Disturbance legacy of a 100-year flood event: large wood accelerates plant diversity resilience on gravel-bed rivers

Kei Uchida *[1], Azumi Okazaki [2], Takumi Akasaka [3], Junjiro Negishi [4], Futoshi Nakamura [5]

1, Institute for Sustainable Agro-ecosystem Services, The University of Tokyo, Nishi-Tokyo, Japan

2, Division of Earth System Science, Graduate School of Environmental Science, Hokkaido University, Sapporo, Japan

3, Laboratory of Conservation Ecology, Department of Agriculture and Animal Science, Obihiro University of Agriculture and Veterinary Medicine, Obihiro, Japan

4, Laboratory of Watershed Conservation and Management, Faculty of Environmental Earth Science, Hokkaido University, Sapporo, Japan

5, Laboratory of Ecosystem Management, Research Faculty of Agriculture, Hokkaido University, Sapporo, Japan

* Correspondence: k.uchida023@gmail.com

Running head: Plant diversity changed after a record flood

Abstract

Understanding biodiversity resilience after a major disturbance is a key issue in basic and applied science. Plant diversity in gravel-bed rivers is affected by flood events, which are one of the most effective disturbance agents in the flow regime, affecting species distribution, and ecosystem dynamics. Although disturbance plays a critical role in community assembly mechanisms, how plant diversity recovers after a severe disturbance, such as a 100-year flood event remains unknown. The present study examined how the disturbance legacy of large wood in gravel-bed river ecosystems contributes to the resilience of plant diversity. The present study demonstrated that the resilience of plant species in disturbance legacy sites, namely deposited large wood sites, was higher than that in open habitat sites. Indicator species analysis revealed that perennial plants were the most important indicator species of disturbance legacy sites. These results suggest that perennial species richness contributes to the resilience of high plant diversity across the disturbance legacy sites in this region. After major flood events, land managers often remove large wood and debris jams to avoid secondary disasters, such as embankment collapse. However, we suggest that large wood should be retained on the gravel beds to aid the recovery of biodiversity and ecosystems. Furthermore, understanding the relationships between disturbance legacies and ecosystem resilience can contribute to the formulation of strategies for sustainable ecosystem management and biodiversity conservation in the future.

Key words: *plants, plant richness, soil nutrients, recovery, regional biodiversity, retention management*

Introduction

The resilience of biodiversity and ecosystems is a key issue in basic and applied science (Scheffer et al. 2001; Thrush et al. 2009). In recent decades, major disturbances resulting from human activities and climate change have led to the degradation of natural ecosystems (Sala et al. 2000; Hirabayashi et al. 2013; Nakamura et al. 2017). The landscape and biodiversity of river ecosystems, including gravel-bed rivers, are affected due to flood events caused by climate change (Dankers & Feyen 2009; Garssen et al. 2015; Arnell & Gosling 2016). Flooding events are one of the most efficient disturbance agents in flow regimes affecting species distributions and ecosystem dynamics (Poff et al. 1997; Fausch et al. 2001; Hastie et al. 2001; Power et al. 2008; Robinson & Uehlinger 2008; Nakamura & Nakamura 2021). Although relationships between disturbance agents and plant community assembly in the riparian ecosystem have been examined (e. g., Lyon & Gross 2005; Biswas & Mallik 2010), information regarding the initial recolonization of the plant community after a major disturbance, such as a 100-year flood event, remains unknown. In the present study, we aimed to achieve a better understanding of ecological resilience, including recovery and recolonization of plant diversity after a severe flood event and the consequences of unpredictable high-magnitude disturbance events.

Dead wood is essential for living organisms (Thorn et al. 2016, 2020). The organic matter and structure of dead wood is a valuable resource for living organisms and can affect species richness and biomass (e.g., Srivastava & Lawton 1998; Thorn et al. 2016). Although large-sized wood (hereafter, large wood) deposited in the river ecosystem can be destroyed and washed away by successive floods, it often remains as a legacy of disturbance events along the active channel axis. Previous studies have focused on large wood in river ecosystems as a disturbance legacy and its influence on aquatic biota (e.g., Angermeier & Karr 1984). No prior studies that have examined the relationships between the disturbance legacy from large woods and the initial recolonization of the plant community after a major 100-year flood event. Severe flood events can result in unvegetated gravel bars in the early successional stages, which can provide a competition-free space for vegetation establishment (Tockner et al. 2006; Kalníková et al. 2018).

In braided rivers, the dynamic vegetation zone is a part of the natural landscape, and it is important for the vegetation patch and plant diversity to recover during the early successional stage. As an initial recolonization stage of plant community, the early successional stage is one of the most important stages for biodiversity resilience after a major disturbance. In particular, the formation of habitat structures from large wood and the transport of organic matter and nutrients from headwater basins to lowland rivers have been investigated (Harmon et al. 1986; Maser & Sedell 1994; Nakamura & Swanson 1994; Inoue & Nakano 1998; Gurnell et al. 2000). Deposition of large wood may lead to the accumulation of fine sediments, soil nutrients, and organic matter (Gurnell et al. 2005; Paetzold, Schubert & Tockner 2005; Pettit & Naiman 2006; Nakamura et al. 2012). A few studies in Europe and the United States have examined the effect of large wood on vegetation cover (Abbe & Montgomery 1996; Gurnell et al. 2000, Pettit & Naiman 2006). In addition, riparian woody plant abundance and species richness were greater in areas with large wood than in open reference areas in a semi-arid South African river ecosystem (Pettit & Naiman 2006). Therefore, we hypothesized that large wood can contribute to the resilience of plant diversity during the early successional stage in a river ecosystem.

In recent decades, the occurrence of severe flooding events has been increasing worldwide (e. g., Hirabayashi et al. 2013). Therefore, further study is needed to examine how biodiversity resilience and ecosystems are maintained after a severe disturbance that causes the degradation of natural ecosystems.

