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1 Restoration of the shifting mosaic of floodplain forests under a flow 2 regime altered by a dam

3
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6 7 **Abstract**

8 A braided gravel-bed river provides essential habitats for various plants and animals.
9 However, human regulation of rivers, such as dams, channelization, and other engineering
10 works, alter flow and sediment regimes, which generally cause the degradation of river
11 and riparian ecosystems. One of the prominent changes prevailing in Japanese rivers is
12 forest expansion over gravel bars, and many native plants and animals that depend on
13 gravel-bed habitat are now endangered. The Satsunai River is typical of rivers
14 experiencing forest expansion, so the Japanese government launched a restoration project
15 in 2012 to partially restore its riparian ecosystems. This is a large-scale experiment
16 developed jointly by an interdisciplinary science team and river managers, who conduct
17 monitoring and evaluation under an adaptive management scheme. The main measure to
18 restore gravel bed habitat was an artificial flood regime, releasing a maximum water
19 volume of 120 m³/s, which was a 2-year return period flood before dam construction. A
20 unique feature of the project is that we considered the role of high-magnitude floods with
21 recurrence intervals greater than 20 years after dam construction. We hypothesize that the
22 artificial floods can be timed seasonally to create sites for regeneration and nesting of
23 riparian species, and the high-magnitude floods contribute to maintaining a shifting
24 mosaic structure of floodplain forest and unvegetated gravel-bar patches. We also used
25 critical non-dimensional shear stress analysis to define “flood-disturbance areas” that can
26 be disturbed under the artificial flow regime created by a dam. Artificial floods have been
27 initiated once a year since 2012 at the end of June, synchronized with the seed dispersal
28 period of *Salix arbutifolia*, which is endangered and a high conservation priority in the
29 project. Thus far, the idea of setting floodplain-disturbance areas and the strategy of using
30 both artificial and high-magnitude floods to restore a shifting mosaic of floodplain habitat
31 patches is appropriate, as we found successful regeneration of *S. arbutifolia* and an
32 exponential decay curve of the age distribution of floodplain forest patches. However, the
33 sediment regime regulated by the dam was not addressed in this research, so future

34 monitoring should track changes in river morphology associated with reduced sediment
35 supply caused by the dam.

36

37 Keywords: Artificial flood, Environmental flow, Gravel-bed river, Riparian ecosystem,
38 *Salix arbutifolia*

39

40 **1. Introduction**

41

42 The habitat mosaic in a braided, gravel-bed river is maintained by frequent migration of
43 multiple river channels and the active movement of sediment (Piegay et al. 2006). Plant
44 and animal species dependent on gravel-bed rivers are adapted to the dynamic features of
45 braided rivers (Poff et al. 1997). However, human modifications in Japan and other
46 developed countries drastically alter braided rivers to a single-thread channel and promote
47 forest establishment on gravel bars and floodplains (Nadler and Schumm 1981; Johnson
48 1994; Bejarano et al. 2011; Takahashi and Nakamura 2011), which threatens native
49 species with extinction (Tiedemann and Rood 2015; Nakamura and Shin 2001). Several
50 factors promote forest expansion, such as reduced flooding resulting from dam
51 management, channel incision associated with channelization, and revetment or spur dike
52 construction.

53 Drastic changes in river and riparian ecosystems can be expected with forest
54 expansion (Nakamura et al. 2017). Plant species, such as *Anaphalis margaritacea* and
55 *Dianthus superbus* L. var. *longicalycinus* and insects, such as *Eusphingonotus japonicus*,
56 which favour gravel-bed habitats, are locally endangered in Japan (Yoshioka et al. 2010).
57 Bird species (e.g., *Charadrius* spp.) that build nests on gravel beds are replaced by forest-
58 nesting birds (Yabuhara et al. 2015). Additionally, energy flow and aquatic food-web
59 structure may change from autochthonous production to allochthonous input (Riley and
60 Dodds 2012), which may result in changes in macroinvertebrate assemblages (Arscott et
61 al. 2003).

62 The Satsunai River, the focal river of this study, was a bar-braided, gravel-bed
63 river in 1960s and 1970s. However, the bar-braided river has been changed to a single-
64 thread river with forest expansion over gravel bars and floodplains (Nakamura et al. 2017,
65 see Fig. 3). One of the probable causes of forest expansion in the Satsunai River was
66 combination effects of spur dikes built since 1945 and artificial levees built since 1950.

67 The gravel beds stabilized by the dikes have provided germination sites for tree species
68 and limited flood disturbance. Another cause of forest expansion is dam construction and
69 reservoir management (Takahashi and Nakamura 2011). The Satsunai River Dam was
70 built in 1998 and is used for multiple purposes, including flood control, water utilization
71 and power generation. As a result, the high peak of snowmelt flooding in spring has been
72 attenuated, and the frequency and magnitude of flood disturbance are greatly reduced in
73 the downstream reaches of the Satsunai River (Nakamura and Shin 2001).

74 Forest expansion causes two major problems in river management. One is an
75 increase in the channel roughness, thereby reducing the transport capacity for floodwater,
76 and the other is a reduction in gravel-bed habitat on which native, rare plant and animal
77 species are dependent. The plant species that characterizes the Satsunai River is *Salix*
78 *arbutifolia*, an endangered species (vulnerable on the IUCN Red List) that occurs in
79 eastern Hokkaido and Nagano Prefectures, Japan, and other countries (Korea, Sakhalin,
80 Kamchatka and the Russian Far East). This species is predominantly observed in gravel-
81 bed rivers with a bar-braided pattern (Shin and Nakamura 2005; Nakamura et al. 2007).

82 In 2012, the Ministry of Land, Infrastructure, Transport and Tourism (MLIT)
83 launched a restoration project along the Satsunai River. This is a large-scale experiment
84 using artificial floods (Robinson and Uehlinger 2003) designed in conjunction with
85 scientists, conducting monitoring and evaluation under an adaptive management scheme.
86 The senior author is the chair of the scientific committee. Some of the present authors are
87 scientific committee members for this project, who suggest how and when the artificial
88 flood should be initiated and what kind of monitoring programme should be implemented.
89 The committee advised synchronizing artificial floods with the seed dispersal period of *S.*
90 *arbutifolia*, because Salicaceous species require exposed mineral soil consisting of sandy
91 pebbles and enough soil moisture for germination (Shin and Nakamura 2005). Based on
92 these recommendations, the project aimed to recreate gravel beds in the Satsunai River
93 and, thereby, maintain flood transport capacity and restore regeneration sites for *S.*
94 *arbutifolia* and habitats for gravel bar-nesting bird species. As in many developed
95 countries, large-scale fundamental restoration, such as dam removal, is not possible, given
96 the constraints of water use, power generation, and flood control. Thus, this project aims
97 to sustain riverine ecosystems with artificial floods that are different from the original
98 flow regime, but provide essential habitats for native riparian species.

99 The main measure to restore the gravel bed in the Satsunai River is artificial

100 flooding, releasing a maximum water volume of 120 m³/s at the end of June, synchronized
101 with the seed dispersal period of *S. arbutifolia*. This magnitude of flow was a 2-year return
102 period flood before dam construction (Nakamura and Shin, 2001). A unique aspect of the
103 project is that we considered the role of high magnitude floods with recurrence interval
104 greater than 20 years after dam construction. This magnitude of flood may exceed the
105 capability of dam operations aiming to completely regulate flood peaks. We hypothesize
106 that the artificial flood can create seasonal regeneration and nesting sites for riparian
107 species, and the high-magnitude flood contributes to maintaining a shifting mosaic
108 structure of floodplain forest patches within a limited extent of the valley floor.

