Title	Contributions of large wood to the initial establishment and diversity of riparian vegetation in a bar-braided temperate river
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Citation	Plant Ecology, 213(5), 735-747 https://doi.org/10.1007/s11258-012-0037-1
Issue Date	2012-05
Doc URL	http://hdl.handle.net/2115/49208
Rights	The final publication is available at www.springerlink.com
Type	article (author version)
File Information	PE213-5_735-747.pdf

Word count (from Abstract to References): 5976

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Contributions of large wood to the initial establishment and diversity of riparian vegetation in a bar-braided temperate river

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ABSTRACT

The purpose of this study was to examine the effects of large wood (LW) on the physical environment and the initial establishment of vascular plant species in the Rekifune River, a large bar-braided monsoonal river in Japan. The physical environment and the diversity and composition of plant species were compared in relation to the orientation of LW pieces. We found that shading effects were more prevalent in the immediate vicinity of LW pieces than in quadrats distant from LW. The effect was especially strong at the center of LW jams (the "jam center"). Fine sand and silt were concentrated in the quadrats downstream from the LW pieces. In contrast, cobbles dominated the upstream quadrats. The highest diversity was found in the jam center, while intermediate values were observed in the quadrats surrounding LW. Indicator Species Analysis detected 21 indicator species only in the jam center. The LW jams favored the deposition of plant fragments and sediment and created shaded areas within and around the structures. Buried seeds may be transported with LW during a flood, and seeds dispersed by wind and stream flows may be trapped by the complex structure of LW jams. The specific environmental conditions and the trapping of seeds and plant fragments result in the early establishment of mid-successional tree species at LW jams. In conclusion, the LW pieces deposited on gravel bars altered the light and substrate conditions and thereby provided specific safe sites for various riparian plant species.

KEYWORDS

large wood, riparian vegetation, indicator species, species diversity, gravel bar, braided river

INTRODUCTION

The geomorphic and ecological roles of large wood (LW) in river ecosystems have been examined in many previous studies (Maser and Sedell 1994; Harmon et al. 1986). One of the primary functions of LW is forming pools and habitat cover (Inoue and Nakano 1998; Nagayama et al. 2009; Nakamura and Swanson 1994). Another well-known function of LW is the retention of sediment, organic matter and nutrients (Wondzell and Swanson 1999; Nakamura and Swanson 1993; Bilby and Likens 1980). However, most of these functions represent instream effects on aquatic organisms and material flows. The volume and location of LW change along the longitudinal gradient of a watershed (Gurnell et al. 2002). Instream LW is abundant in small streams, whereas LW on bars and floodplains dominates in intermediate and large rivers (Seo and Nakamura 2009). However, the majority of studies addressing LW have focused on the influence of instream LW on the aquatic biota of small streams, and studies on the effects of LW deposited on bars and floodplains in large rivers are scarce.

One of the ecological functions of LW pieces deposited on bars is the provision of habitats for the regeneration of various riparian plant species (Naiman et al. 1998). This function is evident in large braided rivers where a wide valley floor develops because abundant LW pieces are scattered over gravel bars and floodplains. Recently, several studies in Europe and the United States have examined the geomorphic processes involved in island development and the establishment of vegetation associated with LW (Abbe and Montgomery 1996; Gurnell et al. 2000), but no such studies have been conducted in the temperate zone in Asian monsoonal regions. Previous studies have clearly indicated that LW facilitates the deposition of fine sediment, organic fragments, and nutrients and thereby creates heterogeneous regeneration habitats for plant species. However, very few studies have focused on the contribution of LW deposited on bars and floodplains to the diversity of plant species.

Pettit and Naiman (2006) investigated riparian woody plants in a semi-arid South African river and found that the abundance and species richness of these plants in LW areas were significantly greater than in open reference areas. However, these results may differ from the situation in the Asian monsoonal temperate zone, where a humid climate dominates. The relatively high humidity in Japan may alter the effect of LW on soil moisture, and floods associated with snowmelt, typhoons, or localized torrential downpours in northern Japan are expected to play an important role in distributing LW pieces and in determining the residence time of LW on gravel bars. Furthermore, Pettit and Naiman (2006) only surveyed naturally established woody plant species, although this study included an examination of the soil seed bank for herbaceous and woody plants. Francis et al. (2008) investigated the influence of LW on plant diversity in the Taliamento River in Italy. They found that specific features of LW jams, notably the scour pool depth at rootwads and the accumulation of fine sediments, were significant with respect to plant diversity.

The objective of the present study was to examine the effects of LW on the physical environment and the initial establishment of vascular plant species in a large monsoonal river. We set sampling quadrats at sites containing a single LW piece and at sites with LW jams (accumulations of multiple LW pieces). The physical environment and the diversity and composition of plant species in these quadrats were compared in relation to the orientation of the pieces. LW pieces on gravel bars are generally aligned parallel to the axis of the active channel (Gurnell et al. 2002; Edwards et al. 1999), and the upstream and downstream ends of the LW pieces may experience considerably different hydraulic conditions during a flood. Therefore, we hypothesized that the structural complexity created by LW pieces increases the heterogeneity of regeneration habitats and thereby enhances the species diversity of riparian plants. Additionally, the species diversity and composition may differ among locations around LW pieces.

This study focused on the early successional stage of riparian vegetation because relatively small differences in species responses in the initial years after a disturbance can have a substantial influence on the future development of plant communities (Bråkenhielm and Liu 1998; Halpern and Spies 1995). We examined the establishment of plant species on gravel bars in the active channel, but not in floodplains because the presence of LW pieces is more significant for the regeneration of riparian species on active bars than in forested floodplains (Pettit and Naiman 2005).

STUDY AREA

The Rekifune River drains the Hidaka mountain range and flows into the Pacific Ocean (Fig. 1). The watershed area associated with the river is 558.5 km^2, and the length of the river is 64.7 km. At the Taiki meteorological station (42°30'N, 143°16'E), which is located near the river, the annual precipitation in 2010 was 1,142 mm; the mean annual air temperature was 6.4 °C; and the mean monthly air temperature ranged from -8.1 °C in January to 21.9 °C in August (Japan Meteorological Agency 2011). The watershed is covered by deposits of Quaternary pyroclastic flows as well as pudding and sandstones.

At the study site, which is situated at the “bar-braided site” of Shin and Nakamura (2005), the river displays bar-braided channels with broadly distributed gravel bars and floodplains. The channel floor is approximately 1 km wide, with an active channel extending for approximately 300 m. The bed gradient is approximately 0.0046. The mean diameter of bed materials obtained using linear-lattice sampling methodology was 11.5 ± 6.6 cm (mean ± SD).

Mature riparian forests are widely distributed along the river, with the species composition being relatively constant throughout the study reach. The pioneer tree species in the area include *Chosenia arbutifolia*, *Toisusu urbaniana*, *Populus maximowiczii*, and *Alnus hirsuta*, whereas late successional species include *Ulmus davidiana* var. *japonica*, *Fraxinus mandshurica* var. *japonica* and *Quercus crispula*. The dominant indigenous herbs on gravel bars are *Picris hieracioides subsp. glabrescens*, *Setaria viridis* and *Artemisia montana,* and the most common alien herb species are *Silene armeria* and *Conyza canadensis*.

Floods occur in early spring associated with snowmelt and in summer due to typhoons or localized torrential downpours. The maximum and minimum water discharges in 2009 at the gauging station near the study site were 322.84 m^3/s and 7.67 m^3/s, respectively. The channel floor is disturbed frequently due to lateral movement of braided channels during floods, and many gravel bars have been maintained throughout the river.

Large wood pieces transported into the bar-braided section of the river during a flood tend to become stranded over gravel bars (Fig. 2). Because of the frequent movement of active channels, the majority of LW pieces on gravel bars may be washed away by successive floods. However, when the direction of flow shifts slightly or abruptly to another direction, some pieces will remain on bars and provide regeneration habitats for riparian plants.

The herbaceous and woody plant species found on the gravel bars are mostly anemochory, but their seeds can be secondarily dispersed by water flows. Some herbaceous species, such as *Phragmites japonica*, vegetatively extend rhizome runners or stolons to allow them to grow in unstable environments and expand their colonies. Additionally, some woody plant species, such as Salicaceae species, sprout from buried shoots and stems.

METHODS

Sampling design

A total of 28 sites were selected on gravel bars within the active channel. The majority of the observed LW pieces were aligned parallel to the axis of the active channel. Sampling quadrats measuring 1 m x 1 m were set at each site in positions defined relative to the orientation of the LW piece (Figs. 2 and 3). We established four neighboring quadrats at each sampling site. These quadrats were located upstream and downstream from the LW and on both sides of the center of the LW. Another four sampling quadrats were established with the same orientations but at a distance of 1 m from the neighboring quadrats. Because it is probable that the effects of LW on the physical environment of gravel bars decrease with increasing distance from the LW, an additional four quadrats, referred to as distant quadrats, were established 4 m from each neighboring quadrat. Several quadrats were intentionally omitted because it seemed probable that other pieces surrounding the target LW piece would have influenced the sampling quadrats in some way (e.g., via sediment deposition). We observed many LW jams (accumulations of multiple LW pieces) in the study area. An additional “jam center” quadrat was established within each LW jam at its center (Fig. 3). Because numerous LW pieces were scattered throughout each gravel bar area, no bar areas were found that showed absolutely no LW effects. Thus, we did not establish control sites that lacked LW pieces.