In Japan, forested areas on hillslopes and in riparian zones have expanded to their highest levels over the past half-century due to land management strategies and drastically declining sediment production rates (Nakamura et al. 2017). In this situation, a large number of flood events have caused the outflow of large wood from riparian forests, and the large woods remains on gravel bars and in riparian areas. This large wood can contribute to the resilience of biodiversity in river ecosystems, but most of it has been removed to prevent wood-laden flood disasters in line with the Japanese river management scheme. In the present study, we hypothesized that legacy retention strategy can increase biodiversity resilience after severe flood events. Previous studies have stated that retention forestry can potentially provide biodiversity resilience (Franklin et al. 1997; Gustafsson et al. 2012; Lyndenmayer et al. 2012), while there are many studies that have examined the effects of large wood on fish habitats (e.g., Shields et al. 2006; Wohl et al. 2016) with the results providing a baseline for fish habitat rehabilitation work (Nagayama & Nakamura 2010). However, to our knowledge, no studies have tested the notion that a retention strategy for large wood in gravel-bed rivers can contribute to the resilience of plant species diversity. Therefore, we need to consider a retention strategy for large wood in gravel-bed rivers, particularly under an era of climate change.

Here, we examined the relationships between the resilience of plant diversity and large wood on gravel bars in the Satunai and Tokachi rivers, Japan. We focused on the role of large wood in creating habitats and how plant diversity can recover during the early successional stage on gravel bars after a major flood event. We hypothesized that the resilience of plant diversity in areas where large wood was deposited on gravel bars would be higher than that of open habitat areas. Our specific predictions were: 1) the resilience of plant species diversity in the presence of disturbance legacies (i.e., sites with large woods) is higher than that in the open habitat sites, and 2) the accumulation of plant species diversity across sites with large woods is higher than that across open habitat sites.

Materials and Methods

Study area

Fieldworks were conducted from September 2017 to August 2019 on the Tokachi and Satsunai Rivers in southern Hokkaido, Japan (Fig. 1). The regional climate is characterized by the mean monthly air temperature being the lowest in January (− 8.0 °C) and the highest in August (20.6 °C), with an annual mean total precipitation of 1,186 mm (2006–2016). The elevation range across sites was 20–210 m.

In typical years, the hydrograph shows characterized by relatively high sustained flow rates between late March and early June because of the snowmelt, with a low flow during summer and occasional floods in late summer and autumn. Mean (±SD) daily flow rates were 26.9 (±5.9) m^3/s and 225.9 (±47.3) m^3/s at the Dainiokawa-bashi gauging station for Satsunai River (1981–2019) and the Moiwa gauging stations of the Ministry of Land, Infrastructure, Transport and Tourism (MLIT) for Tokachi River (1970–2019), respectively. Over a two-week period from late August to early September 2016, three typhoons sequentially landed on Hokkaido Island, followed by another that passed close by. These resulted in approximately 900 mm of precipitation, which is equivalent to the mean total annual precipitation in the Obihiro area for the period 1981–2010, at Totsutabetsu meteorological observatory, MLIT (Negishi et al. 2019). The maximum annual daily flow rates reached record high levels in the area (during approx. 30 years), being three to four times the level as the means from historically available records (Fig S1; 2.8 times and 4.2 times for Dainiokawa-bashi and Moiwa gauging stations). We have estimated the return period of peak discharge of the 2016 flood according to data from historically available records in the previous study (Takahashi & Nakamura 2011). We estimated that the maximum flow discharge for the 100-year return period was 994 m^3/s and 1,866 m^3/s at the Kamisatsunai and Dainiokawa-bashi gauging station, respectively. The recorded peak discharges were 939 m^3/s and 2,368 m^3/s at the above two stations, respectively, during a severe flood event in 2016. Therefore, this flood was considered to be approximately a 100-year flood. After this massive disturbance event, the landscape of the study areas substantially changed. In the Satsunai River, the proportions of gravel-bed land increased (the mean value increasing from 5% to 24% in each survey site) and the areas of vegetated land decreased (Negishi et al. 2019).

Flood events were generally caused by snowmelt in early spring and typhoons or localized torrential downpours during the summer season. The channel floor was frequently disturbed due to the lateral movement of braided channels during floods, and many gravel bars were maintained throughout the river. Large wood was transported into the braided sections of the gravel bars during the floods (Fig. 2). Because of the active channels frequently shifting, most of the large wood on the gravel bars may be washed away by successive floods. However, when the flow direction shifts slightly or abruptly in another direction, some plant fragments can remain on the bars and provide habitats for riparian plants. Several herbaceous species, such as *Phragmites japonica*, vegetatively extend rhizome runners or stolons to allow them to grow in unstable environments and expand their colonies (Fig. 2).

Sampling design for plants and soil nutrients

We established 26 sampling sites on gravel bars within the active channel, as well as 14 sampling sites where large wood was present on the gravel bars during the survey period (Figs. 1 and 2). We also set up 12 sampling sites in open habitat areas where the disturbance legacy of large wood was absent as control sampling sites (Fig. S2). All the study sites were selected using aerial photographs of before and after the severe flood event. After the major flood event in 2016, all the sites were covered by gravel-bed soils and deposited large woods. We confirmed that the recolonization of plant communities initially had equal environmental conditions after the major flood event. This is because the severe flood presumably flushed out all the organisms and vegetation, and according to aerial photographs, the river topography had changed at all the sites due to the debris flow.

At each site, we established four transects in different directions (upper, bottom, right, and left) from the disturbance legacy of large wood (Fig. S2). Along each transect, we placed plots at 0-m, 3-m, and 10-m from the disturbance legacy of large wood, with the 0-m plot being closest to the large wood (Fig. S2). The open habitat sites had a similar transect and plot layout as the woody debris sites, except that the center of the open habitat sites had an empty space (Fig. S2). The open habitat sites were established within a 300-m radius of the disturbance legacy of the large wood sites. All the sites and plots were recorded using a GPS unit (Garmin GPSMAP 64S), therefore, we were able to survey the same plots and sites repeatedly during the survey period.

