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

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Abstract

A braided gravel-bed river provides essential habitats for various plants and animals. However, human regulation of rivers, such as dams, channelization, and other engineering works, alter flow and sediment regimes, which generally cause the degradation of river and riparian ecosystems. One of the prominent changes prevailing in Japanese rivers is forest expansion over gravel bars, and many native plants and animals that depend on gravel-bed habitat are now endangered. The Satsunai River is typical of rivers experiencing forest expansion, so the Japanese government launched a restoration project in 2012 to partially restore its riparian ecosystems. This is a large-scale experiment developed jointly by an interdisciplinary science team and river managers, who conduct monitoring and evaluation under an adaptive management scheme. The main measure to restore gravel bed habitat was an artificial flood regime, releasing a maximum water volume of 120 m^3/s, which was a 2-year return period flood before dam construction. A unique feature of the project is that we considered the role of high-magnitude floods with recurrence intervals greater than 20 years after dam construction. We hypothesize that the artificial floods can be timed seasonally to create sites for regeneration and nesting of riparian species, and the high-magnitude floods contribute to maintaining a shifting mosaic structure of floodplain forest and unvegetated gravel-bar patches. We also used critical non-dimensional shear stress analysis to define “flood-disturbance areas” that can be disturbed under the artificial flow regime created by a dam. Artificial floods have been initiated once a year since 2012 at the end of June, synchronized with the seed dispersal period of *Salix arbutifolia*, which is endangered and a high conservation priority in the project. Thus far, the idea of setting floodplain-disturbance areas and the strategy of using both artificial and high-magnitude floods to restore a shifting mosaic of floodplain habitat patches is appropriate, as we found successful regeneration of *S. arbutifolia* and an exponential decay curve of the age distribution of floodplain forest patches. However, the sediment regime regulated by the dam was not addressed in this research, so future

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

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

1. Introduction

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

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

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

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

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

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

The main measure to restore the gravel bed in the Satsunai River is artificial flooding, releasing a maximum water volume of 120 m^3/s at the end of June, synchronized with the seed dispersal period of *S. arbutifolia*. This magnitude of flow was a 2-year return period flood before dam construction (Nakamura and Shin, 2001). A unique aspect of the project is that we considered the role of high magnitude floods with recurrence interval greater than 20 years after dam construction. This magnitude of flood may exceed the capability of dam operations aiming to completely regulate flood peaks. We hypothesize that the artificial flood can create seasonal regeneration and nesting sites for riparian species, and the high-magnitude flood contributes to maintaining a shifting mosaic structure of floodplain forest patches within a limited extent of the valley floor.

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

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

2. Methods

2.1 Study area

The Satsunai River (catchment area; 725 km^2) runs from Mt. Satsunai (42°41'N, 142°47'E; 1895 m above sea level) in the Hidaka Mountain Range to the Tokachi River in Hokkaido Prefecture, Japan (Fig. 1). The average gradient of the river is 1/100～1/250, and its whole river width in flood stage ranges from 400 m to 500 m. The geology of the basin is composed of sedimentary rocks in the Hidaka Mountain Range, plutonic and metamorphic rocks (granite, gabbro, gneiss, hornfels, and peridotite) in upstream areas, and unconsolidated Quaternary deposits constituting terrace and alluvial fans in downstream areas. The mean annual air temperature from 2010 to 2015 was 5.0 ~ 6.0°C, and the monthly mean air temperature ranged from -8.4°C in January to 18.6°C in August. The average annual precipitation between 1981 and 2010 was 1255 mm (Kamisatsunai observatory; 42°38'N, 143°05'E) (Japan Meteorological Agency 2020, http://www.jma.go.jp/jma/menu/report.html.).

Partial operation of the Satsunai River Dam began in 1997, and full operation began in 1998. The catchment area upstream of the dam is 118 km^2, the maximum volume of water stored is 54 million m^3, and 150 m^3/s was the maximum water discharge that can be released from the sluice gates of the dam. If the capacity of dam reservoirs exceeds the critical water level, the emergency gates located at the top of the dam will release all the water discharge coming into the reservoir from upper basins.

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

Small peak flows are strongly regulated by the dam; specifically, snowmelt peaks in the spring are reduced substantially (Fig. 2). Since completion of the dam, there was a large flood on September 1-7, 2011, initiated by heavy rainfall associated with No. 12 Typhoon, reaching 432.5 mm in total precipitation for 7 days at Nukabira gauging station. The peak discharge was 285 m^3/s at Kamisatsunai Bridge (KP 41.8 km, see Fig. 1, watershed area is 189 km^2), the recurrence interval of which was estimated as once in 20 years after dam construction. Such high-magnitude floods occurring in the summer and autumn seasons are also important in shaping the river and floodplain geomorphology of the Satsunai River.