We classified the quadrats into five habitat groups: upstream (two quadrats); downstream (two quadrats); side (four quadrats); distant (four quadrats); and jam center, located within each LW jam. The numbers of quadrats within these habitat groups were 55, 53, 107, 61 and 11, respectively. Surveys of the vegetation and physical environment were conducted from June 26 through October 3, 2010.

Vegetation survey

We investigated the abundance and species diversity of the vascular plants in the sampling quadrats. Each quadrat was divided into a grid containing 100 cells of 10 cm x 10 cm, and all vascular plant species present in each mesh were identified to the species level (Shimizu 2003; Iwatsuki 1999; Satake et al. 1999a, 1999b). The cover ratio of each species in each quadrat was estimated based on the number of meshes in which the species occurred, and the total cover ratio was estimated based on the number of meshes in which at least one species was present.

Environmental variables

The three environmental variables (relative photon flux density (PFD), surface cover, and soil moisture) considered to be influenced by the deposition of LW were measured in the sampling quadrats.

To clarify the effects of shading associated with LW, the PFD was simultaneously measured 1 m above the ground and immediately above the ground in the center of each quadrat on a cloudy day using two light sensors (LI-250A, Li-Cor Co.). From these results, the percent relative PFD at the ground level was calculated to evaluate the cover effect of LW on the ground.

The ground surface cover, consisting of sediment, litter and twigs, was classified into categories of plant fragments and four grain sizes, following Wentworth (1922): cobble (diameter > 64 mm), pebble (2-64 mm), coarse sand (0.25-2 mm), and fine sand and silt (< 0.25 mm). The ground cover component presenting the highest cover ratio in a given mesh was assigned to that mesh. The cover ratio of each component in each quadrat was estimated based on the number of meshes to which that component was assigned.

TDR (time domain reflectometry; HydroSense, Campbell Scientific, Inc.) was used to measure the water content per a given volume of soil. The water content was measured on a day following three continuous sunny days, when the water stress on plants was relatively high. At five randomly selected points in each quadrat, the soil water content was measured 5, 10, and 15 cm under the ground surface.

Data Analysis

Differences in each of the environmental variables (relative PFD, surface cover, and soil moisture) among the habitat groups were examined using one-way ANOVA. If the variables differed significantly among the habitat groups ($p < 0.05$), Tukey's HSD multiple comparisons were subsequently performed. The overall differences in the physical environments and variations in the environmental conditions among the habitat groups were examined using Principal Component Analysis (PCA). The soil water contents at 10 cm and 15 cm depths were not used in the PCA because the values at some sampling points could not be measured due to soil hardness.

The proportions of alien species in each quadrat were compared among the habitat groups with a one-way ANOVA. ANOVA and Tukey's HSD multiple comparisons were performed using the R statistical package, version 2.12.0 (R Development Core Team 2011).

To describe similarities of the plant communities among the habitat groups, Non-metric Multidimensional Scaling (NMDS) (Kruskal 1964; Mather 1976) was performed on the cover ratio of the vegetation. The cover ratio was divided by 100 and arcsine-square root transformed to improve the normality of the data. The Multi-Response Permutation Procedure (MRPP) (Mielke 1984) was used to test whether the structure and composition of the vegetation differed among the habitat groups. Euclidean distance was used to calculate the average within-group distance. Pearson's correlation coefficients were calculated to indicate the relationship between each of the NMDS axes and species.

The plant species diversity among the habitat groups was compared using the Shannon-Wiener H' index and excluding alien species. Furthermore, Indicator Species Analysis (INSPAN) (Dufrêne and Legendre 1997) was performed to identify the species that characterized each habitat group.

PCA, NMDS, MRPP and INSPAN were performed using PC-ord, ver. 4 (McCune and Mefford 1999).

RESULTS

Environmental conditions

The relative PFD and the occurrence of fine sand and silt, cobble, pebbles, and plant fragments all differed significantly among the five habitat groups (Table 1). However, the values of soil moisture measured at the three depths did not differ significantly among the habitat groups, though the mean surface soil moisture (5 cm depth) was lowest in the distant quadrats. The relative PFD was highest in the distant quadrats and lowest in the jam centers. The fine sand and silt were distributed in the downstream quadrats, whereas cobble was dominant in the distant quadrats. Cobble was scarce and plant fragments dominant at the jam center.

The PCA ordination (Fig 4) showed that the overall environmental conditions at the jam center were very different from the other habitat groups. The variation (SD in the PCA ordination) within each habitat group was similar among the habitat groups. This means that the heterogeneity of the regeneration habitat at the jam center was not considerably different from that in the other habitat groups,

Occurrence and diversity of plant species

The vascular plant species occurring in our study quadrats included 47 herbaceous plants, 22 woody plants, and 2 ferns (Table 2). The dominant herbaceous species were *S. armeria*, *P. hieracioides* subsp. *glabrescens*, and *C. canadensis*, and the dominant woody species was *C. arbutifolia*.

Among the total of 71 species occurring in the study quadrats, 12 were alien species. All of the alien species were herbaceous plants. A total of 56 indigenous species were found, and 3 species identified only to family level were not included in the analyses. Although some alien species, such as *S. armeria* and *C. canadensis*, dominated most of the habitat groups, others (*Taraxacum officinale*, *Trifolium repens*, and *Bidens frondosa*) prevailed only in the jam center (Fig. 5). The proportions of alien species differed slightly among the habitat groups (one-way ANOVA, p=0.045), but no significant difference was found using Tukey's HSD multiple comparison test. Plant species diversity (H') was measured only for the indigenous species of vascular plants. H' was highest in the jam center quadrats, showed intermediate values in the downstream, side, and upstream quadrats, and was lowest in the distant quadrats (Fig. 6).

Community analysis

The results of NMDS ordination (Fig. 7) showed that there were significant differences in the composition and structure of the plant communities among the habitat groups (MRPP: $p < 0.05$). A 3-dimensional representation (final stress = 15.5, $p < 0.05$ for the Monte Carlo test) was chosen by NMDS autopilot in PC-ORD. Three axes represented 84.7% of the variation in the vegetation data. Axes 1, 2 and 3 represented 30.6 %, 21.9% and 32.2 % of the variation, respectively.

The jam center plots occupied the center of the left side on Axis 1 and the upper side on Axis 3, while the plots for the other habitat groups mainly extended from the center to the right side on Axis 1 (Fig. 7). Thus, the species composition at the jam center was very different from that of the other habitat groups. *Carex japonica*, *Bidens frondosa* and *Fraxinus mandshurica* var. *japonica* were specific for the jam center (Fig. 7), although other species coexisted with them (Table 2).

Indicator Species

INSPAN found indicator species only in the jam center quadrats. No indicator species were found in the other habitat groups (Table 2). Eleven herbaceous and 10 woody species were found to represent indicator species in the jam center quadrats (Fig. 8). Among these species, *T. officinale*, *B. frondosa,* and *Salix sachalinensis* were not prevalent at the study sites but occurred preferentially in the jam center quadrats. Species such as *Senecio cannabifolius*, *F. lanuginosa*, and *Tilia japonica* only occurred in the jam center quadrats. The woody species *Betula maximowicziana* occurred in one of the 107 side quadrats, whereas this species was found in 3 of the 11 jam center quadrats. *Populus maximowiczii* occurred in most of the quadrats but was dominant in the jam center quadrats.

DISCUSSION

Variation of physical environments around LW pieces

The physical environments differed among the habitat groups. Shading effects were marked around LW pieces relative to distant quadrats. The degree of shading was especially high at the jam center. However, soil moisture did not exhibit any significant differences among the habitat groups, though surface soil in distant quadrats was slightly drier than at other sites. It is probable that the shading effect associated with LW was not sufficient to alter the soil moisture and that a high groundwater table and high humidity in the riparian zone may weaken differences in soil moisture (Xiong and Nilsson 1997).

Fine sand and silt were concentrated in the downstream quadrats. In contrast, cobbles dominated the upstream quadrats. Gurnell et al. (2005) found the same trend in an island-braided river in Italy. Because LW pieces lie parallel to the direction of flow, usually with their roots pointing upstream (Edwards et al. 1999), the upstream end of a LW piece blocks strong currents. Such an obstruction may create vortex flows on both sides of the LW and areas of very low current velocity at the downstream end of the LW (Abbe and Montgomery 1996). It is probable that the distant quadrats were covered by cobbles because floodwater currents were not hindered, and fine sediment was selectively removed by the high tractive force.