109 Environmental flow regimes, including artificial floods, have been used to
110 reduce ecological degradation, mainly focusing on aquatic species, including mostly fish
111 (Bradford et al., 2011), but other components of riverine ecosystems, such as riparian
112 vegetation, have been disregarded (Rivaes et al. 2015). One of the important concepts
113 concerning the environmental flow regime focuses on the regeneration of riparian tree
114 species is the “recruitment box model”, which considers seasonal streamflow patterns,
115 the dispersal period of seeds, and the elevation of regeneration sites (Rood et al. 2005).

116 Our objective is to determine whether the restoration project in the Satsunai
117 River has been successful, based on monitoring results of flood discharge, floodplain
118 forest dynamics, and the breeding environment of bird species, especially focusing on the
119 persistence of Salicaceous communities dominated by *S. arbutifolia* and the provision of
120 nesting and breeding sites for plover species.

122 **2. Methods**

124 **2.1 Study area**

126 The Satsunai River (catchment area; 725 km²) runs from Mt. Satsunai (42°41'N,
127 142°47'E; 1895 m above sea level) in the Hidaka Mountain Range to the Tokachi River
128 in Hokkaido Prefecture, Japan (Fig. 1). The average gradient of the river is 1/100~1/250,
129 and its whole river width in flood stage ranges from 400 m to 500 m. The geology of the
130 basin is composed of sedimentary rocks in the Hidaka Mountain Range, plutonic and
131 metamorphic rocks (granite, gabbro, gneiss, hornfels, and peridotite) in upstream areas,
132 and unconsolidated Quaternary deposits constituting terrace and alluvial fans in

133 downstream areas. The mean annual air temperature from 2010 to 2015 was 5.0 ~ 6.0°C,
134 and the monthly mean air temperature ranged from -8.4°C in January to 18.6°C in August.
135 The average annual precipitation between 1981 and 2010 was 1255 mm (Kamisatsunai
136 observatory; 42°38'N, 143°05'E) (Japan Meteorological Agency 2020,
137 <http://www.jma.go.jp/jma/menu/report.html>).

138 Partial operation of the Satsunai River Dam began in 1997, and full operation
139 began in 1998. The catchment area upstream of the dam is 118 km², the maximum volume
140 of water stored is 54 million m³, and 150 m³/s was the maximum water discharge that can
141 be released from the sluice gates of the dam. If the capacity of dam reservoirs exceeds the
142 critical water level, the emergency gates located at the top of the dam will release all the
143 water discharge coming into the reservoir from upper basins.

144 Figure 2 shows the hydrographs of natural flows (flows into the reservoir from
145 the upper basin) and controlled flows (flows out of the dam). Although the average
146 discharge in the snowmelt season (from the middle of April to the end of June) is relatively
147 high, clear rising and descending limbs of the hydrograph of snowmelt floods cannot be
148 seen in the Satsunai River, probably because the source catchment area is small and snow
149 conditions are subject to weather variability.

150 Small peak flows are strongly regulated by the dam; specifically, snowmelt peaks
151 in the spring are reduced substantially (Fig. 2). Since completion of the dam, there was a
152 large flood on September 1-7, 2011, initiated by heavy rainfall associated with No. 12
153 Typhoon, reaching 432.5 mm in total precipitation for 7 days at Nukabira gauging station.
154 The peak discharge was 285 m³/s at Kamisatsunai Bridge (KP 41.8 km, see Fig. 1,
155 watershed area is 189 km²), the recurrence interval of which was estimated as once in 20
156 years after dam construction. Such high-magnitude floods occurring in the summer and
157 autumn seasons are also important in shaping the river and floodplain geomorphology of
158 the Satsunai River.

159 The dominant riparian tree species are *Salix pet-susu*, *Salix sachalinensis*, *Salix*
160 *rorida*, *Salix gracilistyla*, *Toisusu urbaniana*, *Populus maximowiczii*, and *S. arbutifolia*.
161 Bird species that build nests on gravel beds are *Charadrius placidus*, *Charadrius dubius*,
162 and *Actitis hypoleucos*. Forest expansion over the gravel bars and floodplains of the
163 Satsunai River has been prominent, particularly since the 1990s (Fig. 3).

164

165 **2.2 Restoration project**

166

167 After thorough discussion within the scientific committee of this project, we decided to
168 initiate an artificial flood at the end of June, given the constraints of water use, power
169 generation, and flood control. The artificial flood was released from the sluice gates once
170 a year from 2012 to present (except in 2016 and 2017 due to construction works in
171 downstream areas) and synchronized with the seed dispersal period of *S. arbutifolia*. In
172 this study, we analysed the monitoring results of artificial floods between 2012 and 2014
173 (Fig. 2). Seed dispersal of *S. arbutifolia* occurs from late June to early July, which is later
174 than that of other Salicaceous species (Nakamura and Shin, 2001). To create an artificial
175 flood, the reservoir water level has been lowered from 474 m (no flood risk period;
176 November 1 - June 30) to 466 m in elevation (flood risk period; July 1 – October 31),
177 which generates the flood for approximately 30 hours, with a peak discharge of
178 approximately 120 m³/s (Fig 2).

179 Another important aspect considered in project planning was the magnitude of
180 the artificial floods. Unfortunately, approximately 120 m³/s was the maximum water
181 discharge that can be released from the dam, owing to the sluice gate structure and water
182 resource allocation. This magnitude of flood was a 2-year return-period flood before dam
183 construction. We expected that the discharge of the artificial flood alone would not be
184 large enough to maintain gravel bars and a downscaled shifting mosaic of floodplain
185 forest patches. Thus, we first discussed “flood-disturbance areas” that can be maintained
186 under the altered flow regime. Second, we built a two-pronged strategy, in which high-
187 magnitude floods are expected to shape the extent of a shifting mosaic within the flood-
188 disturbance areas, while the artificial flood is used for providing non-forested gravel bars
189 which function as germination habitats for Salicaceous species and nesting habitats for
190 plovers. The water discharge of such a high-magnitude flood (e.g., the flood in 2011) can
191 be reduced somewhat by dam operation, but a large amount of water should be released
192 downstream for several days due to the limited capacity of dam and reservoir. During
193 heavy rain, the floodwaters released from the dam site and additional stormwaters from
194 small tributaries would increase the magnitude of flood disturbance in the restoration
195 project area.

196

197 **2.3 Study design**

198

199 1) Flood-disturbance areas

200 We predicted disturbance areas affected by artificial floods using iRIC (International
201 River Interface Cooperative: <http://i-ric.org/en/index.html>). iRIC is a river flow and
202 riverbed variation analysis software package that combines the functionality of
203 MD_SWMS, developed by the U.S. Geological Survey, and RIC-Nays, developed by the
204 Foundation of Hokkaido River Disaster Prevention Research Center, Japan.

205 The comparisons among the results of horizontal two-dimensional flow,
206 morphological changes of the bed and banks in the river by iRIC, and field surveys have
207 indicated that the majority of gravel in the Satsunai River starts to move when
208 nondimensional shear stress, τ_* , becomes greater than 0.05. Here, τ_* can be calculated
209 from the following equation.

$$210 \quad \tau_* = u_*^2 / ((s - 1)gd) \quad (1)$$

211 where u_* is the friction velocity, s is the relative particle density, d is an effective particle
212 diameter that is entrained by the flow, and g is gravity.