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

2.2 Restoration project

After thorough discussion within the scientific committee of this project, we decided to initiate an artificial flood at the end of June, given the constraints of water use, power generation, and flood control. The artificial flood was released from the sluice gates once a year from 2012 to present (except in 2016 and 2017 due to construction works in downstream areas) and synchronized with the seed dispersal period of *S. arbutifolia*. In this study, we analysed the monitoring results of artificial floods between 2012 and 2014 (Fig. 2). Seed dispersal of *S. arbutifolia* occurs from late June to early July, which is later than that of other Salicaceous species (Nakamura and Shin, 2001). To create an artificial flood, the reservoir water level has been lowered from 474 m (no flood risk period; November 1 - June 30) to 466 m in elevation (flood risk period; July 1 – October 31), which generates the flood for approximately 30 hours, with a peak discharge of approximately 120 m^3/s (Fig 2).

Another important aspect considered in project planning was the magnitude of the artificial floods. Unfortunately, approximately 120 m^3/s was the maximum water discharge that can be released from the dam, owing to the sluice gate structure and water resource allocation. This magnitude of flood was a 2-year return-period flood before dam construction. We expected that the discharge of the artificial flood alone would not be large enough to maintain gravel bars and a downscaled shifting mosaic of floodplain forest patches. Thus, we first discussed “flood-disturbance areas” that can be maintained under the altered flow regime. Second, we built a two-pronged strategy, in which high-magnitude floods are expected to shape the extent of a shifting mosaic within the flood-disturbance areas, while the artificial flood is used for providing non-forested gravel bars which function as germination habitats for Salicaceous species and nesting habitats for plovers. The water discharge of such a high-magnitude flood (e.g., the flood in 2011) can be reduced somewhat by dam operation, but a large amount of water should be released downstream for several days due to the limited capacity of dam and reservoir. During heavy rain, the floodwaters released from the dam site and additional stormwaters from small tributaries would increase the magnitude of flood disturbance in the restoration project area.

2.3 Study design

1) Flood-disturbance areas

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

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

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

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

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

2) Shifting mosaic

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

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

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

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

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

3) Survey and analysis of riparian tree species

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

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

We conducted nonmetric multidimensional scaling (NMDS) to show the differences in the structure and composition of tree assemblages among the age classes of habitat patches. The basal area (BA) of each species in each quadrat was obtained from cross-sections at the base of the respective trees, and the relative dominance of each species BA in each quadrat was used for the NMDS analysis. Similarity between pairs of communities was calculated using the Bray–Curtis distance measure. We used R (R Core Team, 2019) and the vegan package (Oksanen et al, 2019) for NMDS.

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

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

3. Results

3.1 Age distribution of floodplain habitat patches

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

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

3.2 Variation in tree assemblages among the age classes

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

3.3 Influences on two plover species

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

4. Discussion

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

The Satsunai River restoration project aims to recover some of the dynamic features of braided rivers using an artificial flood synchronized with plant phenology and high-magnitude floods. However, the maximum discharge that can be released from the sluice gate is limited to approximately 120 m^3/s, which is only a two-year return-period flood before dam construction (Nakamura and Shin 2001). Thus, we decided to create a “downscaled” shifting mosaic of floodplain patches (Hall et al. 2011), delineated by $\tau_* >$ 0.05 created by the high-magnitude floods whose recurrence intervals are greater than once in 20 years after dam construction (Fig. 4), which we called the “floodplain-disturbance area” under the altered flow regime. This project is attempting to restore some dynamism of gravel bar habitat within the confines of a flow regime limited by reservoir management and lateral confines of spur dikes. It cannot restore the full landscape dynamics of the pre-dam, pre-levee watershed. In this sense, the project is "downscaling" the zone of the valley floor subject to inter-annual dynamics imposed by flooding.

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

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

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

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

Retrospective analysis in the Satsunai River conducted by Yabuhara et al. (2015) estimated that large patches (>1.5 ha) of gravel bars have disappeared due to forest encroachment: the number of large gravel bar patches decreased from 13 to 3 over approximately 8 km in river length, and thereby gravel bar-nesting birds decreased by 40%. The young age classes, including unvegetated gravel bars, are nesting and breeding sites for the two plover species. Thus, the restoration project that maintains gravel bars and prevents forest encroachment is likely to contribute to the persistence of plover populations in the Satsunai River. The monitoring results showed that many nesting sites were found in the dam-regulated downstream reaches, and the negative influences of the artificial flood on the nesting success of the two plover species were limited. Most breeding pairs built their nests at higher locations on gravel bars (above the maximum flood level), and chicks might have left before the flood. However, we should continue to monitor the influence of artificial floods on not only nesting sites, but also fledged chicks that cannot fly.