In general, the proportion of fine sediment is correlated with nutrient levels and water-holding capacity (Shin and Nakamura 2005). Although plant fragments dominated the surface cover at the jam center, field observations indicated that LW jams also trapped fine sediment beneath organic fragments. Thus, with respect to vegetation establishment, LW pieces, particularly LW jams, act as a “resource node” (Pettit and Naiman 2005) by accumulating fine sediments and retaining nutrients and organic matter, and they act as “refugia” (Abbe and Montgomery 1996) by providing a barrier to high-velocity flows.

Plant species diversity and composition and invasion of alien species

The species diversity of indigenous species was lowest in the distant and upstream quadrats. In contrast, Francis et al. (2008) found a high species richness and diversity associated with scour pools at rootwads (usually at the upstream end). The probable reason for this association is that wetland species preferring hydric conditions might become established in and around such pools. Of the 16 single LW pieces we investigated, 12 pieces exhibited rootwads. Ten of these rootwads pointed upstream. However, we did not find any pools at the upstream end of LW pieces and detected few differences in soil moisture among the habitat groups. This finding suggested that the variety of physical environments at the rootwads was limited and that damages produced by floodwaters overwhelmed the recruitment of vascular plants.

The distant and upstream quadrats were exposed to floodwaters and suffered from high-velocity flows. Therefore, they were covered by cobbles and exposed to sunlight. Only a limited number of species, such as *Oenothera biennis*, *P. japonica*, and *C. arbutifolia*, were able to adapt to the harsh conditions. *Phragmites japonica* is tolerant to scouring and sedimentation because it recovers vegetatively by extending rhizome runners or stolons (Asaeda and Rajapakse 2008). This species is also tolerant to dislodging by floods. *Chosenia arbutifolia* extends axial roots into coarse gravel, particularly during early growth stages (Ishikawa 1994). Because this species absorbs water from deeper layers by rooting more rapidly than other species and protects itself from physical damage or being flushed away, it can easily become established on gravel bars where water levels change constantly (Shin and Nakamura 2005).

The highest diversity was found in the jam center, while intermediate levels of diversity were observed in the surrounding quadrats, and the lowest levels were detected in the distant quadrats. Thus, our hypothesis was supported in this regard. However, the factors increasing species diversity could not be attributed to the variability of environmental conditions created by LW pieces because there were no significant differences in the variations in these environmental conditions. The overall environmental conditions in the jam center differed significantly from the other groups (Fig. 4), and therefore, the specific site conditions at the jam center may allow many species to establish there. Pettit and Naiman (2006) also found a high density of seedlings and seed banks of various plant species in LW piles. We assumed that the "resource node" and "refugia" functions provided by LW jams enable the establishment of various species, but further research is necessary to explain species diversity with respect to LW.

The species compositions among the habitat groups also differed, particularly between the jam center and the other habitat groups. *C. japonica*, *B. frondosa* and *F. mandshurica* var. *japonica*, which are generally observed in infrequently disturbed wet environments, dominate at the jam center. Thus, the jam center may provide habitat patches with specific conditions that favor these species on relatively unstable, drier gravel bars.

Alien species invaded all the of habitat groups without any preference for a specific habitat group. Thus, LW pieces on gravel bars could provide regeneration habitats not only for indigenous plant species, but also for alien species, such as *S. armeria* and *C. canadensis.*

Significant contributions of LW jams to the biodiversity of riparian vegetation

Although we only investigated the early stage of succession on gravel bars, the species composition during the initial stage following a disturbance can have a substantial influence on the future development of plant communities (Bråkenhielm and Liu 1998; Halpern and Spies 1995). Thus, high species diversity in LW jams may contribute to the overall species richness during the future development of the riparian vegetation.

INSPAN found 21 indicator species only in the jam center and no indicator species in the other quadrats. This result means that LW jams provide specific regeneration habitats for many plant species. Such habitats cannot be created by a single piece of LW.

Woody plants constituted approximately half of the indicator species detected, and 10 out of the 22 woody species found in this study were indicator species for the jam center. Because flood disturbances operate in complex ways both temporally and spatially, the availability of safe sites also varies in time and space. The term “safe site” refers to a site with edaphic conditions or opportunities suitable for successful seedling recruitment (Harper 1977). Riparian trees specialize in colonizing disturbance regimes characteristic of their given geomorphic settings by developing life history strategies adapted to the fluctuating availability of safe sites (Nakamura et al. 2007; Naiman et al. 1998). Under these circumstances, LW jams increase the number and diversity of safe sites. Therefore, propagule sources that reach a suitable safe site will germinate and survive (Karrenberg and Suter 2003).

The woody indicator species that became established only in the jam center included *F. lanuginosa*, *T. japonica*, *Juglans mandshurica* var*. sachalinensis*, *Salix subfragilis* and *U. davidiana* var. *japonica*. These species favor relatively high floodplains or terraces where fine sediment accumulates and slightly dark and humid (or wet) conditions are maintained (Goto and Hayashida 2002; Shin and Nakamura 2005; Nakamura et al. 1997). Some of these species are broadly distributed on hillside slopes (Morimoto et al. 2011; Ishikawa and Ito 1988; Shimano 2000). With the exception of *S. subfragilis*, the seeds of these mid-successional species are larger and heavier than those of pioneer species (e.g., species of the family Salicaceae) and are dispersed by wind or animals (Katsuta et al. 1998).

LW jams facilitate the deposition of plant fragments and sediment and create shaded areas within and around the LW structure in which plant species can become established. Moreover, buried seeds may be transported with LW during a flood, and seeds dispersed by wind and stream flows may be trapped by complex LW structures (Pettit and Naiman 2006), which are associated with the blocking of strong currents and resultant decreases in water velocity. The specific environmental conditions and the trapping of seeds and fragments from various sources at LW jams allow the early establishment of mid-successional tree species at these sites. Although many LW jams are destroyed and washed away by successive floods, a number of the jams may remain if the axis of the active channel shifts to another orientation. As a result, diverse riparian forests develop in these regeneration patches (Nakamura et al. 2007).

Furthermore, we found that *C. arbutifolia* and *P. maximowiczii* were dominant tree species throughout the study area. However, only *P. maximowiczii* was identified as an indicator species in the jam center. *C. arbutifolia* and *P. maximowiczii* both prefer gravel beds as germination sites, but *P. maximowiczii* tends to become established on higher geomorphic surfaces where the disturbance frequency and intensity are lower than on gravel bars in an active channel (Shin and Nakamura 2005; Nakamura et al. 1997). LW jams may create patches including safe sites for *P. maximowiczii* in active channels.

The herbaceous indicator species that became established only in the jam center were *Carex japonica*, *S cannabifolius and Torilis japonica*. These three species are generally distributed in mesic soils on high floodplains and forest edges. These environments were never found on gravel bars in the study area, but the appropriate conditions were provided by LW jams.

The persistence of LW pieces and jams with respect to flood disturbance may be important in attempting to understand how much LW contributes to the future development and diversity of riparian vegetation. The shifting mosaic of bars and floodplain patches in the present study site was examined by Nakamura et al. (2007). Based upon their analysis using serial air photos, the average turnover time following a stand-replacing disturbance in the study area is approximately 37 years, although the central zone of the river floor has been more frequently disturbed than the marginal zones. We believe that the shifting mosaic pattern in the bar-braided section of the river plays a vital role in allowing LW to remain on gravel bars and future development of riparian forests at a half-century time scale.

In conclusion, LW pieces deposited on gravel bars altered the light and substrate conditions in the study area. Thus, they provided various safe sites for riparian plant species. In particular, LW jams play an important role in creating specific habitats, such as the interior environments of LW piles. These habitats cannot occur in the other environments created by a single LW piece. As a result, vascular plant species that prefer fine or coarse sediment, exposed or shaded habitat, or an early- or mid-successional stage are able to coestablish on gravel bars where LW pieces occur. Although we should monitor the future trajectory of the riparian vegetation, the high species diversity found in the initial stage of establishment should contribute to species diversity during mature stages in the dynamic environment of a braided river.

ACKNOWLEDGEMENTS

We thank the members of the Laboratory of Forest Ecosystem Management for assistance in the field. This study was supported by Grants in Aid for Scientific Research (19208013, 23248021) from the Ministry of Education, Science and Culture of Japan and by the Environment Research and Technology Development Fund (S9) of the Ministry of the Environment of Japan.

REFERENCES

Abbe TB, Montgomery DR (1996) Large woody debris jams, channel hydraulics and habitat formation in large rivers. Regul River 12:201-221.

Asaeda T, Rajapakse L (2008) Effects of spates of different magnitudes on a Phragmites japonica population on a sandbar of a frequently disturbed river. River Res Appl 24 (9):1310-1324.

Bilby RE, Likens GE (1980) Importance of organic debris dams in the structure and function of stream ecosystems. Ecology:1107-1113

Bråkenhielm S, Liu Q (1998) Long-term effects of clear-felling on vegetation dynamics and species diversity in a boreal pine forest. Biodivers Conserv 7 (2):207-220.

