

# Interactive effect of canopy and fluvial disturbances on sapling community structure and species diversity in a montane riparian forest<sup>1</sup>

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**Abstract:** Montane riparian forests exhibit a higher diversity of tree species than adjacent stands. This pattern is thought to be generated by the unique disturbance regime of riparian forests, including canopy gap formation and fluvial disturbance (e.g., transport of boulder/gravel sediments), which provides a variety of habitat conditions for regeneration (habitat niche segregation). Although segregation of micro-environmental conditions for seedling establishment has been confirmed, habitat segregation for saplings remains untested. Thus, to determine if the composition and structure of the riparian sapling community is influenced by canopy and fluvial disturbances, we sampled 11 canopy-gap sites and 3 fluvial boulder-deposit sites, as well as beneath-canopy sites that had not been disturbed recently, in a temperate mixed-species deciduous forest. We analyzed the distribution patterns of saplings for 31 canopy and subcanopy species. Saplings were found mainly on the disturbed sites compared with the beneath-canopy sites. A comparison of relative densities for 13 major species in gaps *versus* on fluvial deposits revealed that 5 species were biased significantly to gaps and 4 species to fluvial deposits. Cluster analysis detected 4 species groups with different light requirements. These results suggest riparian habitat partitioning between species through differentiated preferences for the disturbance type × light requirement combination.

**Keywords:** canopy gap, fluvial sediment transport, habitat partitioning, multiple disturbance regimes, regeneration niche, sapling bank.

**Résumé:** Les forêts riveraines de montagne possèdent une plus grande diversité d'espèces d'arbres que les peuplements adjacents. On croit que ce patron de diversité est causé par un régime de perturbation unique à ces forêts riveraines qui comprend la formation de trouées dans le couvert forestier et des perturbations fluviales (p. ex. transport de sédiments composés de blocs et de gravier) créant des conditions d'habitat diversifiées pour la régénération (ségrégation de niches d'habitat). Bien que la ségrégation des conditions micro-environnementales pour l'établissement de semis ait été confirmée, la ségrégation d'habitat dans le cas des gaules n'a pas été étudiée. Ainsi, afin de déterminer si la composition et la structure de la communauté riveraine de gaules sont influencées par les perturbations fluviales et celles du couvert forestier, nous avons échantillonné différents sites dans une forêt mélangée de feuillus en zone tempérée: 11 sites dans lesquels il y avait des trouées du couvert forestier, 3 sites de dépôts fluviaux de blocs, ainsi que des sites sous couvert forestier n'ayant pas été perturbés récemment. Nous avons analysé les patrons de distribution des gaules de 31 espèces du couvert et du sous-couvert forestier. Les gaules se retrouvaient principalement dans les sites perturbés, lorsque comparés aux sites sous couvert forestier. Une comparaison de la densité relative de 13 espèces principales dans les trouées par rapport aux dépôts fluviaux a révélé que 5 espèces se trouvaient préférentiellement dans les trouées et 4 autres sur les dépôts fluviaux. Une analyse typologique a déterminé 4 groupes d'espèces en fonction de leurs exigences de lumière. Ces résultats suggèrent une ségrégation des espèces dans l'habitat riverain en fonction de la combinaison de leurs préférences pour le type de perturbation et les conditions de lumière.

**Mots-clés:** banque de gaules, niche de régénération, régime à perturbations multiples, ségrégation de l'habitat, transport fluvial de sédiments, trouée du couvert forestier.

**Nomenclature:** Satake *et al.*, 1989; Yonekura & Kajita, online.

## Introduction

Disturbance plays a pivotal role in structuring tree communities, and the diversity of tree species often varies among stand types within a landscape. Riparian forests often exhibit higher diversity of tree species than adjacent stands (Salo *et al.*, 1986; Masaki *et al.*, 1999;

Suzuki *et al.*, 2002). A widely accepted inference for the high species diversity of riparian forests is that fluvial disturbances provide diverse environmental conditions and allow many species to coexist. Fluvial disturbance often alters conditions of forest ground surfaces through various processes (e.g., sedimentation, channel change, erosion), providing diverse microhabitats (habitat niche segregation; Duncan, 1993; Nakamura & Inahara, 2007).