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

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Figures and Table captions.

Fig. 1 Watershed of the Satsunai River and kilometre posts

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

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

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.

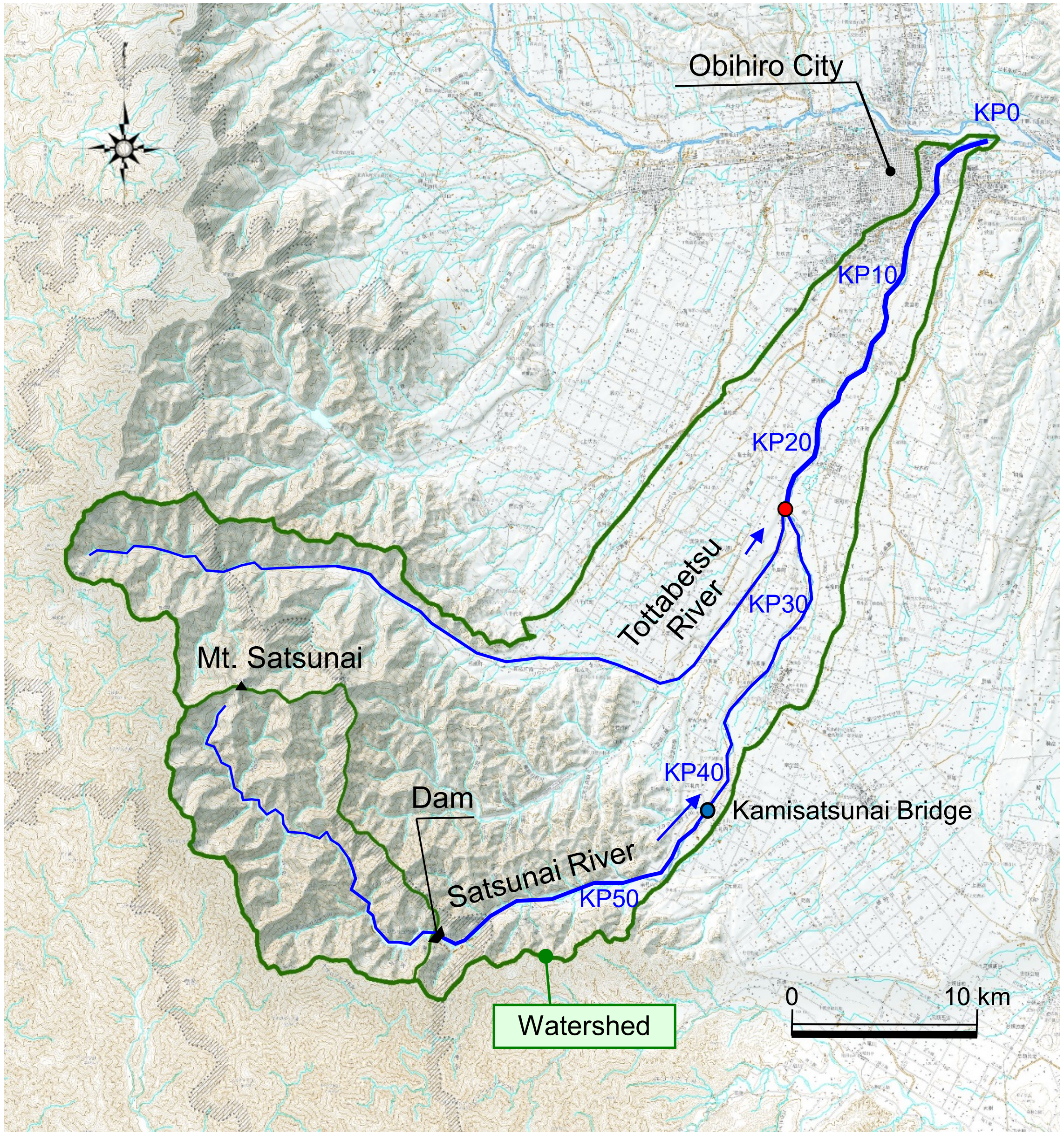
Fig. 5 Age distribution of mosaic patches in the entire study segment (KP 25 km to KP 48 km). The areas of floodplain age classes less than 25 years were approximated by the exponential decay curve (the dotted line), indicating that the pattern of floodplain patches has been sustained in a state of dynamic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

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).