213 We delineated the predicted flood-disturbance areas where τ_* of the artificial
214 flood and the 2011 flood exceeds 0.05 and examined to what extent we can maintain
215 gravel beds and the regeneration dynamics of Salicaceous species represented by *S.*
216 *arbutifolia*. The research and calculation segments were from KP 25 km (the confluence
217 of the Tottabetsu River (a tributary) and the Satsunai River) to KP 48 km (see Fig. 1).

218

219 2) Shifting mosaic

220 The floods create a shifting mosaic pattern of habitat patches with different disturbance
221 frequencies and intensities. Here, the ‘shifting mosaic’ refers to the mosaic of floodplain
222 habitat patches that continually change their spatial distributions in floodplain valleys
223 throughout successional development (Bormann and Likens, 1979). Nakamura and
224 Kikuchi (1996) developed the following equation governing the age distribution of
225 floodplain habitat patches.

$$226 \quad \partial n(x, t) / \partial t = -\partial n(x, t) / \partial x - e(x) \cdot n(x, t) \quad (2)$$

227 where $n(x, t)$ is the area of age x years when the time is t (years), and $e(x)$ represents the
228 percent loss of x -year-old sediment per unit area per year. Assuming the steady state
229 condition of the age distribution ($\partial n(x, t) / \partial t = 0$) and $e(x)$ being constant (α), equation (2)
230 becomes

$$231 \quad dn(x) / dx = -\alpha n(x) \quad (3)$$

232 Equation (3) means that the floodplain habitat aged x years decays exponentially with age.
233 Thus, if the shifting mosaic is maintained continuously (state of dynamic equilibrium),
234 the age distribution of floodplain habitat patches should be approximated by the
235 exponential decay curve. We examined the age distribution of habitat patches in the
236 floodplain-disturbance areas within $\tau_* > 0.05$, calculated by iRIC. The ages of the habitat
237 patches were determined from a series of aerial photos and field confirmation.

238

239 3) Survey and analysis of riparian tree species

240 We compared air-photos of 1987, 1991, 1995, 2000, 2005, 2010, and 2015 to determine
241 age classes of forest patches. The patches were grouped in tree age classes: 1-5 years, 6-
242 10 years, 11-15 years, 16-20 years, 21-25 years, and greater than 25 years (Fig. 4). First,
243 we delineated forest patches older than 25 years by identifying the patches which found
244 in 1987 and were not disturbed by flooding until 2015. The forest patches which were
245 gravel bars in 1987 but revegetated in 1991 and 1995 and suffered no disturbance until
246 2015 were designated as 20-25 years old. The forest patches which were gravel bars in
247 1995 but revegetated in 2000 and suffered no disturbance until 2015 were designated as
248 15-20 years. Similar methods were used for determination of age classes of 0-5, 5-10, and
249 10-15 years. The habitat patches were digitized and entered into a GIS with their ages
250 (Fig. 4)

251 To investigate the species composition of riparian trees, five quadrats were
252 established in each of the age classes of forest patches; therefore, 25 quadrats in total were
253 distributed over the gravel bars and floodplains from KP 25 km to KP 48 km (Fig. 1). The
254 size of the quadrats varies with tree height: 5×5 m, 10×10 m, 10×20 m, 15×15 m, 15×20
255 m, 20×20 m, and 25×25 m. In each quadrat, the height and diameter at the base of
256 individual trees were measured, and the species was identified for trees taller than 1.3 m.
257 Among the trees in each quadrat, the individuals producing seeds were identified, and the
258 ages of some individuals were estimated from tree-ring core samples using an increment
259 borer.

260 We conducted nonmetric multidimensional scaling (NMDS) to show the
261 differences in the structure and composition of tree assemblages among the age classes
262 of habitat patches. The basal area (BA) of each species in each quadrat was obtained from
263 cross-sections at the base of the respective trees, and the relative dominance of each
264 species BA in each quadrat was used for the NMDS analysis. Similarity between pairs of

265 communities was calculated using the Bray–Curtis distance measure. We used R (R Core
266 Team, 2019) and the vegan package (Oksanen et al, 2019) for NMDS.

267

268 4) Effect of the artificial flood on gravel bar-nesting bird species

269 Plover species require a gravel bed for nesting and breeding. However, the end of June,
270 when an artificial flood is released, overlaps with the breeding season of gravel bar-
271 nesting bird species. To investigate the effects of artificial floods on the breeding
272 performance of two plover species (*Charadrius placidus* and *C. dubius*), the incubation
273 behaviour of breeding pairs, the existence of their chicks, and their nesting sites were
274 identified and monitored before and after the flood along the Satsunai River. We
275 investigated the gravel bars from KP0 to KP48 km to identify the location of the nesting
276 (incubation) sites of the two species from May to June 2014. The elevation of each of the
277 nesting sites and the maximum level of artificial flooding were compared to judge
278 whether the sites were submerged or not during the flood.

279

280 **3. Results**

281

282 *3.1 Age distribution of floodplain habitat patches*

283

284 The age and spatial distribution of habitat patches are mapped in Fig. 4. The gravel bars
285 and the age classes ranging from 1 to 25 years were distributed in the central parts of the
286 floodplains, and the age classes older than 25 years were distributed on the outer sides of
287 the riverbed along the artificial levees. The floodplain areas where τ_* of the 2011 flood
288 was > 0.05 closely coincide with the boundaries of floodplain patches younger than 25
289 years old. The $\tau_* > 0.05$ areas of the artificial flood were narrower than those of the 2011
290 flood and correspond to floodplain patches of less than 10-15 years.

291 The areas of floodplain age classes less than 25 years were approximated by the
292 exponential decay curve (Fig. 5), indicating that the pattern of floodplain patches has been
293 sustained in a state of dynamic equilibrium.

294

295 *3.2 Variation in tree assemblages among the age classes*

296

297 Tree assemblage changes with increasing age classes arranged along axis-1 in NMDS

298 ordination, although there are substantial variations within a single age class (Fig. 6 and
299 Table 2). Species richness increases slightly, whereas species diversity does not change
300 with age class. The relative dominance of *S. arbutifolia* was approximately 30 % in all
301 age classes except the 1-5 year age class, in which it was only 6.5 % (Table 1). *S.*
302 *arbutifolia* was distributed near the centre of the NMDS ordination, indicating that it is a
303 common species among all age classes. The relative dominance of Salicaceous species
304 was high in young age classes (Table 1), distributed on the left side of the NMDS
305 ordination, whereas late-successional species such as *Ulmus davidiana* var. *japonica*,
306 *Acer mono*, and *Quercus crispula* are distributed on the right side of the NMDS ordination
307 and appear in older age classes (Tables 1 and 2, and Fig. 6).

308

309 ***3.3 Influences on two plover species***

310

311 We identified the incubation behaviour at 43 sites and/or the existence of their chicks on
312 gravel bars. Among the 43 sites, we could specify the exact locations of 24 nesting sites,
313 but could not for the other 19 sites. Thus, we analysed influences of the artificial flood at
314 the 24 nesting sites. The comparison between the elevations of nests and the maximum
315 level of artificial flooding indicated that 16 nests located on higher-elevation gravel bars
316 avoided flood disturbance, while 8 nests located on lower-elevation were submerged by
317 the flood (Fig. 7). Among the 8 nests, two nesting sites could avoid flooding because these
318 sites were located behind higher geomorphic surfaces that block floodwater, but the other
319 6 nesting sites were flooded. We confirmed incubation behavior at two nesting sites just
320 before the artificial flood, whereas the nests of other sites were empty, meaning that the
321 chicks had been already fledged or breeding failed. Among the two nests having
322 incubation behavior during the flood, one of them was above the flood peak while the
323 other one was submerged by the artificial flood and, therefore, eggs were flushed out.