The disturbance-mediated niche effect on riparian forest trees has often been examined in lowland floodplains

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where flooding is the major disturbance (Duncan, 1993; Nakamura, Yajima & Kikuchi, 1997; Hall & Harcombe, 1998; Vervuren, Blom & de Kroon, 2003; Lin *et al.*, 2004). In montane riparian forests, on the other hand, habitat alterations are caused mainly by fluvial sediment transport, rather than water logging, and canopy gaps (Nakamura & Inahara, 2007). Montane fluvial sediments usually contain many types of surface conditions, including boulders, gravel, organic soils, woody fragments, and bumpy microtopography (Nakamura & Inahara, 2007), which provide a variety of habitat conditions for plants. Canopy gap formation also provides several gradients of environmental conditions, including increased light, decaying wood, and, when available, bare soils on uprooted mounds (*e.g.*, Cornett, Reich & Puettmann, 1997; Lafon, 2006). Combination of these disturbances can greatly increase habitat heterogeneity.

Niche segregation in montane riparian forests has often been confirmed for seedling establishment. For example, seedlings partition rooting substrates, such that establishment of some species is enhanced on fluvial gravel deposits, whereas for other species, establishment is enhanced on mineral soils on uprooted mounds and decaying logs (Kubo *et al.*, 2000; Sakio *et al.*, 2002; Masaki *et al.*, 2007). However, because microsite segregation facilitating seedling establishment often operates at smaller spatial scales (*e.g.*, rooting substrate) than later life stages (Schupp, 1995; Dovciak, Reich & Frelich, 2003), elucidation of riparian habitats for saplings should also be important for evaluation of regeneration niches. In closed forests, saplings of different species often partition the light gradient (*e.g.*, Kobe, 1999; Kato & Yamamoto, 2000; Gravel, Beaudet & Messier, 2008). In addition, riparian forest saplings may also be affected by fluvial disturbances. For example, flooding induced changes in competitive rankings of saplings along the light gradient on a Texas floodplain (Hall & Harcombe, 1998; Lin *et al.*, 2004). Thus, canopy gaps and fluvial disturbances can interactively enrich the species diversity of a riparian sapling community. Unfortunately, very few studies have examined the differences in habitat suitability for sapling communities in relation to montane riparian disturbances, and empirical evidence is available only for specific pairs of species (Sakio, 1993; 1997).

In this study, we investigated the distribution and habitat preferences of a sapling community in a temperate, mixed-species montane riparian forest of northern Japan. We determined if saplings are segregated among species in the environmental space defined by disturbance type (canopy gap or fluvial deposits) and light gradient. We tested the following hypotheses: 1) species diversity and sapling densities are higher in disturbed sites than in undisturbed, closed-canopy sites; 2) the dependence of sapling occurrence on disturbance type differs among species; 3) saplings of different species have different preferences for light habitat; and 4) disturbance types and light requirements in combination synergistically diversify the niches available for the sapling community.

## Methods

### STUDY SITE AND DISTURBANCE REGIME

This study was conducted in the Kanumazawa Riparian Research Forest (KRRF: 4.71 ha), northern Japan (39°06'N, 140°52'E). The climate is cool temperate, with an annual mean temperature of 9.2 °C, highest monthly mean of 20.5 °C (in August), and *ca* 2000 mm of annual rainfall. The area has high snow fall in winter, with a maximum depth of approximately 2 m. KRRF has no record of human disturbance, such as logging, in the past.