In total, we surveyed 137 plots in 12 disturbance legacy large wood sites and 141 plots in 12 open habitat sites in autumn 2017; 135 plots in 12 disturbance legacy sites and 120 plots in 10 open habitat sites in early summer 2018; 168 plots in 14 disturbance legacy sites and 144 plots in 12 open habitat sites in autumn 2018; 119 plots in 11 disturbance legacy sites and 125 plots in 11 open habitat sites in summer 2019. Two open habitat sites and two large wood sites (four sites in total) were not surveyed in autumn 2017 because of rising water levels due to rainfall events. In addition, several plots in different sites in each survey period were excluded because of the rising water levels due to rainfall events.

We recorded and identified all vascular plants in each plot during the survey period. In the subsequent analyses, we divided the plant species into annual and perennial plants because the plant growth rate is dependent on these life-history traits (Aaarsen et al 1997). We also collected soil samples (approx. 100 cm^3) from each plot during autumn 2018 for soil nutrient analyses. All the soil samples were air-dried in winter 2018. For the analyses, 10 g of dried soil was mixed with 25 mL of double-distilled water. The mixtures were shaken and left for one hour, after which the pH of the solution was measured using a HORIBA pH meter (D51, Japan). Following this, the soil NH_4^+ (indophenol blue colorimetric method) and the PO_4^{3-} (molybdenum blue colorimetric method) contents were determined using test kits from Kyoritsu Rika Kenkyu-jo, Japan.

Statistical analyses

Plant diversity, soil nutrients, and vegetation height between large wood sites and open habitat sites after a major flood event

We compared plant diversity indices (total, annual, and perennial plant species), soil nutrients (pH, NH_4^+, and PO_4^{3-}), and vegetation height between the large wood sites and open habitat sites after a severe flood event. We examined all the statistical analyses separately according to year and season through four surveys. These datasets were analyzed using generalized linear mixed models (GLMMs) with Tukey's HSD. In the GLMMs, response variables included the plant species richness indices (total, annual, and perennial plants), while the explanatory variables were the presence or absence of a disturbance legacy of large wood and distance from the center of the site (Fig. S2). We examined the relationships between vegetation height and the presence or absence of a disturbance legacy of large wood and the distance from the center of the site. We also analyzed the relationships between soil nutrients (pH, NH_4^+, and PO_4^{3-}) and the presence or absence of a disturbance legacy of large wood and distance from the center of the site (Fig. S2). In addition, we analyzed the relationships between plant diversity and soil nutrients using GLMMs. The response variables were total plant diversity, while the explanatory variables were soil nutrients (pH, NH_4^+, and PO_4^{3-}). In all the GLMMs, the site ID was included as a random term. The significance levels of the partial regression coefficients for the explanatory variables were examined at 95% and 99% confidence intervals of the estimated coefficients. Statistical analyses (GLMM and Tukey's HSD) were performed the package *lme4* and *multcomp* using R 3.1.1 (R Development Core Team 2012).

Rarefaction curves for species accumulation

The sample-based interpolation was calculated by plotting the total plant species richness at a given number of plots for the large wood sites and the open habitat sites. In the analyses, we divided plant species into total, annual, and perennial species. This method provides a measure of the accumulation rates of different species with increasing sample size (Colwell et al. 2012; Solar et al. 2016).

Identifying indicator species between large wood sites and open habitat sites

We examined the data to identify indicator species for the disturbance legacy at large wood sites versus the open habitat sites. We then conducted an indicator species analysis (INSPAN; Dufrêne & Legendre 1997).

Results

The highest total, annual, and perennial plant species richness were observed in the 0-m plots of the disturbance legacy large wood sites during all the survey periods (Fig. 3). The total and perennial plant species richness in the 3-m plots were higher at the large wood disturbance legacy sites than at the open habitat sites during all the survey periods, except for early summer 2018 (Fig. 3). In contrast, the total, annual, and perennial plant species richness in the 10-m plots did not significantly differ between the disturbance legacy sites and the open habitat sites (Fig. 3). The richness of the total, annual, and perennial plant species in the open habitat sites was consistently lowest during the survey period (Fig. 3). The vegetation height in the 0-m plots of the disturbance legacy sites was the highest during all the survey periods (Fig. S3). The soil PO_4^{3-} content in the 0 m plots in the large wood sites was highest (Fig. S4), and the soil PO_4^{3-} content was significantly correlated with total plant species richness (Fig. S5).

Rarefaction curves from sample-based interpolation demonstrated that total, annual, and perennial plant species were higher in the large wood sites than in the open habitat sites during the survey periods (Fig. 4). These results indicate that differences in species richness (*sensu* beta diversity) between the large wood sites were higher than those in the open habitat sites. In addition, rarefied plant species richness gradually decreased during the survey period (Fig. 4).

According to the INSPAN, 20 species were indicator species for the large wood sites (Table 1). Two were woody species, four were annual species, 12 were perennial species, and two were fern species. In general, all the recorded indicator species characterize riparian forest and grassland habitats.

Discussion

The present study demonstrated that the resilience of plant species diversity in the presence of disturbance legacies at large wood sites was higher than that in the absence of disturbance legacies at open habitat sites. In addition, plant richness at 0- and 3-m from the large wood was higher than that at 10 m from the large wood. According to the rarefaction analyses, accumulated species richness across the large wood sites was higher than that across the open habitat sites; in other words, disturbance legacy sites harbored different species compositions across the riverside gravel-beds (*sensu* high beta diversity). The rarefied plant species richness indices, such as total plant richness across the surveyed area, gradually decreased during the early successional stage because vegetation cover and height gradually increased, possibly suppressing the growth of annual species.