324

325 **4. Discussion**

326

327 Before dam and spur dike construction, the original shifting mosaics of floodplain patches
328 were sustained over the entire valley floor between the artificial levees in the Satsunai
329 River. After flow regulation and spur dike and artificial levee constructions, however,
330 gravel bars started to be colonized by trees, and the number and area of gravel bars has

331 been greatly reduced.

332 The Satsunai River restoration project aims to recover some of the dynamic
333 features of braided rivers using an artificial flood synchronized with plant phenology and
334 high-magnitude floods. However, the maximum discharge that can be released from the
335 sluice gate is limited to approximately 120 m³/s, which is only a two-year return-period
336 flood before dam construction (Nakamura and Shin 2001). Thus, we decided to create a
337 “downscaled” shifting mosaic of floodplain patches (Hall et al. 2011), delineated by $\tau_{*} >$
338 0.05 created by the high-magnitude floods whose recurrence intervals are greater than
339 once in 20 years after dam construction (Fig. 4), which we called the “floodplain-
340 disturbance area” under the altered flow regime. This project is attempting to restore some
341 dynamism of gravel bar habitat within the confines of a flow regime limited by reservoir
342 management and lateral confines of spur dikes. It cannot restore the full landscape
343 dynamics of the pre-dam, pre-levee watershed. In this sense, the project is “downscaling”
344 the zone of the valley floor subject to inter-annual dynamics imposed by flooding.

345 The “recruitment box model” of Rood et al. (2005) considers seasonal
346 streamflow patterns, the dispersal period of seeds, and the elevation of regeneration sites.
347 The concept recommends “ramping flows” involving gradual flow decline after the peak
348 of snowmelt floods. The ramping flow (gradual flow recession) is possible, if the
349 recession limb of the hydrograph of the snowmelt flood is gradual and continues for more
350 than several months. However, the catchment area of Satsunai River Dam is small (118
351 km²), therefore, recession of the hydrograph is not gradual; but, rather, it is spiky,
352 exhibiting flow pulses created by daily snowmelt associated with periodic high air
353 temperature, sunny weather, and rain-on-snow events in spring (Fig. 2).

354 Under the constraints of water use and the above hydrology, we used the artificial
355 flood for approximately 30 hours at the end of June. Although the duration of the artificial
356 flood was short compared with that of “ramping flows” recommended by Rood et al.
357 (2003) and Rood et al. (2005), the flood pulse creates fresh gravel bars and provides
358 enough soil moisture for Salicaceous species to germinate. Soil moisture requirements for
359 seed germination vary among species (Nagasaka et al., 1994). For example, although *P.*
360 *maximowiczii* and *S. sachalinensis* can germinate under limited moisture conditions, *S.*
361 *arbutifolia* cannot. Thus far, the idea of setting floodplain-disturbance areas based on
362 critical nondimensional shear stress under a dam-regulated flow regime was appropriate,
363 as we found successful regeneration of *S. arbutifolia* and other Salicaceous species (Table

364 1) and a downscaled shifting mosaics of forest patches (Fig. 4). We found many middle-
365 and late-successional tree species within the floodplain-disturbance areas, but eventually
366 large floods will erode them and they will be replaced by Salicaceous species along with
367 lateral migration of the braided river channel. Currently, there are many large-diameter
368 and tall mature trees of *S. arbutifolia*, *T. urbaniana*, and *P. maximowiczii* outside of the
369 floodplain-disturbance areas (coloured red in Fig. 4). However, we expect that they will
370 gradually be replaced by late-successional species such as *Ulmus davidiana* var. *japonica*
371 and *Acer mono* (Takagi and Nakamura, 2003).

372 Nakamura et al. (2007) investigated stand-level forest dynamics in the Reikifune
373 River near the Satsunai River. They found habitat separation between seedling and
374 conspecific mature trees, which indicates that riparian tree species, including *S.*
375 *arbutifolia*, require more than one habitat type to complete their lifecycles. The minimum
376 age of the reproductive mature trees of *S. arbutifolia* was 11 years in the Satsunai River.
377 If we can sustain a shifting mosaic of habitat patches over 25 years (Fig. 4), *S. arbutifolia*
378 will complete its lifecycle and survive in the Satsunai River. The mature ages of other
379 pioneer Salicaceous species were 8 years for *T. urbaniana*, and 11 years for *P.*
380 *maximowiczii*; therefore, they can survive these managed conditions as well. The key
381 factors maintaining the diversity of floodplain tree species, including *S. arbutifolia*, are
382 the development of diverse geomorphic surfaces providing regeneration and habitat
383 niches, the timing of maturation, and the lifespan of early and mid-successional species
384 (Nakamura et al. 2007). Even though the flood-disturbance areas are greatly reduced after
385 dam regulation, high-magnitude floods, whose recurrence interval is greater than 20 years,
386 may function to reset most of the active valley floor (flood-disturbance areas) to the
387 younger age classes, and maintain a small shifting mosaic of floodplain habitat patches
388 (Hall et al. 2011). As indicated by continuity equation (3), the exponential decay curve of
389 the age distribution over 25 years (Fig. 5) may guarantee the dynamic equilibrium of
390 floodplain patches and, therefore, the conservation of early successional riparian tree
391 species. However, the relative dominance of *S. arbutifolia* in the 1-5 year age class was
392 not high, and we do not know why this occurred. We have to continue to monitor the
393 seedling dynamics in young age classes and may change the timing of artificial floods, if
394 necessary.

395 Retrospective analysis in the Satsunai River conducted by Yabuhara et al. (2015)
396 estimated that large patches (>1.5 ha) of gravel bars have disappeared due to forest

397 encroachment: the number of large gravel bar patches decreased from 13 to 3 over
398 approximately 8 km in river length, and thereby gravel bar-nesting birds decreased by
399 40%. The young age classes, including unvegetated gravel bars, are nesting and breeding
400 sites for the two plover species. Thus, the restoration project that maintains gravel bars
401 and prevents forest encroachment is likely to contribute to the persistence of plover
402 populations in the Satsunai River. The monitoring results showed that many nesting sites
403 were found in the dam-regulated downstream reaches, and the negative influences of the
404 artificial flood on the nesting success of the two plover species were limited. Most
405 breeding pairs built their nests at higher locations on gravel bars (above the maximum
406 flood level), and chicks might have left before the flood. However, we should continue to
407 monitor the influence of artificial floods on not only nesting sites, but also fledged chicks
408 that cannot fly.

409 To date, the restoration strategy using both artificial and high-magnitude floods
410 to restore a shifting mosaic of floodplain habitat patches has been successful. However,
411 the sediment regime regulated by the dam was not addressed in this research.
412 Unfortunately, we do not have any monitoring data on sediment transport before and after
413 dam construction, although the longitudinal profile of the riverbed has been monitored.
414 Fortunately, there is no evidence of channel incision in the section downstream of the
415 Satsunai River Dam. Sediment deposition in the reservoir should be monitored and
416 carefully examined to understand how much sediment has been trapped by the reservoir.
417 We have to monitor how the reduction of sediment delivery from the dam alters the
418 morphology of the downstream river channel and thereby the downscaled shifting mosaic
419 in the Satsunai River. As an adaptive management project, we should reconsider and
420 revise the artificial flood scheme in the future according to the monitoring results
421 regarding recruitment and succession of riparian tree species, the fate of plovers, and also
422 the effect of the next high-magnitude flood.