KRRF is a deciduous broad-leaved forest characterized by a species-rich riparian stand and a beech-dominated terrace stand. In the riparian stand, the canopy consists of riparian specialists such as *Cercidiphyllum japonicum*, *Aesculus turbinata*, *Acer mono*, *Pterocarya rhoifolia*, and *Ulmus laciniata*, as well as habitat generalists *Fagus crenata* and *Quercus crispula* (Suzuki *et al.*, 2002). The height of the canopy is >30 m, and the forest floor is often covered by the evergreen shrub *Camellia japonica* var. *decumbens* or ferns (*e.g.*, *Arachniodes standashii*, *Polystichum tripterum*) (Hoshizaki, Suzuki & Sasaki, 1997). Detailed descriptions of KRRF can also be found in previous papers (Hoshizaki, Suzuki & Nakashizuka, 1999; Masaki *et al.*, 2005; 2008).

Canopy gap formation and mass movement of sediments resulting from fluvial processes are the major disturbances in KRRF. Canopy gap formation occurs approximately once every 1 to 3 y; gaps of various magnitude (single or multiple treefall) and size of affected area are created by a variety of means (stem snapping, uprooting, or standing-dead) (Appendix I). Some of these canopy openings provide good rooting substrate (fallen logs and mounds) for some species in KRRF (Masaki *et al.*, 2007), as reported in other forests (Sugita & Tani, 2001; Christie & Armesto, 2003). The size of the gaps ranges from 24 to 413 m<sup>2</sup>, with a mean of 162 m<sup>2</sup>, which falls within the usual range for temperate deciduous forests (Yamamoto, 1992; McCarthy, 2001; Yamamoto *et al.*, 2011; Torimaru, Itaya & Yamamoto, 2012).

The fluvial disturbances in KRRF, triggered by heavy rain events, include sedimentation, erosion, and channel change. Recent fluvial disturbances occurred in 1988, 1998, and 2007. In the 1988 fluvial sediment transport event, 2 new sites (680 m<sup>2</sup> and 615 m<sup>2</sup>), comprising mixtures of boulders (here defined as sediments about 30 cm in diameter or larger), gravel, and small amounts of woody debris, were created (Appendix IIa). In the 1998 flow event, part of the boulder-gravel deposit site was washed out, leaving large amounts of woody debris (Appendix IIb,c). In the 2007 flow event, 2 sites were created; one was a new site (144 m<sup>2</sup>), while the other (340 m<sup>2</sup>) was re-loaded over the previous fluvial-disturbed site (Appendix II d,e). Hereafter, we refer to the debris deposits resulting from fluvial processes as “fluvial deposits”.

Between 1988 and 2012 (our observation period), canopy gap formation and fluvial sediment transport events occurred independently. Fluvial disturbances were less frequent than gap formation but created larger areas for plant regeneration (Appendix I; for review, see Nakamura & Inahara, 2007). Environmental conditions

(e.g., light availability and rooting substrate) were highly heterogeneous in this forest owing to the multiple disturbance regime.

#### SAPLING CENSUS

We sampled all 3 fluvial deposits and 11 canopy gaps in and around the riparian stand of KRRF (Figure 1; Table I; Appendix I). We also sampled beneath-canopy sites that remained without recent disturbance in order to obtain average densities of saplings in KRRF. In the disturbed sites,