According to INSPAN results, native perennial plants were the most important indicator species for the large wood sites. This suggests that native perennial species richness contributes to the resilience of high plant diversity in the presence of disturbance legacy in this region. Additionally, 10% of the indicator species were woody plants including the riparian woody plants, *Salix schwerinii*, and *Alnus hirsuta*, and 60% were perennial plants including herbaceous plants such as *Picris hieracioides* subsp. *japonica*, and *Aster microcephalus* var. *yezoensis*. A previous study reported that the abundance and seedling density of woody plants were significantly greater in woody debris areas than in open reference areas (Pettit & Naiman 2006). In another study, many plant fragments were deposited in large wood areas, resulting in the growth of woody plants, including family *Salix* spp., compared with areas far from large wood (Nakamura et al. 2012). Woody species such as *Populus suaveolens*, *Toisusu urbaniana*, and *Salix schwerinii* regenerated rapidly on gravel bars in headwater streams and braided rivers, because these species can regenerate from fragmented branches on gravel beds after major flood disturbance events (Nakamura 2012; Nakamura & Nakamura 2021). The present study demonstrated that not only woody plants but also herbaceous perennial plants regenerated in the disturbance legacy areas. Although species with high regeneration rates (i.e., annual plant species) may recolonize during the early successional stage after massive disturbances (cf. Aaarsen et al. 1997), the present study showed that many perennial and woody plants recovered in the disturbance legacy areas. These results suggest that plant tissues and roots were deposited in areas with large wood after a massive disturbance, increasing the ecosystem's resilience.

In the present study, the soil $PO4^{3-}$ content was highest in the 0-m plots in the large wood sites, and this nutrient was significantly correlated with total plant species richness. In addition, the soil $PO4^{3-}$ content at the large wood sites was higher in the 0-m plots than in plots further away from the large woods. We suggest that the large woods can trap not only organic matter but also soil nutrients, which in turn, contribute to the resilience of plant diversity. A large proportion of the surrounding areas in the Satsunai and Tokachi Rivers are agricultural lands. Therefore, phosphorus might flow in the river ecosystem directly from the agricultural lands in particulate organic forms as well as inorganically bound forms. P-loaded particles can also be deposited in such areas, which eventually mineralize to become available in the soil as PO_4^{3-}. According to a study in the Hokkaido area, the highest diversity was found in the center of the area where large pieces of wood were jammed together, while intermediate levels of diversity were observed in surrounding quadrats, and the lowest levels were detected in the distant quadrats (Nakamura et al. 2012). This study also reported that large wood facilitates the deposition of plant fragments and creates shaded areas within and around the large wood for growing plant species (Nakamura et al. 2012). Although seeds and plants are not deposited in gravel-bed environments (O'Donnell et al. 2014), the specific environmental conditions of areas with large wood can trap seeds and plants, allowing the early establishment of mid-successional tree species (Pettit & Naiman 2006). The foliage cover and litter biomass in areas near large wood were found to be higher than in areas far from debris in a woodland environment (Goldin & Brookhouse 2015). Considered together, the results of the present and previous studies suggest that the deposition of plant seeds and fragments, and soil nutrients, which facilitate the growth of various plant species, may promote rapid recovery from severe flood disturbance.

Interestingly, the accumulated species richness across the large wood sites was higher than that across the open habitat sites; in other words, the large woods harbored different species compositions along the streams. Plant species composition can differ substantially between upstream and downstream areas according to the environmental conditions of the river channel and the area surrounding the river (Nilsson et al. 1991; Poff et al. 2007). The present study results indicate that woody debris catches various plant species depending on the regional environment gradient, whereas plant composition was similar across sites without large wood. These results indicate that plant foliage was washed and disturbed by running water in the gravel bar, which resulted in re-colonization by disturbance-tolerant species in the bar environment. This phenomenon may be explained by annual plants regenerating under frequent disturbances from running water in the open habitat sites (cf. Grime 1974, Aaarsen et al. 1997).

It is possible that the size of the disturbance legacy affected plant community resilience. Larger amounts of woody debris can trap larger plant parts and more soil nutrients. Additionally, larger patches of debris potentially creating a more heterogeneous environment. Heterogeneity is important for post-disturbance regeneration, as it results in more niches where different species can establish under varied conditions (Peterson & Pickett 2000). Future studies should focus on investigating how differences in legacy size contribute to the composition of plant species associated with biodiversity resilience.

Conclusions and implications for a strategy of legacy retention

The present study demonstrated that large wood promoted the resilience of plant diversity in gravel-bed river basins. Perennial plant species contributed to the resilience of plant diversity after the flood event. In addition, different large wood sites along the rivers and streams harbored differences in species composition, maintaining the heterogeneity of plant communities (*sensu* high beta diversity). We propose that the disturbance legacy of large wood in the gravel bed environment promoted plant diversity and based on findings of previous studies, also promoted plant growth (Abbe & Montgomery 1996; Gurnell et al. 2000, Pettit & Naiman 2006). Findings of the present study suggest that the legacy of large wood remnants after a massive flood disturbance can create a new riparian landscape, which drives plant diversity resilience, and may increase the number of high-trophic level organisms (cf. Haddad et al. 2009; Uchida & Ushimaru 2014, 2016).

Over recent decades, a number of major floods have occurred resulting from human activities and climate change, which have led to the degradation of natural ecosystems (Sala et al. 2000; Hirabayashi et al. 2013; Nakamura et al. 2017). In the future, these trends will continue due to human activities (IPCC 2013). Following large flood events, the ministries that manage land in the developed countries, including Japan, USA, and EU, need to eliminate large wood and debris to prevent secondary disasters in river ecosystems such as embankment collapse (Ministry Land, Infrastructure, Transport and Tourism 2018). However, we suggest that river managers could retain the several large woods on the gravel-bed environments because the disturbance legacy can contribute to the recovery of biodiversity and ecosystems. At present, no studies have emphasized that a retention strategy for large wood in gravel-bed rivers can contribute to biodiversity resilience after a record flood event. Therefore, we need to consider the retention strategy of large wood on the gravel bed river under an era of climate change. Previous studies have propounded that the strategy of retention forestry can contribute to biodiversity conservation in forest ecosystems (Franklin et al. 1997; Gustafsson et al. 2012; Lyndenmayer et al. 2012). The aims of retention forestry are to maintain the supply of ecosystem services, provide biodiversity, and achieve temporal and spatial continuity of key habitat elements for early- and late-successional specialist species (Gustafsson et al. 2012; Lyndenmayer et al. 2012). Overall, we suggest that researchers and policymakers should consider the relationships between disturbance legacies and ecosystem resilience. Understanding this relationship could prevent future disasters and inform sustainable ecosystem management to conserve biodiversity.