Dufrêne M, Legendre P (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol Monogr 67:345-366

Edwards PJ, Kollmann J, Gurnell AM, Petts GE, Tockner K, Ward JV (1999) A conceptual model of vegetation dynamics on gravel bars of a large Alpine river. Wetl Ecol Manag 7 (3):141-153.

Francis R, Tibaldeschi P, McDougall L (2008) Fluvially-deposited large wood and riparian plant diversity. Wetl Ecol Manag 16 (5):371-382.

Goto S, Hayashida M (2002) Seed dispersal by rodents and seedling establishment of walnut trees (Juglans ailanthifolia) in a riparian forest. J Jpn For Soc 84:1-8

Gurnell A, Tockner K, Edwards P, Petts G (2005) Effects of deposited wood on biocomplexity of river corridors. Front Ecol Environ 3 (7):377-382.

Gurnell AM, Petts GE, Harris N, Ward JV, Tockner K, Edwards PJ, Kollmann J (2000) Large wood retention in river channels: the case of the Fiume Tagliamento, Italy. Earth Surf Process Landforms 25 (3):255-275.

Gurnell AM, Piégay H, Swanson FJ, Gregory SV (2002) Large wood and fluvial processes. Freshw Biol 47 (4):601-619.

Halpern CB, Spies TA (1995) Plant Species Diversity in Natural and Managed Forests of the Pacific Northwest. Ecol Appl 5 (4):913-934.

Harmon ME, Franklin JF, Swanson FJ, Sollins P, Gregory SV, Miller J, Anderson NH, Gline SP, Aumen NG, Sedell JR, Lienkaemper GW, Cromack Jr. K, Cummins KW (1986) Ecology of coarse woody debris in temperate ecosystems. Adv Ecol Res 15:133-302

Harper JL (1977) Population Biology of Plants. Academic Press, London

Inoue M, Nakano S (1998) Effects of woody debris on the habitat of juvenile masu salmon (Oncorhynchus masou) in northern Japanese streams. Freshw Biol 40 (1):1-16.

Ishikawa S (1994) Seedling growth traits of three salicaceous species under different conditions of soil and water level. Ecol Rev 23 (1):1-6

Ishikawa Y, Ito K (1988) The regeneration process in a mixed forest in central Hokkaido, Japan. Plant Ecol 79 (1):75-84.

Iwatsuki K (1999) Ferns and Fern Allies of Japan. Heibonsha, Tokyo (in Japanese)

Japan Meteorological Agency (2011) Climate statistics. Available via Japan Meteorological Agency. http://www.jma.go.jp/jma/menu/report.html. Accessed 1 Sep. 2011

Karrenberg S, Suter M (2003) Phenotypic trade-offs in the sexual reproduction of Salicaceae from flood plains. Am J Bot 90 (5):749-754.

Katsuta M, Mori T, Yokoyama T (1998) Seeds of Woody Plants in Japan: Broadleaf Tree. Japan Forest Tree Breeding Association, Tokyo (in Japanese)

Kruskal JB (1964) Nonmetric multidimensional scaling: a numerical method. Psychometrika 29:115-129

Maser C, Sedell JR (1994) From the forest to the sea: The ecology of wood in streams, rivers, estuaries, and oceans. St. Lucie Press, Delray Beach, FL

Mather PM (1976) Computational methods of multivariate analysis in physical geography. John Wiley & Sons, London

McCune B, Mefford MJ (1999) Multivariate analysis on the PC-ORD system. Version 4. MjM Software, Gleneden Beach, Oregon

Mielke PWJ (1984) Meteorological applications of permutation techniques based on distance functions. In: Krishnaiah PR, Sen PK (eds) Handbook of statistics, vol 4. North-Holland Publishing, Amsterdam, pp 813-830

Morimoto J, Morimoto M, Nakamura F (2011) Initial vegetation recovery following a blowdown of a conifer plantation in monsoonal East Asia: Impacts of legacy retention, salvaging, site preparation, and weeding. For Ecol Manag 261 (8):1353-1361.

Nagayama S, Kawaguchi Y, Nakano D, Nakamura F (2009) Summer microhabitat partitioning by different size classes of masu salmon (Oncorhynchus masou) in habitats formed by installed large wood in a large lowland river. Can J Fish Aquat Sci 66 (1):42-51.

Naiman RJ, Fetherston KL, McKay SJ, Chen J (1998) Riparian Forests. In: Naiman RJ, Bilby RE (eds) River Ecology and Management. Springer, New York, pp 289-323

Nakamura F, Shin N, Inahara S (2007) Shifting mosaic in maintaining diversity of floodplain tree species in the northern temperate zone of Japan. For Ecol Manag 241:28-38.

Nakamura F, Swanson FJ (1993) Effects of coarse woody debris on morphology and sediment storage of a mountain stream system in western Oregon. Earth Surf Process Landforms 18 (1):43-61.

Nakamura F, Swanson FJ (1994) Distribution of coarse woody debris in a mountain stream, western Cascade Range, Oregon. Can J For Res 24 (12):2395-2403.

Nakamura F, Yajima T, Kikuchi S-i (1997) Structure and composition of riparian forests with special reference to geomorphic site conditions among the Tokachi River, northern Japan. Plant Ecol 133 (2):209-219.

Pettit N, Naiman R (2005) Flood-deposited wood debris and its contribution to heterogeneity and regeneration in a semi-arid riparian landscape. Oecologia 145 (3):434-444.

Pettit NE, Naiman RJ (2006) Flood-deposited wood creates regeneration niches for riparian vegetation on a semi-arid South African river. J Veg Sci 17 (5):615-624.

R Development Core Team (2011) R: a language and environment for statistical computing. 2.12.0 edn. R Foundation for Statistical Computing, Vienna

Satake Y, Hara H, Watari S, Tominari T (1999a) Wild Flowers of Japan: Herbaceous Plants

I, II, III. Heibonsha, Tokyo (in Japanese)

Satake Y, Hara H, Watari S, Tominari T (1999b) Wild Flowers of Japan: Woody Plants I, II. Heibonsha, Tokyo (in Japanese)

Seo JI, Nakamura F (2009) Scale-dependent controls upon the fluvial export of large wood from river catchments. Earth Surf Process Landforms 34 (6):786-800.

Shimano K (2000) A power function for forest structure and regeneration pattern of pioneer and climax species in patch mosaic forests. Plant Ecol 146 (2):207-220.

Shimizu T (2003) Naturalized Plants of Japan. Heibonsha, Tokyo

Shin N, Nakamura F (2005) Effects of fluvial geomorphology on riparian tree species in Rekifune River, northern Japan. Plant Ecol 178:15-28.

Wentworth CK (1922) A Scale of Grade and Class Terms for Clastic Sediments. J Geol 30 (5):377-392

Wondzell SM, Swanson FJ (1999) Floods, channel change, and the hyporheic zone. Water Resour Res 35 (2):555-567.

Xiong S, Nilsson C (1997) Dynamics of leaf litter accumulation and its effects on riparian vegetation: A review. Bot Rev 63 (3):240-264.

Table 1 Mean and SD of environmental variables by habitat groups

Habitat group	upstream	Downstream	side	distant	jam center
Number of quadrats	55	53	107	61	11
Relative PFD (%)	0.87±0.12^{b}	0.88±0.09^{bc}	0.88±0.09^{b}	0.93±0.07^{c}	0.55±0.26^{a}
Surface cover (%)					
Cobble	27.78±20.3^{ab}	22.4±17.77^{ac}	24.86±17.44^{ab}	31.92±17.68^{b}	8.45±7.97^{c}
Pebble	29.47±20.93^{ab}	26.34±25.25^{ab}	32.21±26.8^{b}	28.59±20.59^{ab}	9±10.37^{a}
Coarse sand	26.45±28.82	21.36±25.35	24.27±27.37	22.2±23.12	4.82±9.62
Fine sand and silt	15.8±18.52^{b}	29.79±30.47^{a}	18.38±24.67^{b}	17.3±23.39^{ab}	11.36±12.93^{ab}
Plant fragments	0.49±2.87^{b}	0.11±0.82^{b}	0.28±1.93^{b}	0±0^{b}	66.36±18.53^{a}
Soil moisture (%)					
5 cm depth	1.41±0.5	1.34±0.42	1.42±0.47	1.27±0.4	1.45±0.44
10 cm depth	2.66±0.83	2.54±0.53	2.87±1.09	2.54±0.62	2.47±0.69
15 cm depth	5.11±2.6	4.42±1.3	6.12±3.23	5.18±1.41	5.4±4.88

Lowercase letters indicate significant differences (Tukey HSD multiple comparisons, $p<0.05$)