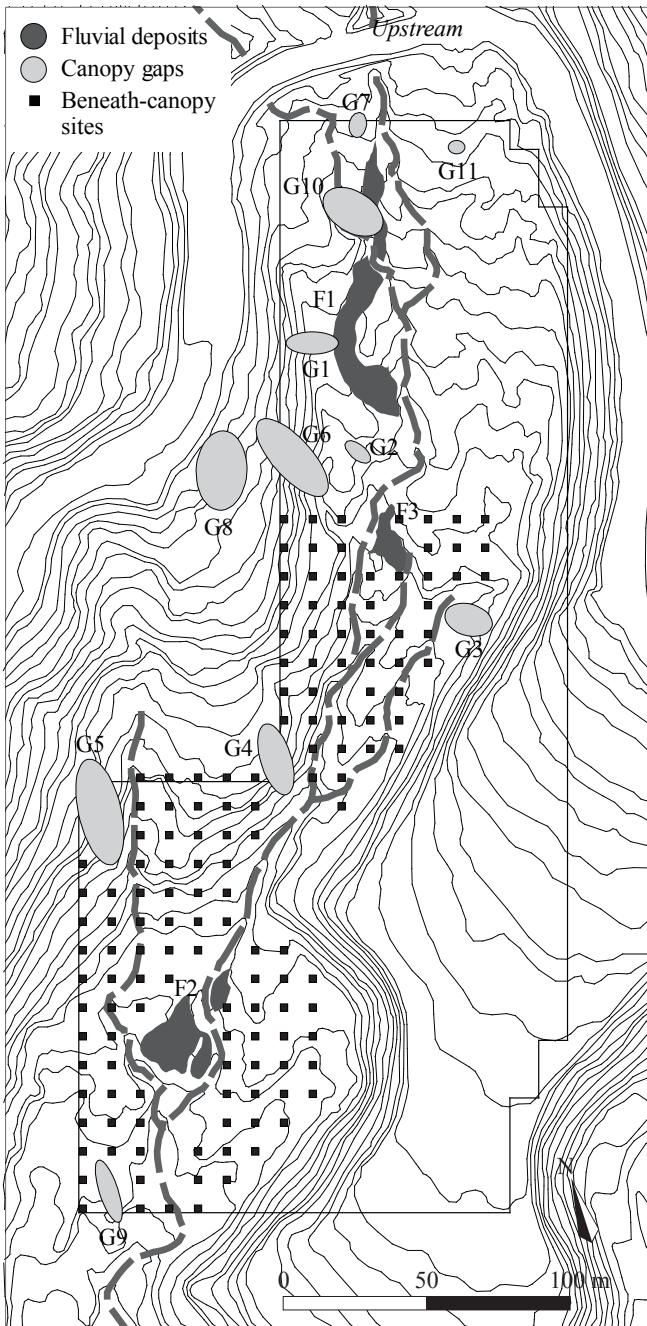


FIGURE 1. Topographical map of the Kanumazawa Riparian Research Forest (KRRF) and spatial arrangement of sampling sites. The thick solid frame and thick dashed lines represent the 4.71-ha KRRF plot and current channels, respectively. Dark grey represent fluvial deposits. Contour interval is 2 m.

$2 \times 2$ -m quadrats (total  $n = 646$ ) were established in 2005 (canopy gaps) and 2007 (fluvial deposits). On the fluvial deposits, the quadrats were tightly arranged over the site (total area 1436 m<sup>2</sup>), whereas in the gaps they were positioned at the centre of each gap, depending on the shape of the gap (total area 564 m<sup>2</sup>). In the beneath-canopy sites, quadrats of the same size were placed in a 10-m-interval grid in the forest at sites that had not suffered recent severe disturbances (total area 584 m<sup>2</sup>; Figure 1; see Masaki *et al.*, 2008 for further details).

In this study, saplings were defined as young stems of woody species (excluding lianas) larger than 30 cm in height and less than 5 cm in diameter at breast height but excluding current-year seedlings. All saplings in each quadrat were identified, and their heights were measured between July and September. In this study, we used data from the most recent 2 censuses for each site; 2007 and 2011 for fluvial deposits, 2005 and 2011 for gaps, and 2006 and 2010 for beneath-canopy sites. We analyzed canopy and subcanopy species (31 species; 1543 saplings in total) and excluded shrub species because most shrub species show vigorous vegetative propagation and because data for shrubs were not available at the beneath-canopy sites.

#### LIGHT CONDITIONS

Light conditions were evaluated for each quadrat. At the centre of the quadrat, a hemispherical photograph was taken at 2-m height under overcast sky conditions in summer 2007 or 2011. During this period, no substantial changes occurred in the canopy at each site. Photographs were analyzed to calculate canopy openness using CanopOn 2 version 2.03c (Takenaka, online). Openness data were log-transformed in order to minimize overestimation of openness under high light and to maintain homogeneity of variances. Each value was then converted to 1 of 5 light levels (I to V) established at regular intervals (on a log scale) across the full range (1.5–26.2%) of observed openness (*i.e.*, I: 1.5–2.6% openness; II: 2.7–4.7%; III: 4.8–8.3%; IV: 8.4–14.7%; V: 14.8–26.2%; corresponding to increase by 0.25 on  $\log_{10}$  scale), in order to perform hierarchical cluster analysis (see below).