423

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425

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545 **Figures and Table captions.**

546

547 Fig. 1 Watershed of the Satsunai River and kilometre posts

548

549 Fig. 2 Hydrographs (water discharge) of natural flows (flows into the reservoir from the
550 upper basin) and controlled flows (flows out of the reservoir). A, B, and C are
551 hydrographs in 2012, 2013, and 2014, respectively.

552

553 Fig. 3 Forest expansion over the gravel bars and floodplains of the Satsunai River

554

555 Fig. 4 A mosaic pattern of floodplain forest patches along the KP 41.4 km - KP 45.4 km
556 segment. We compared air-photos of 1987, 1991, 1995, 2000, 2005, 2010, and 2015 to
557 determine age classes of forest patches.

558

559 Fig. 5 Age distribution of mosaic patches in the entire study segment (KP 25 km to KP 48
560 km). The areas of floodplain age classes less than 25 years were approximated by the
561 exponential decay curve (the dotted line), indicating that the pattern of floodplain patches
562 has been sustained in a state of dynamic equilibrium.

563

564 Fig. 6 NMDS ordination of quadrats (A) and tree species (B). Tree assemblage changes
565 with increasing age classes arranged along axis-1 of the NMDS ordination (A). *Salix*
566 *arbutifolia* was distributed near the centre of the NMDS ordination, indicating that it is
567 a common species among all age classes (B). Salicaceous species was distributed on the
568 left side of the ordination, whereas late-successional species such as *Ulmus davidiana*
569 *var. japonica*, *Acer mono*, and *Quercus crispula* are distributed on the right side of the
570 ordination (B).

571

572 Fig. 7 Elevation of nest sites with reference to the maximum level of the artificial flood.
573 The negative value of relative elevation means that the nest sites were submerged by the
574 flood.

575

576 Table 1 Species richness and diversity and the dominance of Salicaceous species. Values
577 are the mean \pm SD. To investigate the species composition of riparian trees, five quadrats
578 were established in each of the age classes of forest patches; therefore, 25 quadrats in
579 total were distributed over the gravel bars and floodplains from KP 25 km to KP 48 km.

580

581 Table 2 Abbreviations for species name

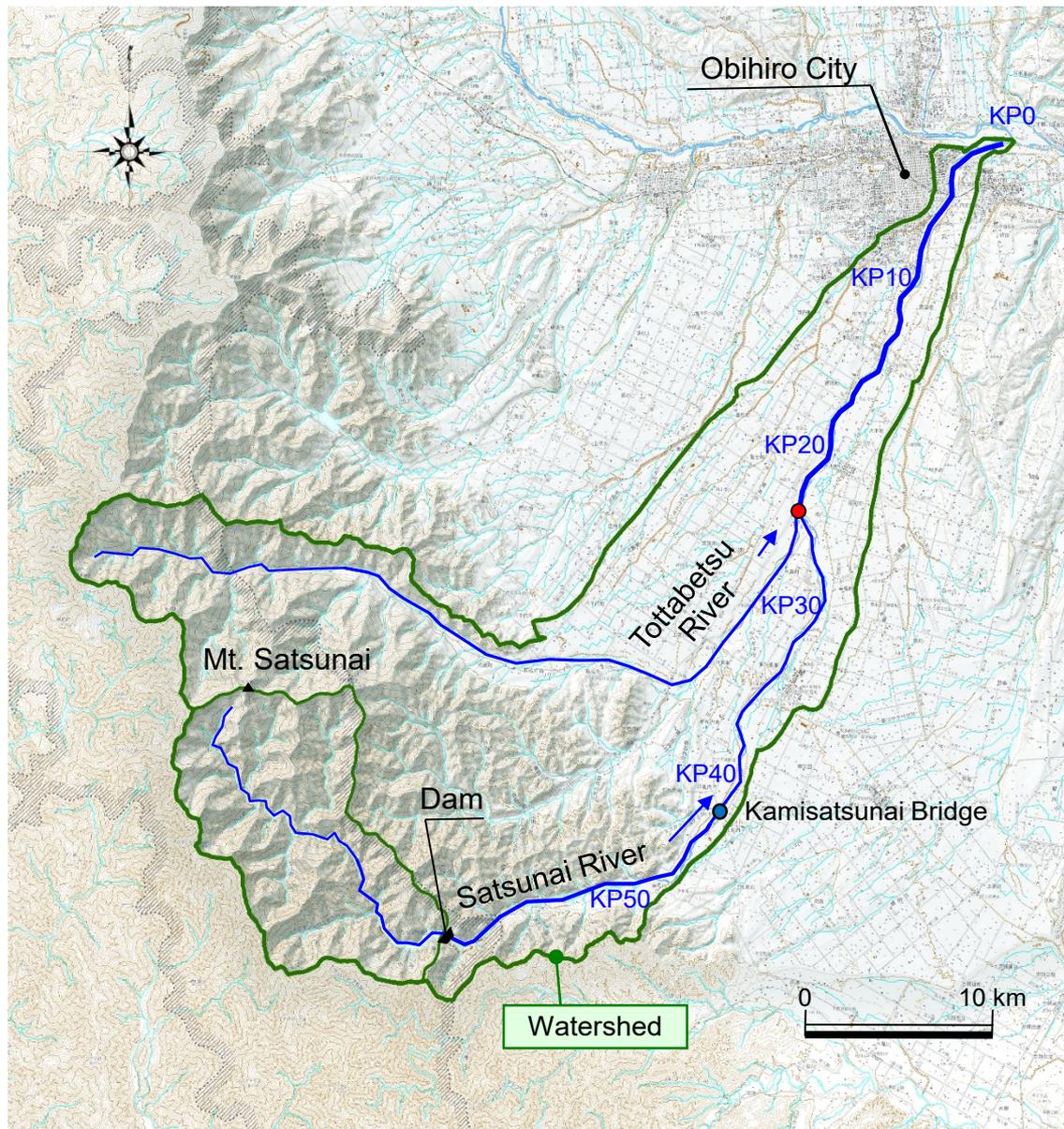
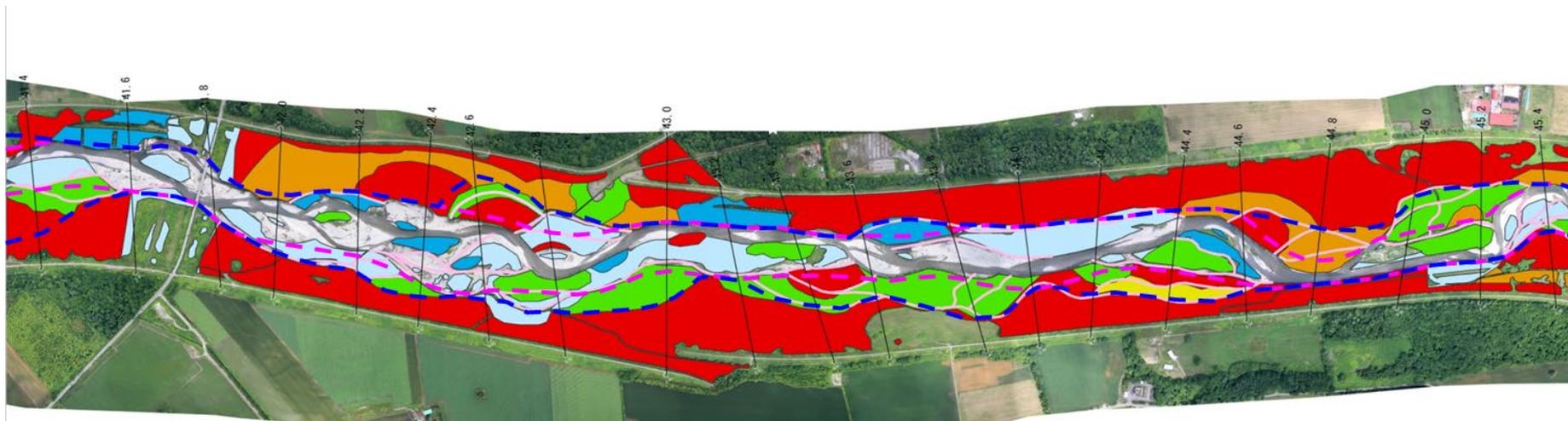