Table 2 Plant species in the study area and their occurrence ratio by habitat groups

species	abbr.	alien species	indicator speceis*	occurrence ratio**				
				up stream	down stream	side	distant	jam center
herbaceous plants								
Petasites japonicus subsp. *giganteus*			jam center	0.07	0.11	0.07	0.03	0.36
Viola selkirkii				0	0	0.01	0	0
Arabis stelleri var. *japonica*				0.07	0.04	0.03	0.03	0
Lotus corniculatus var. *japonicus*				0.04	0.09	0.07	0.05	0
Trifolium pratense		●		0	0.06	0	0	0
Trifolium repens		●	jam center	0	0.04	0.05	0.03	0.18
Stenactis annuus	*ean*	●	jam center	0.18	0.13	0.04	0.08	0.45
Taraxacum officinale		●	jam center	0.07	0.04	0.02	0.03	0.45
Moehringia lateriflora				0.02	0.02	0.01	0	0
Dianthus armeria		●		0	0	0.03	0	0
Silene armeria	*sa*	●		0.91	0.94	0.89	0.97	0.45
Ranunculus silerifolius var. *glaber*			jam center	0	0.02	0	0	0.18
Aquilegia buergeriana var. *oxysepala*				0.04	0	0	0	0.09
Thalictrum aquilegifolium var. *intermedium*				0	0.02	0	0	0
Galium verum var. *trachycarpum* f. *album*				0	0.02	0	0	0
Torilis japonica				0	0	0	0	0.09
Elsholtzia ciliata	*ec*			0.05	0.04	0.02	0	0.09
Oenothera biennis	*ob*	●		0.29	0.34	0.36	0.13	0.45
Dianthus superbus var. *superbus*				0.07	0.06	0.02	0.03	0

Rumex acetosella		●		0.04	0.06	0.06	0.03	0
Anaphalis margaritacea				0	0	0.01	0	0
Picris hieracioides subsp. glabrescens	*ph*			0.69	0.64	0.67	0.49	0.82
Patrinia villosa				0.04	0	0	0	0
Hypericum kamtschaticum				0	0	0.02	0	0
Persicaria sieboldi				0.07	0	0	0	0.09
Persicaria longiseta				0.02	0.02	0	0	0
Reynoutria sachalinensis				0	0	0.01	0.02	0
Artemisia montana	*am*			0.27	0.25	0.21	0.13	0.45
Bidens frondosa	*bf*	●	jam center	0.04	0.02	0.04	0	0.27
Senecio cannabifolius			jam center	0	0	0	0	0.09
Conyza canadensis	*cc*	●		0.53	0.57	0.58	0.41	0.55
Aster ageratoides subsp. *ovatus* f. *yezoensis*			jam center	0.2	0.09	0.11	0.03	0.27
Solidago gigantea var. *leiophylla*		●		0.04	0.04	0.04	0.03	0.09
Setaria viridis	*sv*			0.36	0.28	0.33	0.3	0.45
Phragmites japonica				0.07	0.09	0.07	0.03	0.18
Festuca ovina				0.04	0.04	0.03	0.02	0
Poa pratensis		●		0.02	0.02	0.03	0.02	0
Muhlenbergia japonica				0.02	0	0	0.03	0.09
Phalaris arundinacea				0.07	0.02	0.03	0.03	0.09
Carex incisa	*ct*			0.02	0	0	0	0
Carex japonica	*cj*		jam center	0	0	0	0	0.18
Carex thunbergii				0.13	0.06	0.05	0.03	0.09
Equisetum arvense				0.04	0.02	0.04	0.08	0
Equisetum hyemale			jam center	0	0.06	0.05	0	0.18

ferns							
Thelypteris nipponica			0.02	0	0	0	0
Thelypteris palustris			0.04	0	0	0	0.09
woody plants							
Populus maximowiczii	*pm*	jam center	0.55	0.64	0.64	0.41	0.82
Chosenia arbutifolia	*ca*		0.67	0.7	0.63	0.72	0.45
Toisusu urbaniana			0.05	0.11	0.08	0.07	0
Salix hultenii var. *angustifolia*			0	0	0.02	0.02	0.09
Salix gracilistyla			0	0	0	0.02	0.09
Salix rorida	*sr*		0.13	0.21	0.09	0.03	0.27
Salix subfragilis		jam center	0	0	0	0	0.09
Salix sachalinensis		jam center	0.02	0.08	0.05	0.02	0.55
Salix pet-susu			0	0.08	0.04	0	0
Juglans mandshurica var. *sachalinensis*			0	0	0	0	0.09
Betula platyphylla var. *japonica*			0	0	0.01	0	0
Betula maximowicziana		jam center	0	0	0.01	0	0.27
Ulmus davidiana var. *japonica*		jam center	0	0	0	0	0.09
Schizopragma hydrangeoides			0.02	0	0.01	0	0
Hydrangea paniculata		jam center	0.02	0.04	0.04	0.03	0.27
Rubus mathumuranus			0	0.02	0	0	0
Malus toringo			0	0.02	0	0	0
Lespedeza bicolor			0.02	0	0	0.02	0
Pachysandra terminalis			0.02	0.02	0	0.02	0
Tilia japonica		jam center	0	0	0	0	0.18
Fraxinus mandshurica var. *japonica*	*fm*	jam center	0	0	0.01	0	0.09

Fraxinus lanuginosa	jam center	0	0	0	0	0.18

*Indicator species and their habitat group selected by Indicator Species Analysis are shown. **Occurrence ratio = number of quadrats where a species occurred / total number of quadrats of a habitat group. ***The three species identified only to the family level, which were Onagraceae sp., *Ixeris* sp., and Viola sp., are not shown.

Figure captions

Fig. 1 Location of the Rekifune River in Hokkaido, Japan

Fig. 2 LW pieces on gravel bars in the study area

Fig. 3 Arrangement of sampling quadrats at the study site. Quadrats representing five habitat groups were set around LW pieces. See details in Methods

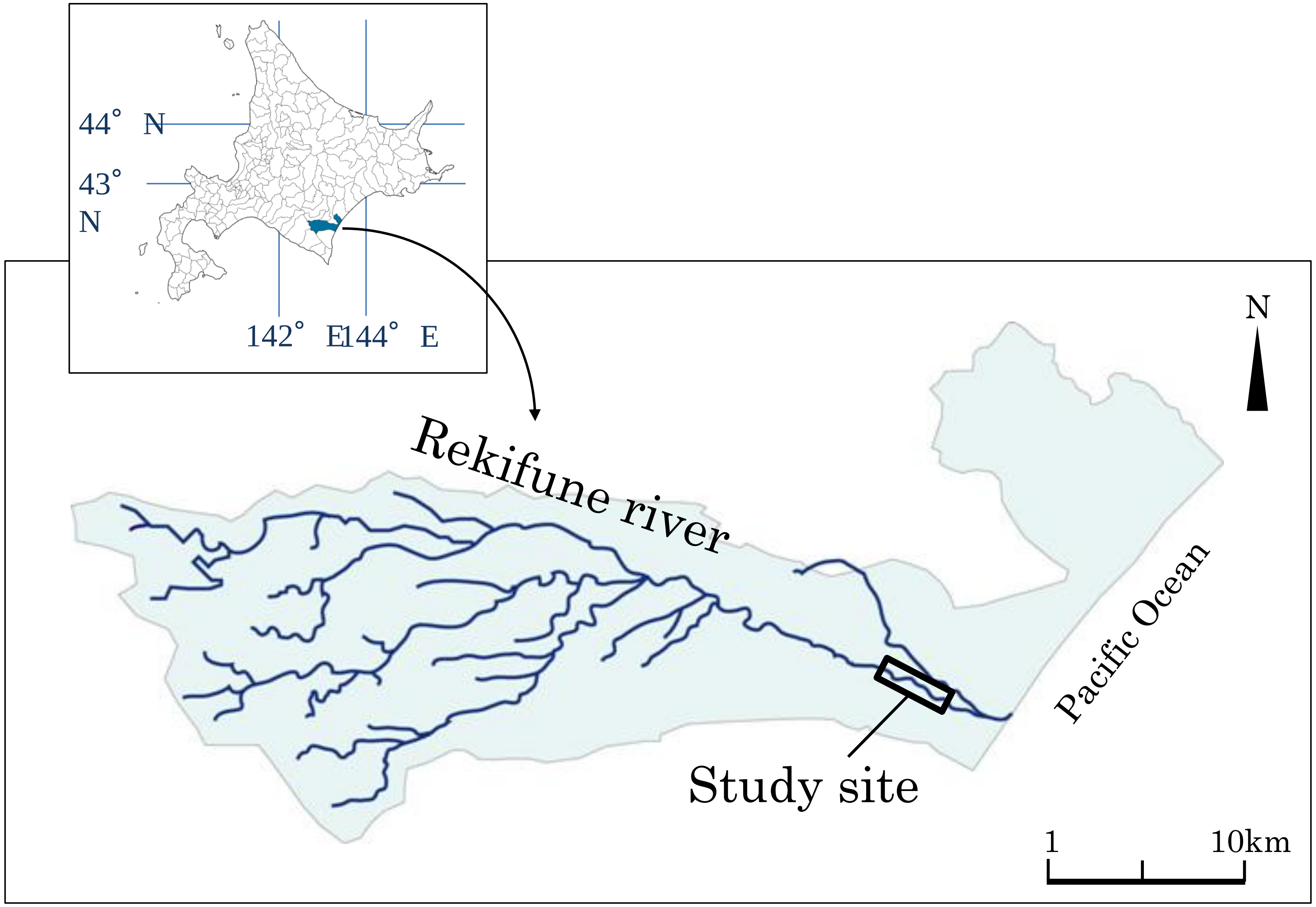
Fig. 4 PCA ordination of the first two principal components for the seven environmental variables. The sample quadrats were averaged by the habitat groups, and the error bars represents ± 1 SD. The first two PCA axes for the environmental variables explained 49.5% of the variance (28.3% and 21.2%, respectively). The first two eigenvectors for environmental variables were relative PFD=(0.46, -0.42), fine sand and silt = (-0.37, -0.05), coarse sand = (-0.21, -0.65), pebble= (0.45, 0.34), cobble = (0.45, 0.21), plant fragments = (-0.35, 0.46), and soil moisture at 5 cm = (-0.26, 0.18).