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

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

Table 2 Abbreviations for species name



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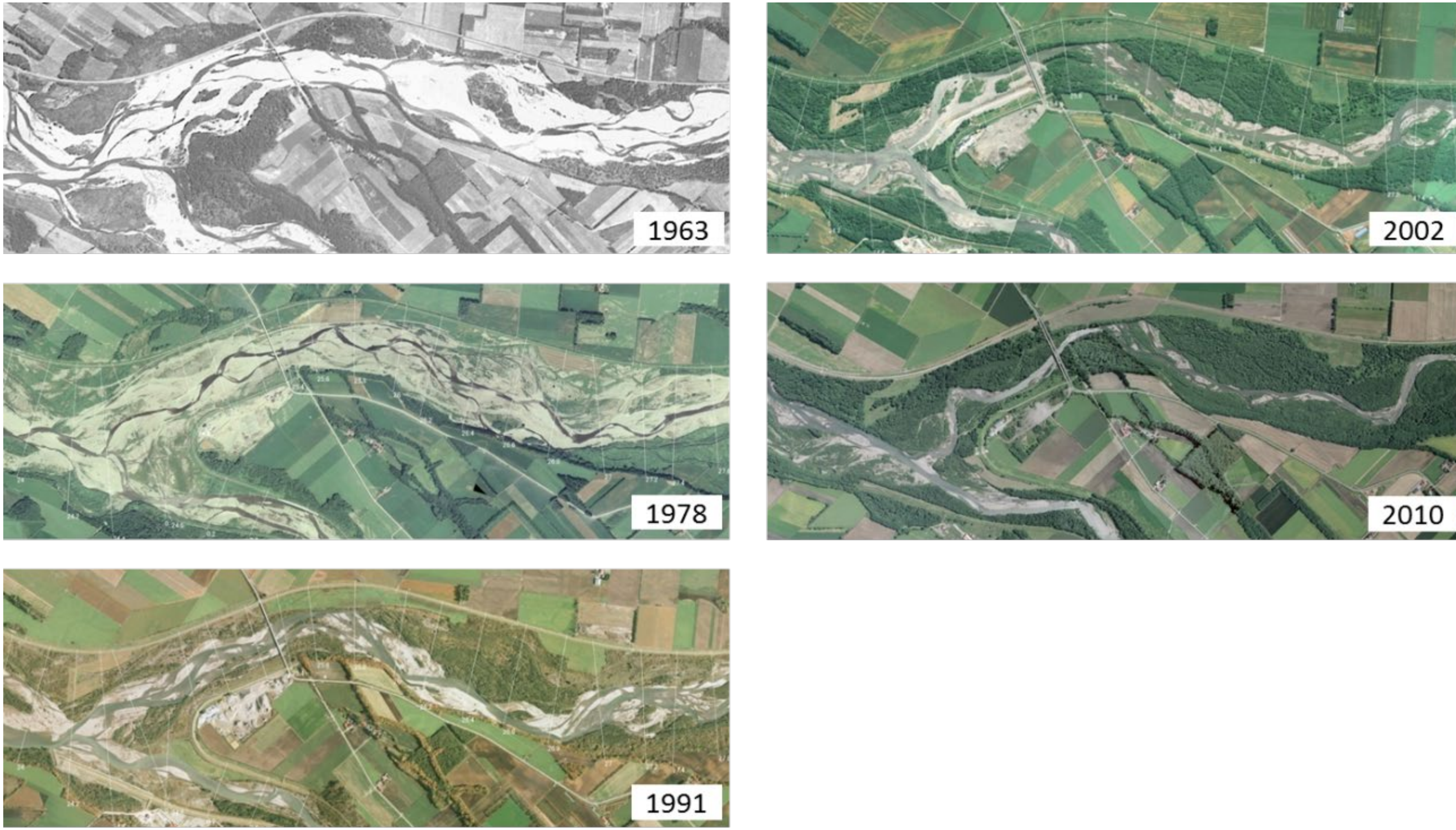