Fig. 1 Watershed of the Satsunai River and kilometre posts



Fig. 3 Forest expansion over the gravel bars and floodplains of the Satsunai River



- Areas within $\tau * > 0.05$ by the 2011 flood (1/20 years recurrence interval)
- Areas within $\tau * > 0.05$ by the artificial flood

- Age class
- >25
 - 21-25
 - 16-20
 - 11-15
 - 6-10
 - 1-5 years

Fig. 4 A mosaic pattern of floodplain forest patches along the KP 41.4 km - KP 45.4 km segment. We compared air-photos of 1987, 1991, 1995, 2000, 2005, 2010, and 2015 to determine age classes of forest patches.

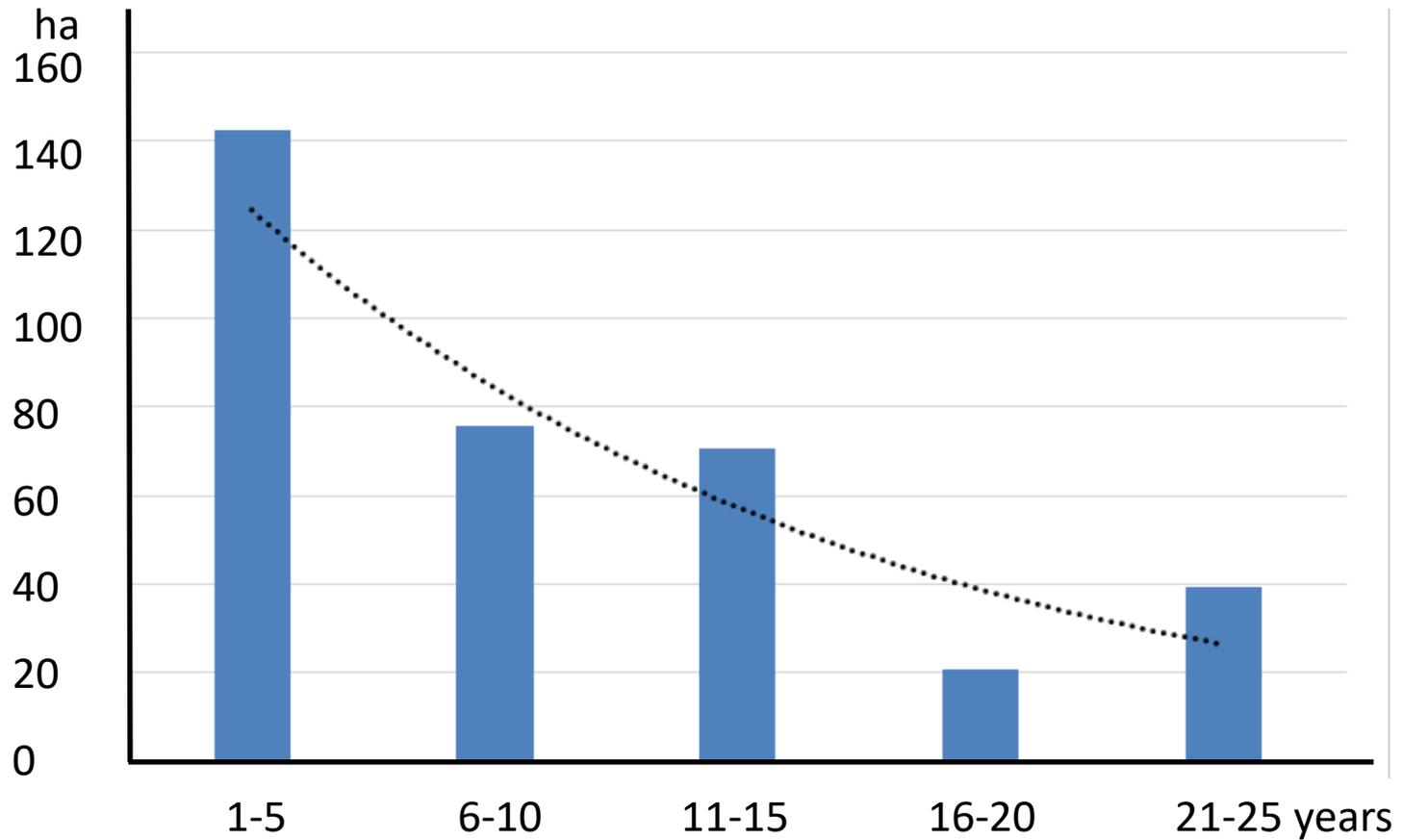


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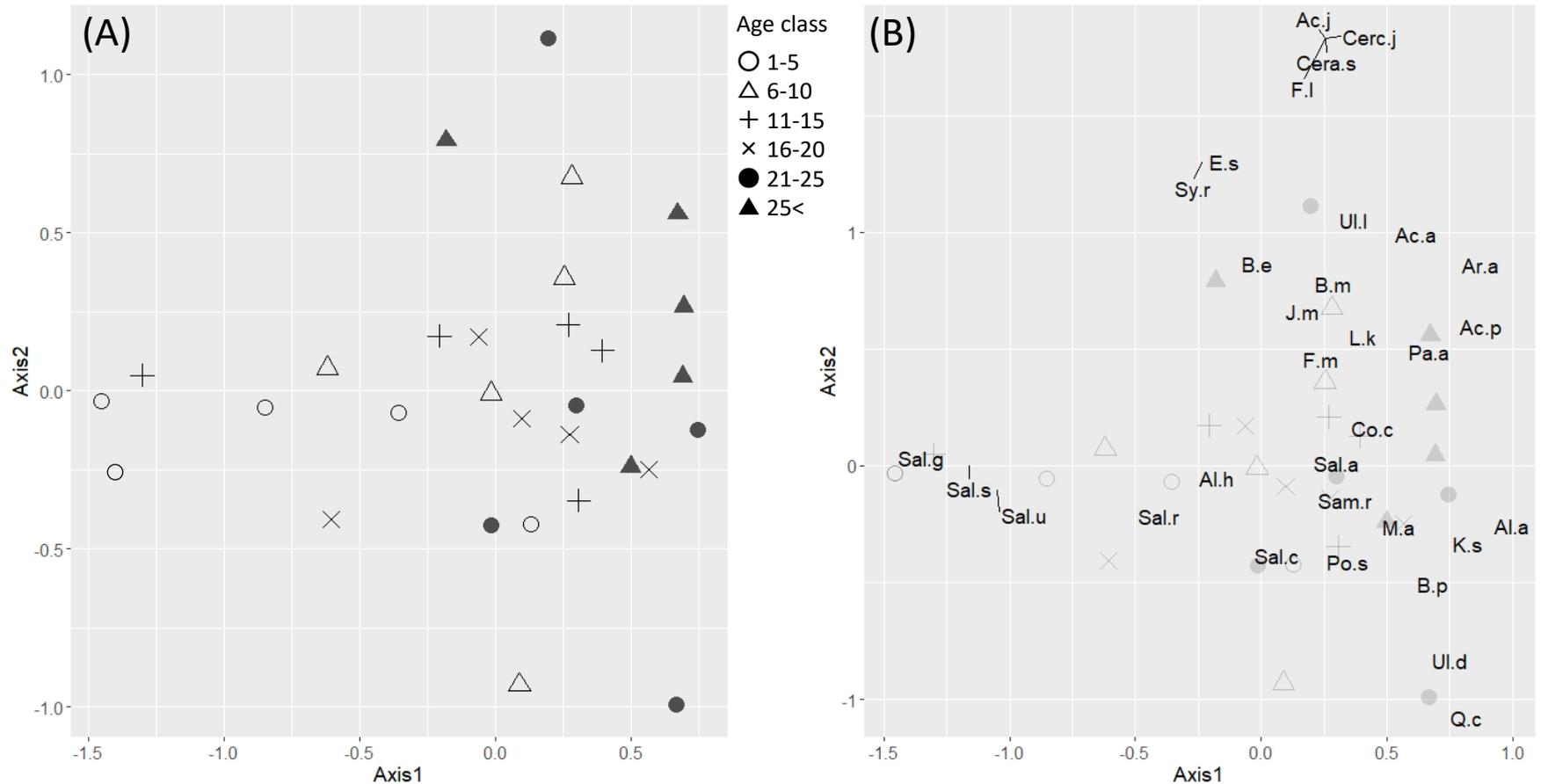