Acknowledgements

We sincerely appreciate for Dr. Yasushi Hashimoto and Dr. Terutaka Mori for constructive comments on the study. We thank also Yuki Iwachido, Ko Nakamura, Misaki Hirano, Hayata Goto, Daisuke Shimada, and Taiki Nangi for their assistance in field surveys. This research was supported by grants from the Ministry of Land, Infrastructure, Transport, and Tourism of Japan.

References

Aaarsen L.W., 1997. High productivity in grassland ecosystems: effected by species diversity or productive species? Oikos 80, 183–184.

Abbe, T.B., & Montgomery, D.R., 1996. Large woody debris jams, channel hydraulics and habitat formation in large rivers. Regulated Rivers: Research & Management 12, 201–221.

Angermeier, P.L., & Karr, J.R., 1984. Relationships between Woody Debris and Fish Habitat in a Small Warmwater Stream. Transactions of the American Fisheries Society 113, 716–726.

Arnell, N.W., & Gosling, S.N., 2016. The impacts of climate change on river flood risk at the global scale. Climatic Change 134, 387–401.

Biswas, S., Mallik, AU., 2010. Disturbance effects on species diversity and functional diversity in riparian and upland plant communities. Ecology 91, 28–35.

Colwell, R.K., Chao, A., Gotelli, N.J., Lin, S., Mao, C.X., Chazdon, R.L., & Longino, J.T., 2012. Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. Journal of Plant Ecology 5, 3–21.

Dankers, R., & Feyen, L., 2009. Flood hazard in Europe in an ensemble of regional climate scenarios. Journal of Geophysical Research 114, D16108, doi:10.1029/2008JD011523

Shields, F.D., Knight, S.S., Stofleth, J.M. 2006. Large wood addition for aquatic habitat rehabilitation in an incised, sand-bed stream, Little Topashaw Creek, Mississippi. River Research & Applications 22, 803– 817.

Dufrêne, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological monographs 67, 345–366.

Fausch,K.D., Taniguchi, Y., Nakano, S., Grossman, G.D., Townsend, C.R., 2001. Flood disturbance regimes influence rainbow trout invasion success among five holarctic regions. Ecological Applications 11, 1438–1455.

Franklin, J.F., Berg, D.F., Thornburg, D., Tappeiner, J.C. (Edited by: Kohm, K.A., Franklin, J.F.), 1997. Alternative silvicultural approaches to timber harvesting: Variable retention harvest systems Creating a Forestry for the 21st Century: The Science of Ecosystem Management.

Fedrowitz, K., Koricheva, J., Baker, S.C., Lindenmayer, D.B., Palik, B., Rosenvald, R., Beese, W., Franklin, J.F., Kouki, J., Macdonald, E., Messier, C., Sverdrup-Thygeson, A., Gustafsson, L., 2014. Can retention forestry help conserve biodiversity? A meta-analysis. Journal of Applied Ecology 51, 1669–1679.

Garssen, A.G., Baattrup-Pedersen, A., Voesenek, L.A.C.J., Verhoeven, J.T.A., Soons, M.B., 2015. Riparian plant community responses to increased flooding: a meta-analysis. Global Change Biology 21, 2881–2890.

Goldin, S.R., Brookhouse, M.T., 2015. Effects of coarse woody debris on understorey plants in a

temperate Australian woodland. Applied Vegetation Science 18, 134–142.
Grime, J.P., 1974. Vegetation classification by reference to strategies. Nature 250, 26–31.
Gurnell, A.M., Petts, G.E., Harris, N., Ward, J.V., Tockner, K.P., Edwards, J., Kollmann, J. 2000. Large wood retention in river channels: the case of the Fiume Tagliamento, Italy. Earth Surface Possesses and Landforms 25, 255–275.
Gurnell, A., Tockner, K., Edwards, P., Petts, G., 2005. Effects of deposited wood on biocomplexity of river corridors. Ecological Applications 3, 377–382.
IPCC Climate change 2013. The physical science basis. Stocker TF, Qin D, Plattner G-K, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM (eds). Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, pp 1535.
Gustafsson, L., Baker, S.C., Bauhus, J., Beese, W.J., Brodie, A., Kouki, J., Lindenmayer, D.B., Lõhmus, A., Martínez Pastur, G., Messier, C., Neyland, M., Palik, B., Sverdrup-Thygeson, A., Volney, W.J.A., Wayne, A., Franklin, J.F., 2012. Retention Forestry to Maintain Multifunctional Forests: A World Perspective. BioScience 62, 633–645.
Haddad, N.M., Crutsinger, G.M., Gross, K., Haarstad, J., Knops, J.M.H., Tilman, D., 2009. Plant species loss decreases arthropod diversity and shifts trophic structure. Ecology Letters 12, 1029–1039.
Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack Jr., K., Cummins, K.W., 1986. Ecology of Coarse Woody Debris in Temperate Ecosystems. Advances in Ecological Research 15, 133–302.

Hastie, L.C., Boon, P.J., Young, M.R., Way, S., 2001. The effects of a major flood on an endangered freshwater mussel population. Biological Conservation 98, 107–115.

Hirabayashi, Y., Mahendran, R., Koirala, S.K., Konoshima, L., Yamazaki, D., Watanabe, S., Kim, H., Kanae, S., 2013. Global flood risk under climate change. Nature Climate Change 3, 816–821.

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

Kalníková, V., Chytrý, K., Chytrý, M., 2018. Early vegetation succession on gravel bars of Czech Carpathian streams. Folia Geobotanica 53, 317–332.

Lyon, J., Gross, N.M., 2005. Patterns of plant diversity and plant–environmental relationships across three riparian corridors. Forest Ecology and Environment 204, 267–278.

Maser, C., Sedell, J.R., 1994. From the forest to the sea: the ecology of wood in streams, rivers, estuaries, and oceans. St. Lucie Press, Delray Beach.

Nagayama, S., Nakamura, F. 2010. Fish habitat rehabilitation using wood in the world. Landscape and Ecological Engineering 6, 289–305.