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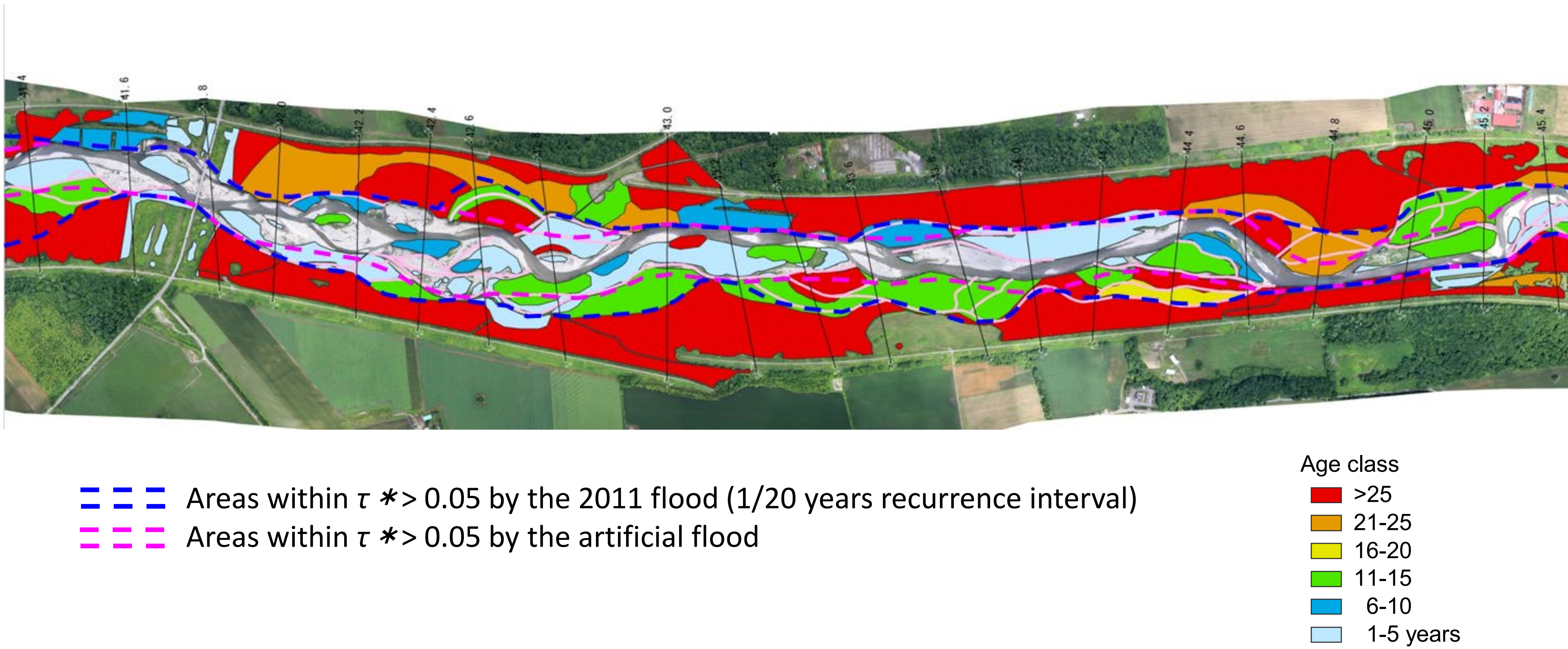

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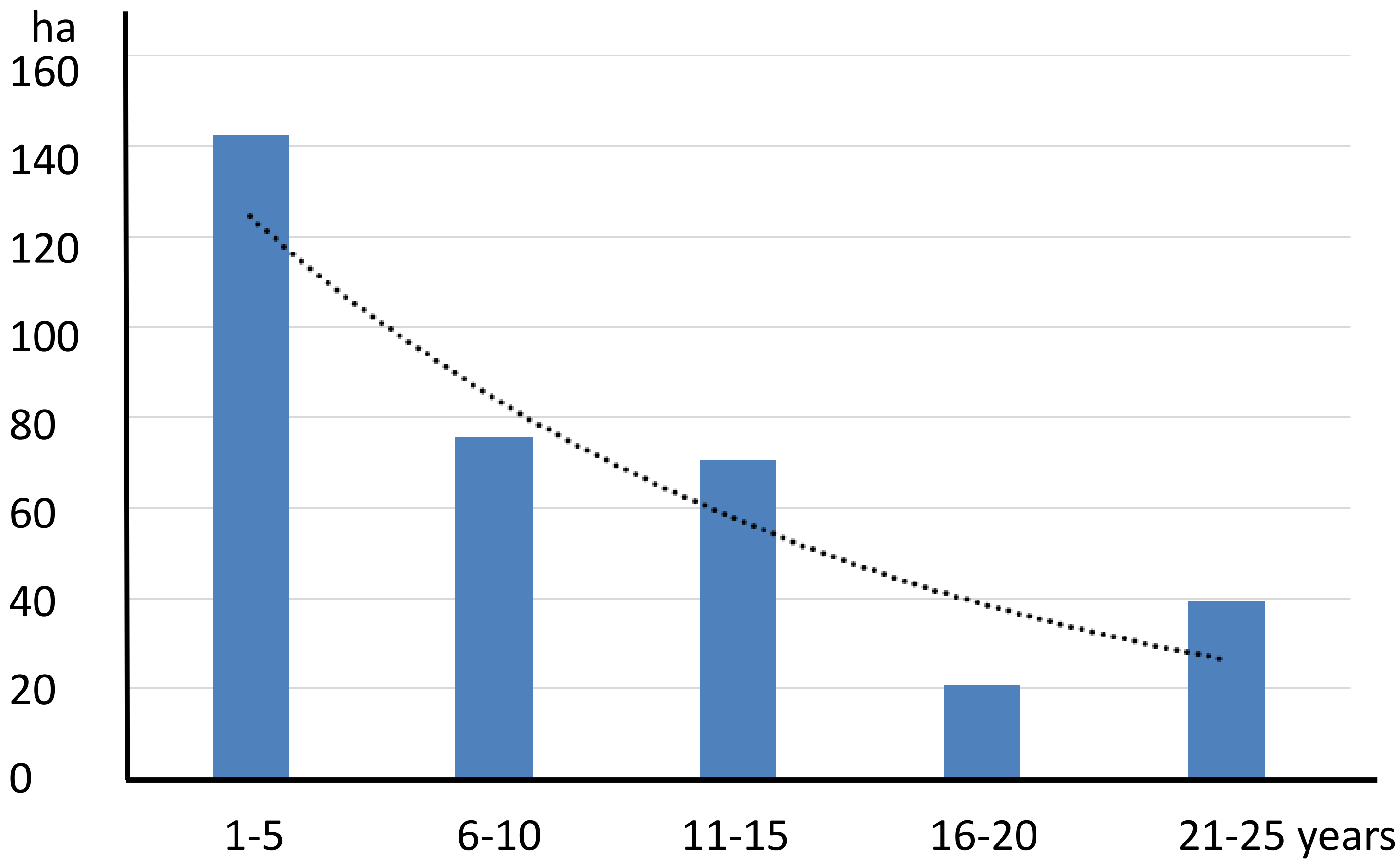