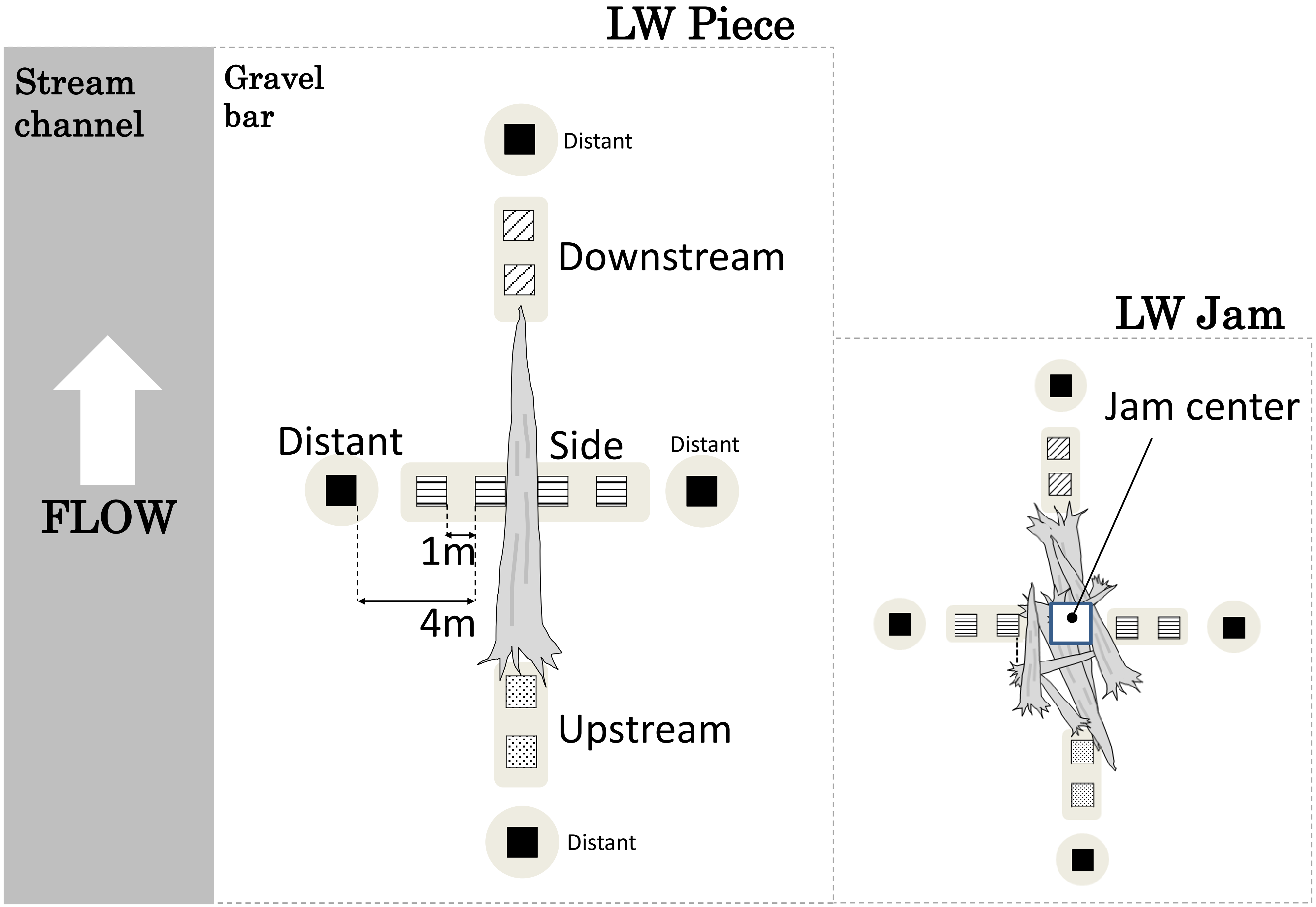
Fig. 5 Occurrence ratio of 12 alien species by habitat group. The species are arranged in descending order of their average occurrence ratios. Occurrence ratio = number of quadrats where a species occurred / total number of quadrats of a habitat group. *See Table 2 for full names, including subspecies and variety

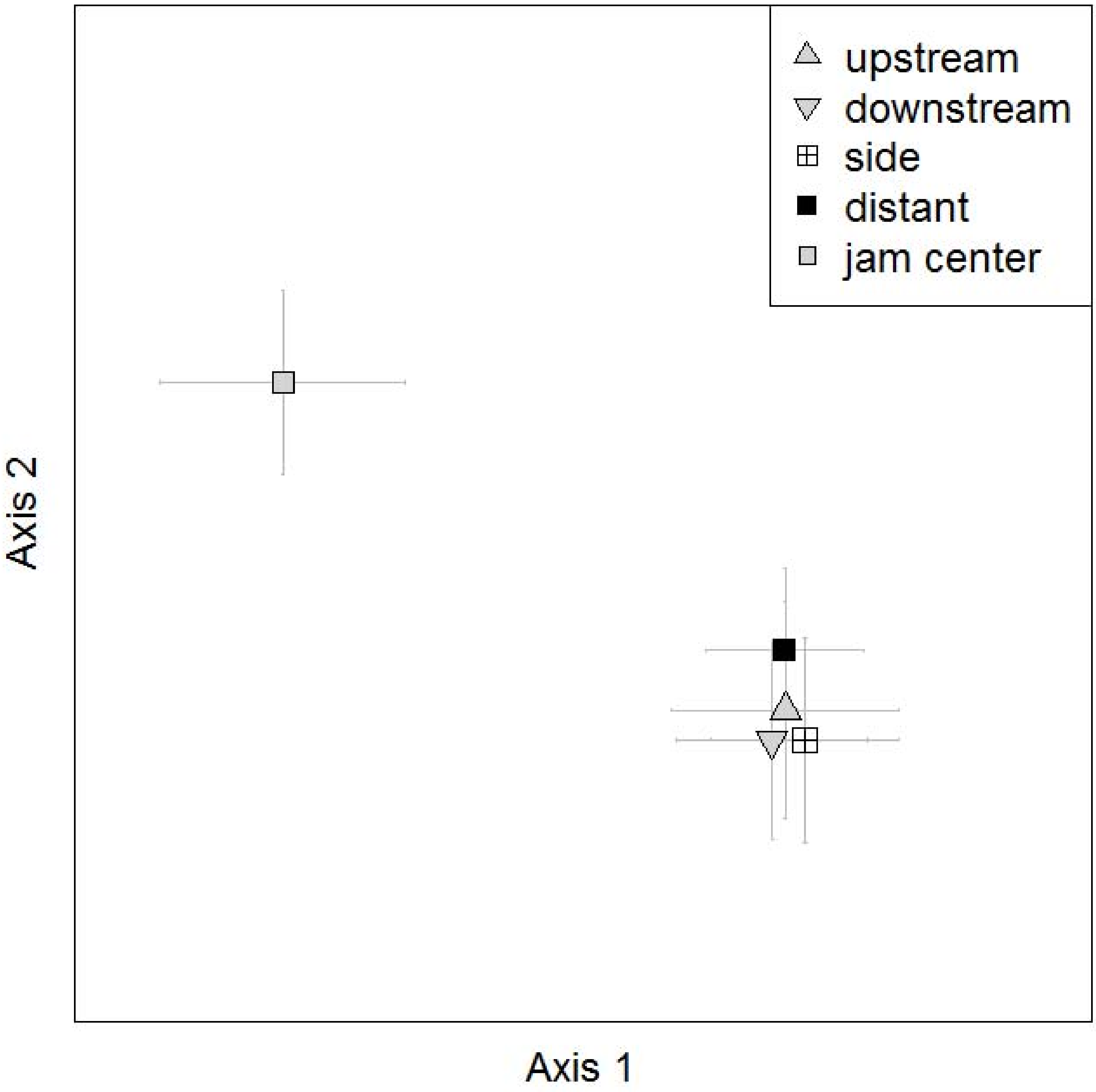
Fig. 6 Mean and SD of the Shannon-Wiener H' index by habitat group. Lowercase letters indicate significant differences by Tukey's HSD multiple comparison tests ($p<0.05$)