Fig. 6 NMDS ordination of quadrats (A) and tree species (B).

Tree assemblage changes with increasing age classes arranged along axis-1 of the NMDS ordination (A). *Salix arbutifolia* was distributed near the centre of the NMDS ordination, indicating that it is a common species among all age classes (B). Salicaceous species was distributed on the left side of the ordination, whereas late-successional species such as *Ulmus davidiana* var. *japonica*, *Acer mono*, and *Quercus crispula* are distributed on the right side of the ordination (B).

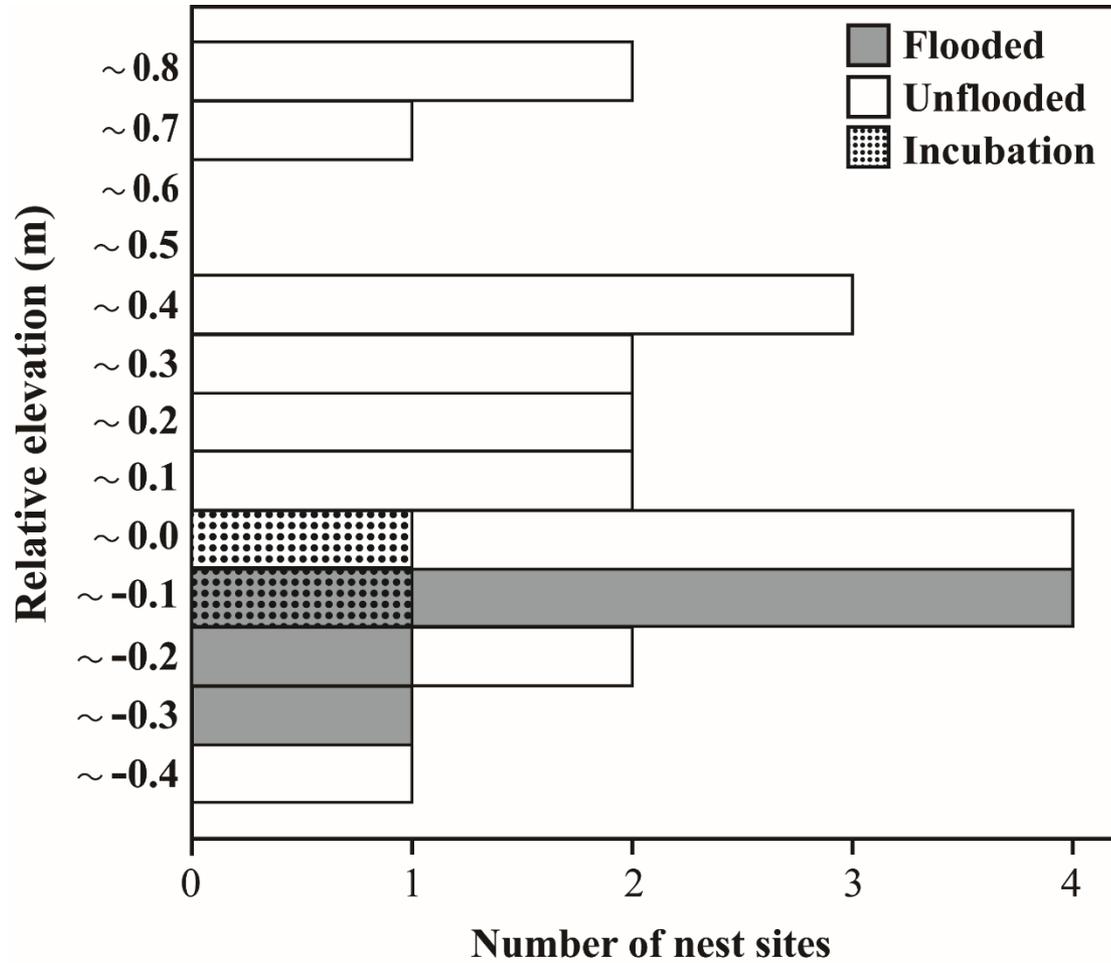


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		Age class					
		1-5	6-10	11-15	16-20	21-25	25<
Species richness		4.40 \pm 1.67	8.00 \pm 4.64	8.20 \pm 3.70	8.00 \pm 1.58	10.80 \pm 5.31	9.40 \pm 1.34
Simpson diversity index (D)		0.61 \pm 0.12	0.45 \pm 0.32	0.51 \pm 0.15	0.55 \pm 0.10	0.44 \pm 0.15	0.61 \pm 0.03
Shannon diversity index (H')		1.12 \pm 0.37	0.97 \pm 0.69	0.98 \pm 0.33	1.08 \pm 0.16	0.97 \pm 0.30	1.18 \pm 0.08
Basal Area (m ² /ha)	Total	17.00 \pm 7.46	24.40 \pm 4.48	29.08 \pm 9.87	36.04 \pm 18.93	49.39 \pm 8.14	41.03 \pm 5.35
	<i>Salix arbutifolia</i>	1.08 \pm 1.93	9.46 \pm 10.59	5.48 \pm 4.65	16.22 \pm 16.48	19.87 \pm 19.39	14.02 \pm 7.46
	Other Salicaceous species	15.92 \pm 6.95	13.53 \pm 7.65	22.93 \pm 13.05	18.84 \pm 10.88	24.98 \pm 17.10	24.63 \pm 7.21
	Other than Salicaceous species	0.00 \pm 0.00	1.42 \pm 1.52	0.67 \pm 0.43	0.98 \pm 0.58	4.54 \pm 3.69	2.38 \pm 1.00
Relative dominance (%)	<i>Salix arbutifolia</i>	6.49 \pm 9.03	35.44 \pm 38.63	22.34 \pm 20.79	37.34 \pm 30.23	38.55 \pm 38.04	34.06 \pm 17.57
	Other Salicaceous species	93.51 \pm 9.03	59.10 \pm 36.35	75.17 \pm 21.12	60.03 \pm 31.30	51.97 \pm 37.44	60.20 \pm 16.66
	Other than Salicaceous species	0.00 \pm 0.00	5.46 \pm 5.80	2.49 \pm 1.76	2.63 \pm 1.59	9.48 \pm 8.36	5.74 \pm 2.17