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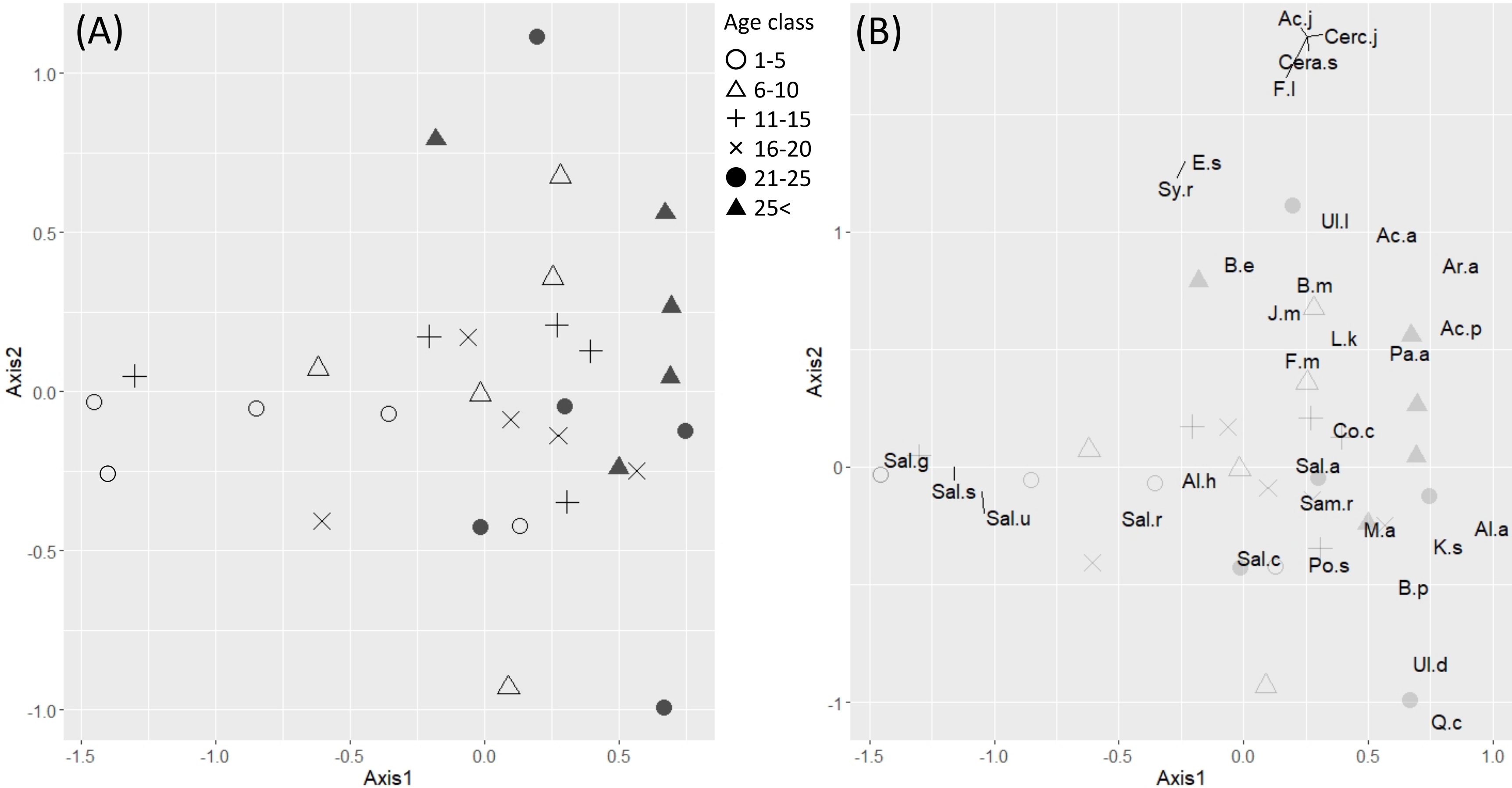