Fig. 7 NMDS ordination of community plant cover data. The sample quadrats were averaged by the habitat groups, and the error bars represent ± 1 SD. The positions of plant species exhibiting a correlation coefficient of $r > |0.2|$ on Axis 1 or 3 are shown in lowercase letters. See Table 2 for abbreviations for plant species

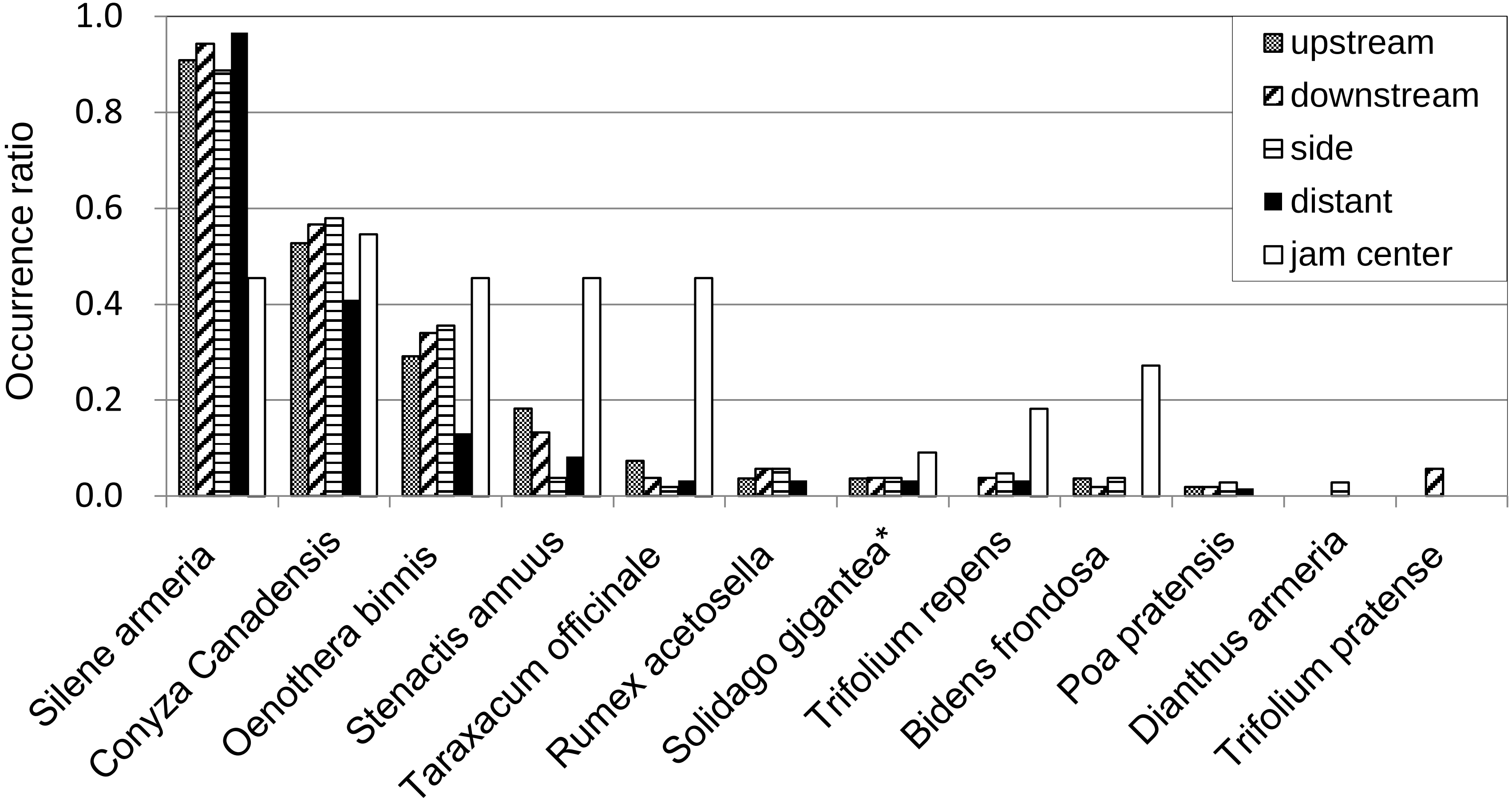
Fig. 8 Occurrence ratio of 21 indicator species by habitat group. Indicator species with significant indicator values were grouped into herbaceous and woody plants and arranged in descending order of their indicator values. *See Table 2 for full names, including subspecies and variation