Table 2 Abbreviations for species name

Abbreviations	Species name
Ac.j	<i>Acer japonicum</i> Thunb.
Ac.p	<i>Acer pictum</i> Thunb. subsp. mono (Maxim.) H.Ohashi
Ac.a	<i>Acer amoenum</i> Carriere var. <i>matsumurae</i> (Koidz.) K.Ogata
Al.h	<i>Alnus hirsuta</i> (Spach) Turcz. ex Rupr. var. <i>hirsuta</i>
Al.a	<i>Alnus alnobetula</i> (Ehrh.) K.Koch subsp. <i>maximowiczii</i> (Callier) Chery
Ar.a	<i>Aria alnifolia</i> (Siebold et Zucc.) Decne.
B.e	<i>Betula ermanii</i> Cham.
B.m	<i>Betula maximowicziana</i> Regel
B.p	<i>Betula platyphylla</i> Sukaczew var. <i>japonica</i> (Miq.) H.Hara
Cerc.j	<i>Cercidiphyllum japonicum</i> Siebold et Zucc. ex Hoffm. et Schult.
Sal.a	<i>Salix arbutifolia</i> Pall.
Co.c	<i>Cornus controversa</i> Hemsl. ex Prain
E.s	<i>Euonymus sieboldianus</i> Blume
F.l	<i>Fraxinus lanuginosa</i> Koidz. f. <i>serrata</i> (Nakai) Murata
F.m	<i>Fraxinus mandshurica</i> Rupr.
J.m	<i>Juglans mandshurica</i> Maxim. var. <i>sachalinensis</i> (Komatsu) Kitam.
K.s	<i>Kalopanax septemlobus</i> (Thunb.) Koidz.
L.k	<i>Larix kaempferi</i> (Lamb.) Carri?re
M.a	<i>Morus australis</i> Poir.
Po.s	<i>Populus suaveolens</i> Fisch.
Pa.a	<i>Padus avium</i> Mill.
Cera.s	<i>Cerasus sargentii</i> (Rehder) H.Ohba var. <i>sargentii</i>
Q.c	<i>Quercus crispula</i> Blume
Sal.g	<i>Salix gracilistyla</i> Miq.
Sal.s	<i>Salix schwerinii</i> E.L.Wolf subsp. <i>yezoensis</i> (C.K.Schneid.) Vorosch.
Sal.r	<i>Salix rorida</i> Laksch.
Sal.u	<i>Salix udensis</i> Trautv. et C.A.Mey.
Sam.r	<i>Sambucus racemosa</i> L. subsp. <i>kamtschatica</i> (E.L.Wolf) Hult?n
Sy.r	<i>Syringa reticulata</i> (Blume) H.Hara
Sal.c	<i>Salix cardiophylla</i> Trautv. et C.A.Mey. var. <i>urbaniana</i> (Seemen) Kud?
Ul.d	<i>Ulmus davidiana</i> Planch. var. <i>japonica</i> (Rehder) Nakai
Ul.l	<i>Ulmus laciniata</i> (Trautv.) Mayr ex Schwapp.

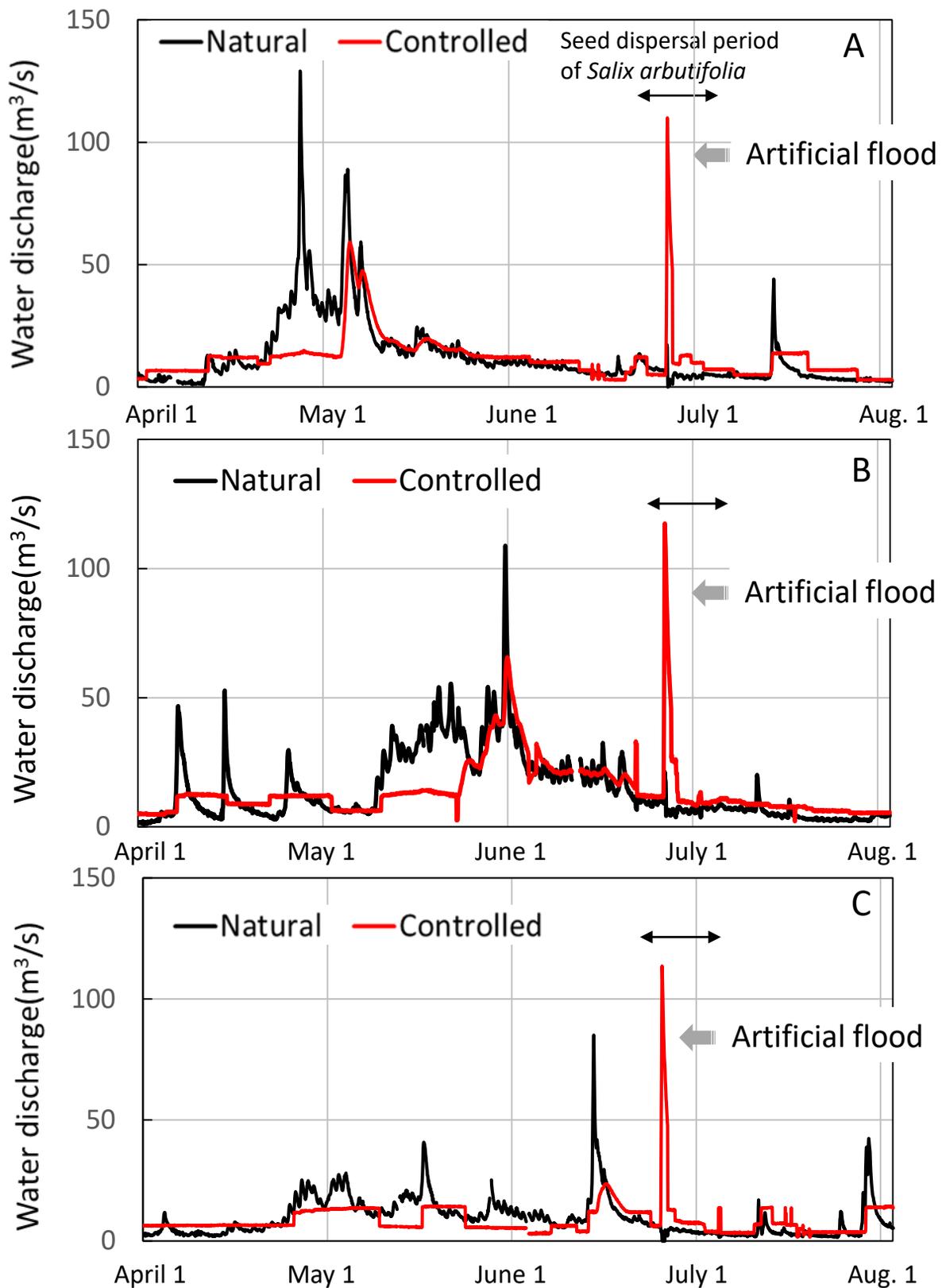


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