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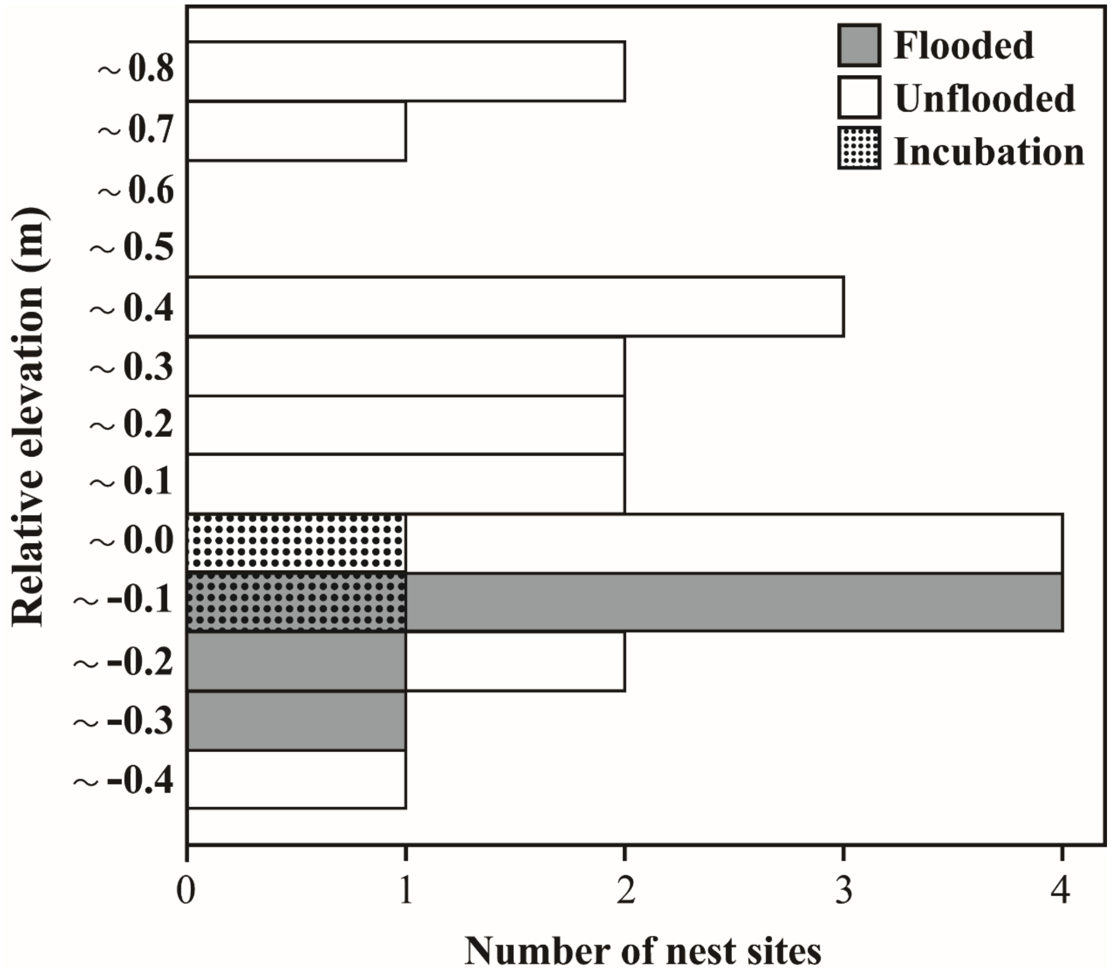

