.9	3.30	20.8	0.88	0.63	0.21	0.48
Ki3	4.1	1.87	1.33	24.5	13.8	3.14	18.3	0.66	0.64	0.23	0.51
Ki4	7.2	2.21	1.57	23.1	12.2	4.28	22.1	0.59	0.28	0.06	0.40
Ki5	8.8	1.88	1.92	16.9	20.6	4.24	19.2	0.55	0.54	0.15	0.34
Ki6	10.8	2.14	1.04	18.9	12.6	4.48	30.8	0.51	0.47	0.13	0.27
Ki7	16.2	2.32	1.21	21.7	29.8	10.28	40.8	0.48	0.49	0.23	0.47
Ki8	17.1	1.55	1.12	27.2	51.9	9.28	35.8	0.53	0.63	0.14	0.46
Ki9	17.9	1.58	1.01	16.4	62.5	10.13	35.0	0.42	0.41	0.08	0.47
Pe1	0	1.35	4.90	21.0	10.6	2.89	7.5	0.74	0.52	0.22	0.48
Pe2	0	1.24	3.19	18.3	15.5	2.86	18.3	0.96	0.53	0.27	0.45
Pe3	0.1	1.68	2.47	14.9	15.1	2.95	11.3	0.78	0.45	0.17	0.42
Pe4	1.0	1.55	2.15	21.1	24.9	4.77	8.3	0.68	0.92	0.26	0.52
Pe5	2.4	1.49	3.35	27.6	15.7	4.83	2.9	0.65	0.42	0.20	0.51
Pe6	4.3	2.19	1.98	26.8	16.5	5.99	5.0	0.67	0.40	0.17	0.28
Pe7	9.0	1.98	1.13	12.6	35.1	9.38	45.8	0.76	0.48	0.26	0.52
Pe8	9.8	2.17	2.08	34.8	18.3	5.68	17.9	0.53	0.40	0.11	0.43
Pe9	11.7	2.08	1.91	20.4	28.5	6.74	29.6	0.69	0.51	0.11	0.45
Ke1	4.8	1.60	1.51	15.1	10.5	1.73	32.9	0.44	0.36	0.17	0.30
Ke2	7.8	1.56	1.72	11.1	21.5	2.29	56.7	0.49	0.56	0.20	0.38
Ke3	14.4	1.66	1.22	9.1	19.7	2.28	68.8	0.56	0.38	0.18	0.27
Ke4	17.9	2.46	2.11	21.5	11.8	4.12	57.1	0.53	0.33	0.10	0.30
Ke5	14.5	1.79	0.83	4.9	53.7	3.81	76.3	0.52	0.21	0.09	0.24
Ke6	14.6	1.58	1.44	9.4	33.6	2.93	53.3	0.54	0.53	0.18	0.43
Ke7	11.3	1.87	1.89	22.6	32.7	7.15	39.2	0.67	0.61	0.21	0.40
Ke8	10.5	1.97	0.99	18.3	41.2	6.60	46.7	0.57	0.52	0.13	0.51
Ke9	10.2	2.15	1.48	17.2	29.0	7.38	19.6	0.61	0.54	0.23	0.48



493 Figure 4. A relationship between agricultural intensity (catchment %pasture) and flood

494 magnitude (relative shear stress). There is no significant correlation between %pasture

495 and relative shear stress (Pearson's correlation).

496

497