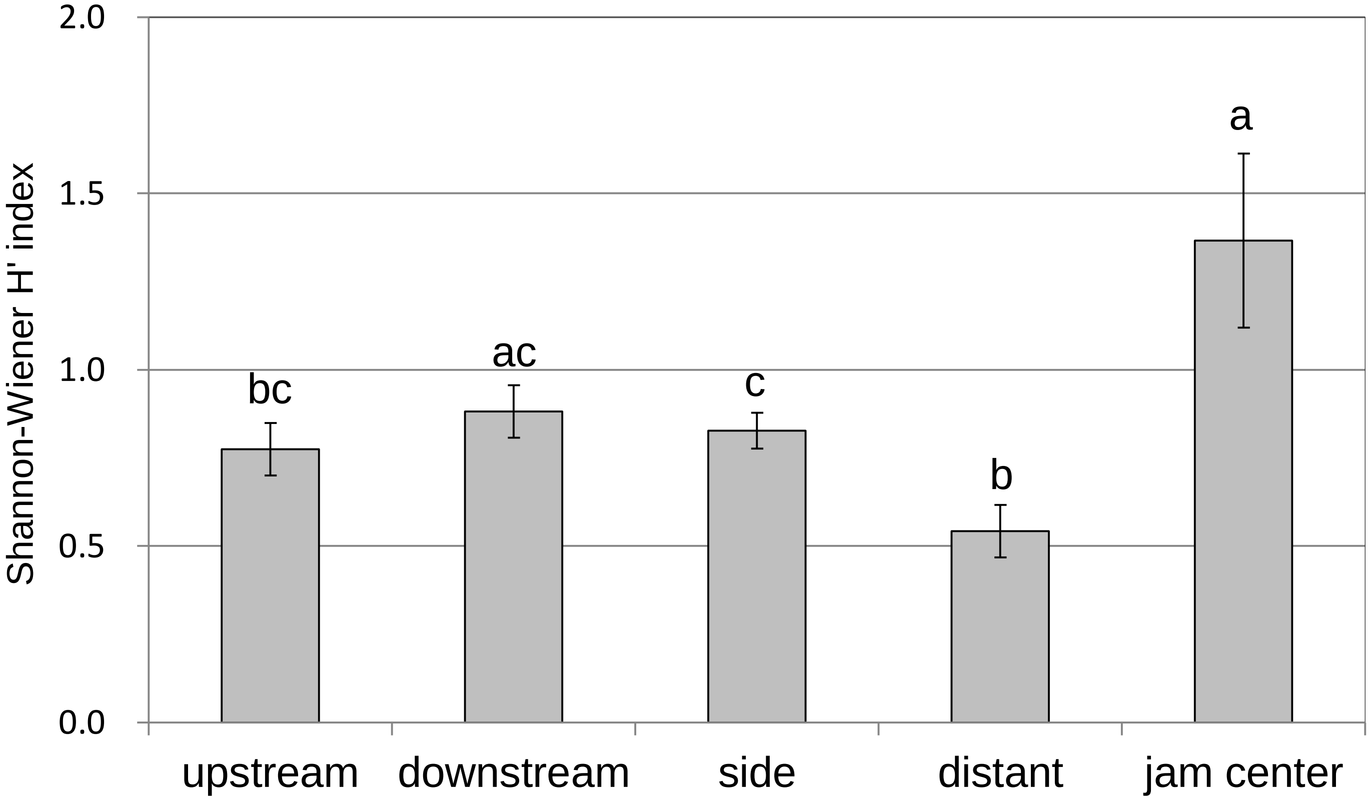

44° N
43° N
142° E
144° E
N
Rekifune river
Pacific Ocean
Study site
1
10km

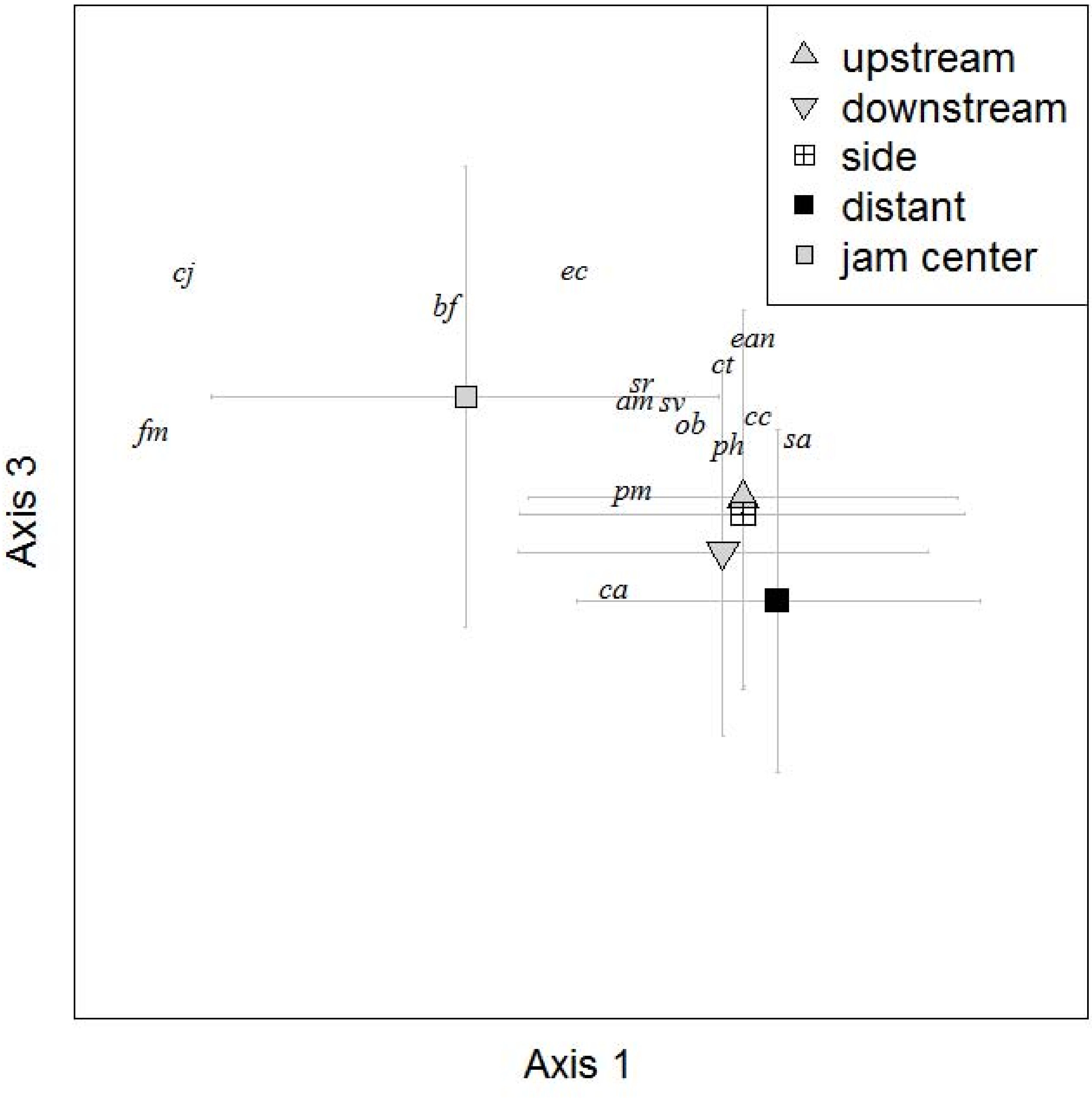

LW Piece
Stream channel
Gravel bar
Distant
Downstream
FLOW
Distant
Side
Distant
1m
4m
Upstream
Distant
LW Jam
Jam center

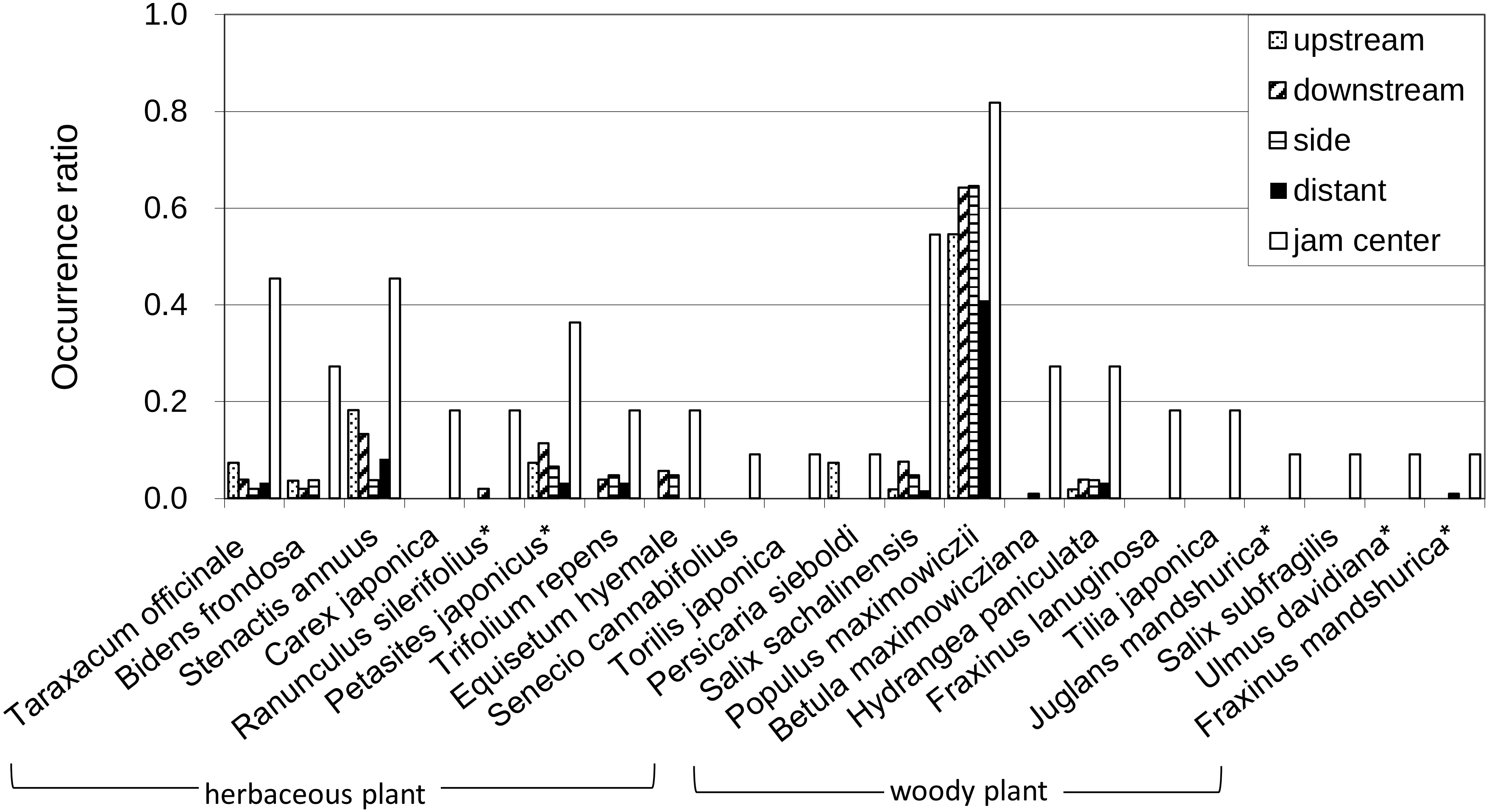


upstream
downstream
side
distant
jam center
Axis 1
Axis 2


Occurrence ratio
1.0
0.8
0.6
0.4
0.2
0.0
upstream
downstream
side
distant
jam center
Silene armeria
Conyza Canadensis
Oenothera binnis
Stenactis annuus
Taraxacum officinale
Rumex acetosella
Solidago gigantea*
Trifolium repens
Bidens frondosa
Poa pratensis
Dianthus armeria
Trifolium pratense


Shannon-Wiener H' index
2.0
1.5
1.0
0.5
0.0
bc
ac
c
b
a
upstream
downstream
side
distant
jam center


upstream
downstream
side
distant
jam center
cj
ec
bf
ean
ct
sr
am
sv
ob
cc
sa
fm
ph
pm
ca
Axis 3
Axis 1


Occurrence ratio
1.0
0.8
0.6
0.4
0.2
0.0
upstream
downstream
side
distant
jam center
Taraxacum officinale
Bidens frondosa
Stenactis annuus
Carex japonica
Ranunculus silerifolius*
Petasites japonicus*
Trifolium repens
Equisetum hyemale
Senecio cannabifolius
Torilis japonica
Persicaria sieboldi
Salix sachalinensis
Populus maximowiczii
Betula maximowicziana
Hydrangea paniculata
Fraxinus lanuginosa
Tilia japonica
Juglans mandshurica*
Salix subfragilis
Ulmus davidiana*
Fraxinus mandshurica*
herbaceous plant
woody plant