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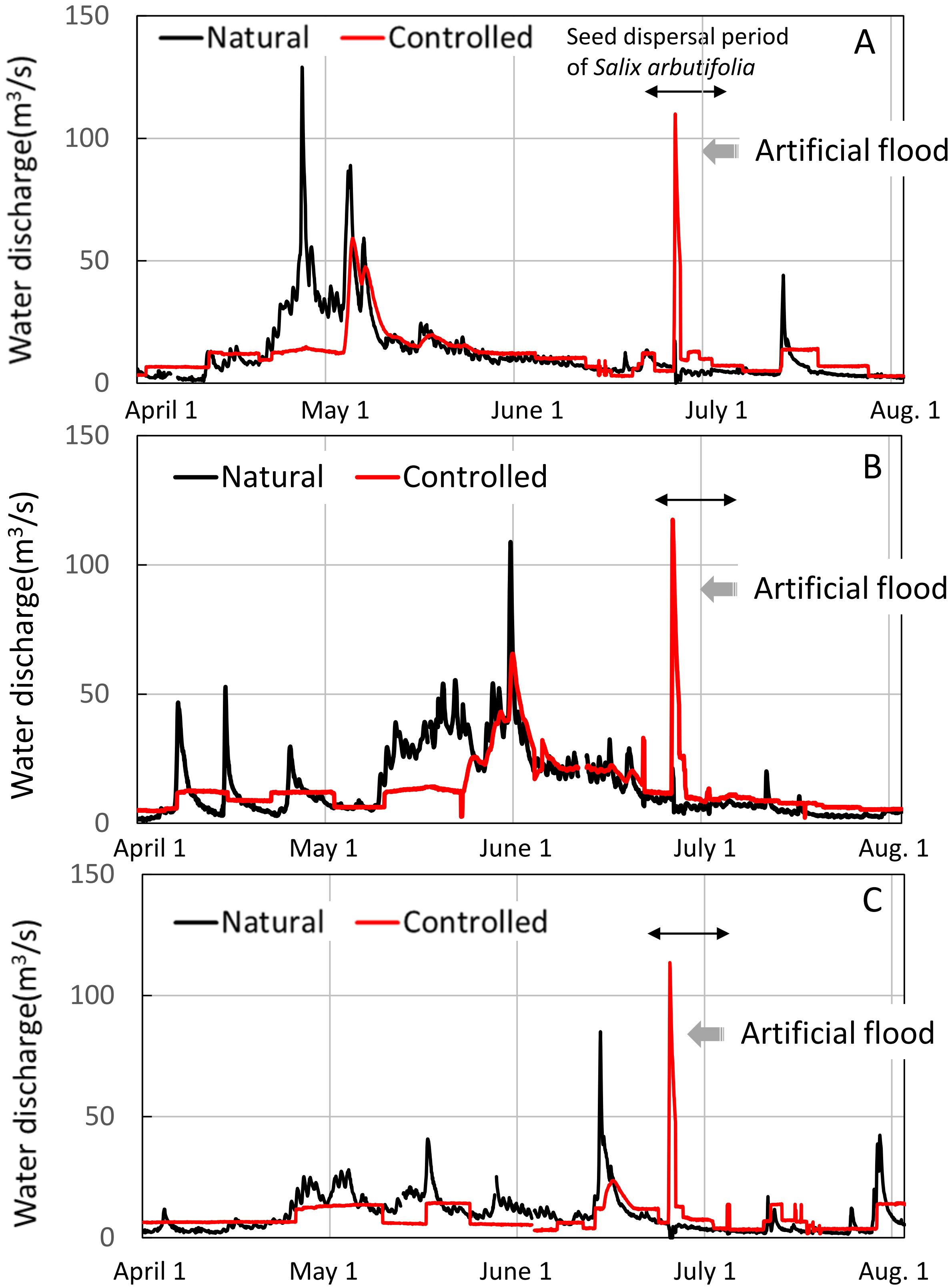
		Age class					
		1-5	6-10	11-15	16-20	21-25	25<
Species richness		4.40 ± 1.67	8.00 ± 4.64	8.20 ± 3.70	8.00 ± 1.58	10.80 ± 5.31	9.40 ± 1.34
Simpson diversity index (D)		0.61 ± 0.12	0.45 ± 0.32	0.51 ± 0.15	0.55 ± 0.10	0.44 ± 0.15	0.61 ± 0.03
Shannon diversity index (H')		1.12 ± 0.37	0.97 ± 0.69	0.98 ±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

Table 2 Abbreviations for species name

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



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