Nakamura, F., Swanson, F.J., 1994. Distribution of coarse woody debris in a mountain stream, western Cascade Range, Oregon. Canadian Journal of Forest Research 24, 2395–2403.

Nakamura, F., Fuke, N., Kubo, M., 2012. Contributions of large wood to the initial establishment and diversity of riparian vegetation in a bar-braided temperate river. Plant Ecology 213, 735–747.

Nakamura, F., Seo, J.I., Akasaka, T., Swanson, F.J., 2017. Large wood, sediment, and flow regimes: Their interactions and temporal changes caused by human impacts in Japan. Geomorphology 279, 176–187.

Nakamura, F., Nakamura, S.I., 2021. Fluvial geomorphic disturbances and life-history traits of riparian tree species. p. 291–315. Plant Disturbance Ecology The Process and the Response. Edited by Johnson, E.A., Miyanishi, K.

Negishi, J.N., Terui, A., Nessa, B., Miura, K., Oiso, T., Sumitomo, K., Kyuka, T., Yonemoto, M., Nakamura, F., 2019. High resilience of aquatic community to a 100-year flood in a gravel-bed river. Landscape and Ecological Engineering 15, 143–154.

Nilsson, C., Ekblad, A., Gardfjell, M., Carlberg, B., 1991. Long-Term Effects of River Regulation on River Margin Vegetation. Journal of Applied Ecology 28, 963–987.

O'Donnell, J., Fryirs, K., Leishman, M.R., 2014. Digging deep for diversity: riparian seed bank abundance and species richness in relation to burial depth. Freshwater Biology 59, 100–113.

Paetzold, A., Schubert, C.J., Tockner, K., 2005. Aquatic terrestrial linkages along a braided-river: riparian arthropods feeding on aquatic insects. Ecosystems 8, 748–759.

Peterson, C.J., Pickett, S.T.A., 2000. Patch type influences on regeneration in a western Pennsylvania, USA, catastrophic windthrow. Oikos 90, 489–500.

Pettit, N., Naiman, R., 2005. Flood-deposited wood debris and its contribution to heterogeneity and regeneration in a semiarid riparian landscape. Oecologia 145, 434–444.

Pettit, N., Naiman, R., 2006. Flood-deposited wood creates regeneration niches for riparian vegetation on a semi-arid South African river. Journal of Vegetation Science 17, 615–624.

Poff, N.L., Allan, J.D., Bain, M.B., Karr, J.R., Prestegaard, K. L., Richter, B.D., Sparks, R.E., Stromberg, J.C., 1997. The natural flow regime. BioScience 47, 769–784.

Poff, N.L., Olden, J.D., Merritt, D.M., Pepin, D.M., 2007. Homogenization of regional river dynamics by dams and global biodiversity implications. PNAS 104, 5732–5737.

Power, M.E., Parker, M.S., Dietrich, W.E., 2008. Seasonal reassembly of a river food web: floods, droughts, and impacts of fish. Ecological Monographs 78, 263–282.

Robinson, C.T., Uehlinger, U., 2008. Experimental floods cause ecosystem regime shift in a regulated river. Ecological Applications 18, 511–526.

Sala, O.E., Stuart, C.F., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., et al., 2000. Global biodiversity scenarios for the year 2100. Science 287, 1770–1774.

Scheffer, M., Carpenter, S., Foley, J.A., Folke, C., Walkerk, B., 2001. Catastrophic shifts in ecosystems. Nature 413, 591–596.

Solar, R. R. C., Barlowc, J., Andersene, A. N., Schoereder, J. H., Berenguer, E., Ferreira, J. N., Gardner, T. A. 2016. Biodiversity consequences of land-use change and forest disturbance in the Amazon: A multi-scale assessment using ant communities. Biological Conservation 197, 98–107.

Srivastava, D.S., Lawton, J.H., 1998. Why more productive sites have more species: an experimental test of theory using tree-hole communities. American Naturalist 152, 510–529.

Takahashi, M., Nakamura, F. 2011. Impacts of dam-regulated flows on channel morphology and riparian vegetation: a longitudinal analysis of Satsunai River, Japan. Landscape and Ecological Engineering 7, 65–77.

Thorn, S., Bässler, C., Bernhardt-Römermann, M., Cadotte, M., Heibl, C., Schäfer, H., … Müller, J., 2016. Changes in the dominant assembly mechanism drive species loss caused by declining resources. Ecology Letters, 19, 163–170.

Thorn, S., Seibold, S., Leverkus, A.B., Michler, T., Müller, J., Noss, R.F., Stork, N., Vogel, S., Lindenmayer, D.B., 2020. The living dead: acknowledging life after tree death to stop forest degradation. Frontiers in Ecology and the Environment 18, 505–512.

Thrush, S.F., Hewitt, J.E., Dayton, P.K., Coco, G., Lohrer, A.M., Norkko, A., Norkko, J., Chiantore, M.,

2009. Forecasting the limits of resilience: integrating empirical research with theory. Proceeding of the Royal Society B. 276, 3209–3217.

Tockner, K., Paetzold, A., Karaus, U., Claret, C., Zettel, J., 2006. Ecology of braided rivers. In Smith GHS, Best JL, Bristow CS, Petts GE (eds) Braided rivers: process, deposits, ecology and management. Blackwell Publishing, Oxford, pp 339–359.

Uchida, K., Ushimaru, A., 2014. Biodiversity declines due to land abandonment and intensification of agricultural lands: patterns and mechanisms. Ecological Monographs 84, 637−658.

Uchida, K., Hiraiwa, M., Ushimaru. A., 2016. Plant and herbivorous insect diversity loss are greater than null model expectations due to land-use changes in agro-ecosystems. Biological Conservation 201, 270−276.

Wohl, E., Bledsoe, B.P., Fausch, K.D., Kramer, N., Bestgen, K.R., Gooseff, M.N. 2016. Management of large wood in streams: An overview and proposed framework for hazard evaluation. Journal of the American Water Resources Association 52, 315– 335.

Table 1 Indicator species analysis (INSPAN) results. Bold and underlined fonts indicate significant indicator species in the large wood sites. There were no indicator species in the open habitat sites. The Indval value is an indicator of unique species from INSPAN (*see* Materials and Methods).

Species	Life history trait	Disturbance legacy of large woods	Indval value	*p* value	Frequency (plots)
Phragmites japonica	perennial herbaceous	presence	0.826	**0.002**	34
Persicaria lapathifolia	annual herbaceous	presence	0.697	**0.026**	31
Picris hieracioides subsp. *japonica*	perennial herbaceous	presence	0.671	**0.001**	17
Fallopia sachalinensis	perennial herbaceous	presence	0.670	**0.005**	21
Salix schwerinii	woody	presence	0.652	**0.020**	26
Cyperus amuricus	perennial herbaceous	presence	0.651	**0.008**	21
Aster microcephalus var. *yezoensis*	perennial herbaceous	presence	0.612	**0.001**	16
Chenopodium album var. *centrorubrum*	annual herbaceous	presence	0.611	**0.045**	26
Chenopodium album	annual herbaceous	presence	0.607	0.077	25
Rubus parvifolius	perennial herbaceous	presence	0.582	**0.004**	16
Phalaris arundinacea	perennial herbaceous	presence	0.575	**0.015**	19
Petasites japonicus subsp. *giganteus*	perennial herbaceous	presence	0.557	**0.005**	16
Equisetum arvense	fern	presence	0.507	**0.023**	14
Equisetum hyemale	fern	presence	0.411	**0.007**	9
Persicaria nepalensis	perennial herbaceous	presence	0.372	0.056	11
Persicaria thunbergii	perennial herbaceous	presence	0.363	**0.027**	8
Patrinia villosa	perennial herbaceous	presence	0.359	**0.021**	9
Erigeron annuus	annual herbaceous	presence	0.354	0.055	11
Alnus hirsuta var. *tinctoria*	woody	presence	0.346	0.070	10
Cardamine leucantha	perennial herbaceous	presence	0.340	**0.041**	9

Fig. 1 Distribution of the study sites along the Tokachi and Satsunai Rivers. Triangles represent the study sites (several sites overlapped each other). Annual maximum hourly flow rates were recorded at Dainiokawa-bashi, and Moiwa (*see* Materials and Methods and Fig. S1). Alphabetical numbers represent overlapping site numbers.

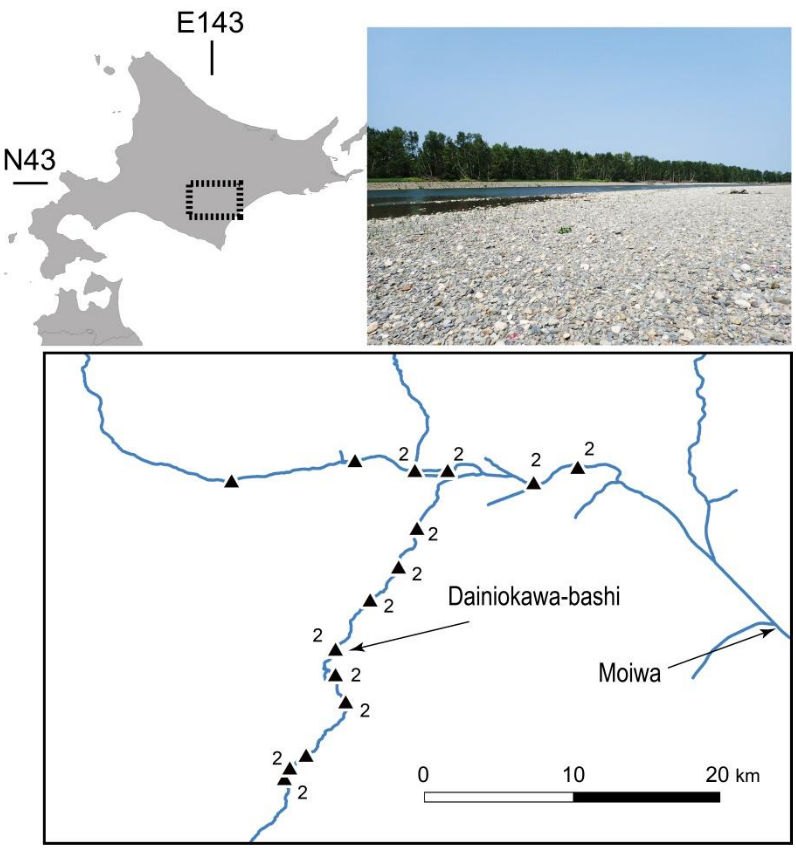

Fig. 2 Photographs representing the large wood sites and the open habitat sites.

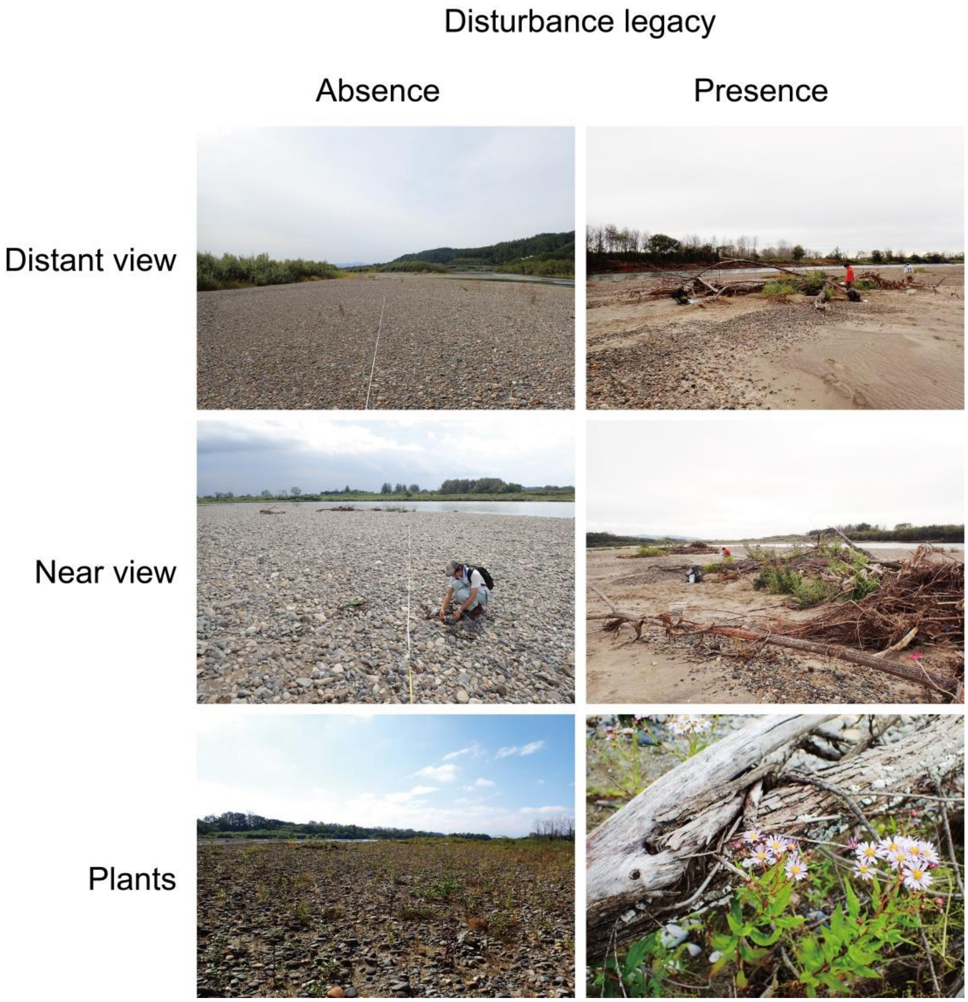

Fig. 3 Species richness at plots with absence (A) or presence (P) of large woods at different distances from the center of the site (Fig. S2). In the box plots, the black horizontal lines represent the medians, the box perimeters represent the first and third quartiles, and the whiskers above and below the boxes represent the10th and 90th percentiles. Letters indicate significant differences according to GLMM with Tukey HSD (*see* Statistical analyses).

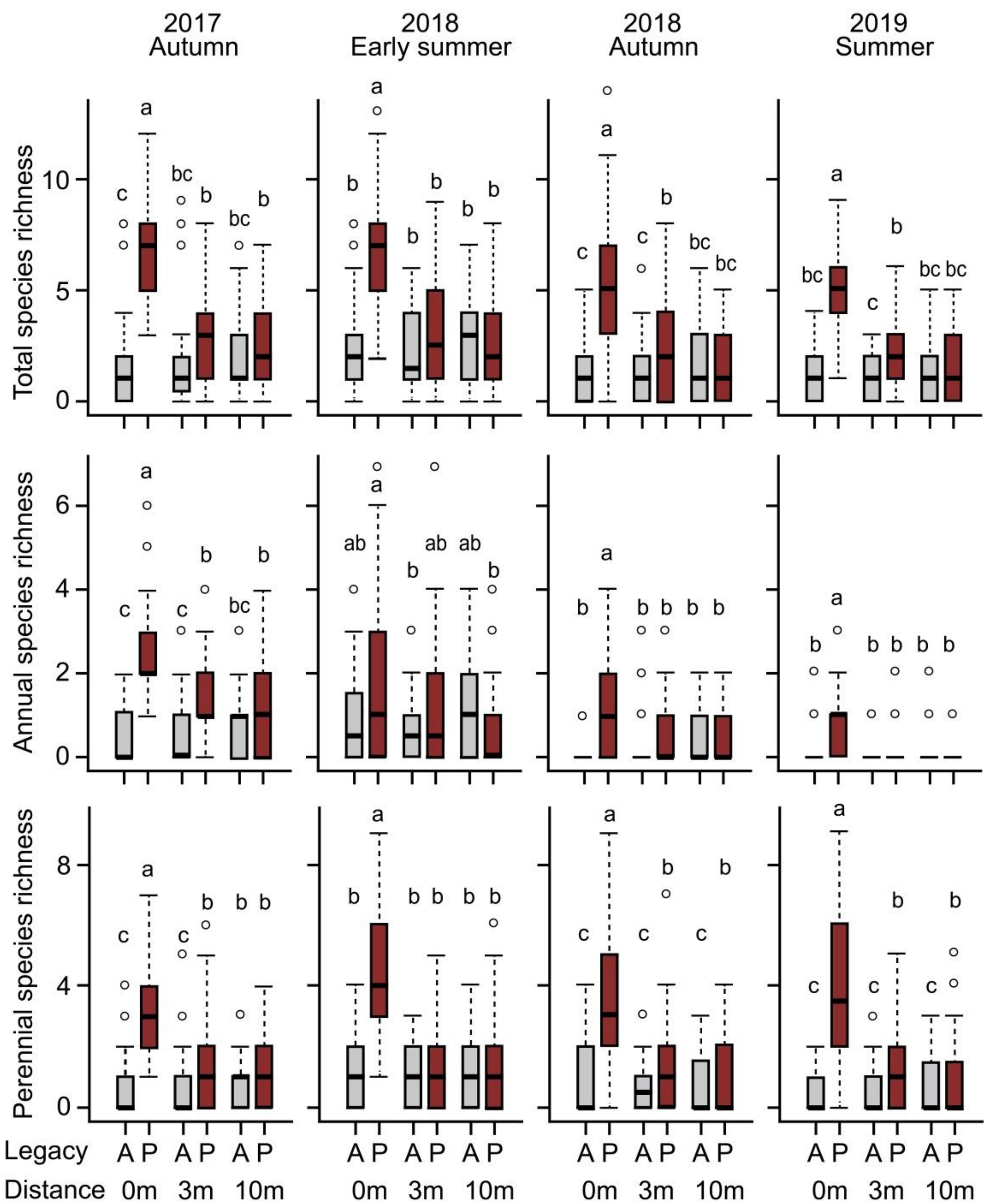

Fig. 4 Species rarefaction curves in the areas of absence or presence of large woody debris. Bold curves represent estimated species richness according to interpolation. The areas between dashed curves represent the 95% confidence intervals for the estimated species richness.