#### DATA ANALYSIS

To test the effect of disturbances on species richness of saplings, we compared species-area curves for the 3 types of site (canopy gaps, fluvial deposits, and beneath-canopy sites). The unbiased estimator of species richness (Mao Tau estimator; see Colwell, Mao & Chang, 2004) and the 95% confidence intervals were calculated through randomization of  $2 \times 2$ -m sampling quadrats with 2000 runs, using EstimateS version 8.2.0 (Colwell, online).

Then, to test the preference of saplings for disturbance type (fluvial deposits *versus* canopy gaps), a simple comparison of sapling densities (by species) was carried out between those on fluvial deposits and those in canopy gaps. Site preference of each major species was examined using a binomial test. Here, “major” species refers to those that had more than 10 stems on the disturbed sites (13 species, 1275 saplings).

To explore how the distribution patterns of each species depended on light conditions, hierarchical cluster analysis was performed to group the 13 major species. After sapling densities were placed in the matrix of 13 species by 5 light levels, we calculated the Chao index to assess similarity. This index has been shown to be more tolerant to “false zeroes” (*i.e.*, species missing from samples) than other classic indices (*e.g.*, Jaccard index; Chao *et al.*, 2005). These analyses were carried out with R version 2.9.2 (R Development Core Team, 2009) and the “MASS” and “vegan” packages.

### Results

#### SPECIES COMPOSITION AND RICHNESS OF SAPLING BANK

Of the saplings recorded over the 3 site types ( $n = 1543$ ), densities at the disturbed sites (68.1 and 60.1 stems · 100 m<sup>-2</sup> for fluvial-deposit and canopy-gap

sites, respectively) were higher than the overall density in beneath-canopy sites (38.7 stems · 100 m<sup>-2</sup>). Numbers of species recorded in each site type were similar (17–23 species per type) (Table I).

Sapling composition and abundance differed substantially among the 3 types (Table II). Of the 31 species over the 3 site types, 22 species had higher densities on disturbed sites than in beneath-canopy sites. Fifteen species were found only in the disturbed sites. Of those, 6 and 5 species were distributed only on the fluvial deposits and in the canopy gaps, respectively. Conversely, non-riparian specialists, such as *F. crenata*, *Q. crispula*, and *A. japonicum*, were more abundant in beneath-canopy sites.

Species-area curves differed between disturbed sites and beneath-canopy sites. Within the range in which the 3 site types can directly be compared (<564 m<sup>2</sup>), the cumulative number of species was generally higher for disturbed sites than for beneath-canopy sites; there was no

TABLE I. Basic information on the study sites and sapling abundance.

Site type	Area (m <sup>2</sup> )	No. of quadrats	No. of stems	Density (stems · 100 m <sup>-2</sup> )	No. of species	Canopy openness (%)	
						Mean ± SD	Range
Fluvial deposits	1436	359	978	68.1	23	5.2 ± 1.9	1.2–11.2
Canopy gaps	564	141	339	60.1	20	5.8 ± 4.6	2.2–20.5
Beneath-canopy sites	584	146	226	38.7	17	3.8 ± 0.8	0.8–8.0

TABLE II. Species composition, number of stems, and density (stems · 100 m<sup>-2</sup>) of saplings at each site. Species are listed in decreasing order of total sample size for fluvial deposits and canopy gaps.

Species	Code	Fluvial deposits		Canopy gaps		Beneath-canopy sites	
		Stems	Density	Stems	Density	Stems	Density
a) Canopy species							
<i>Ulmus laciniata</i>	Ul	303	21.10	45	7.98	18	3.08
<i>Pterocarya rhoifolia</i>	Pr	275	19.15	35	6.21	35	5.99
<i>Cercidiphyllum japonicum</i>	Cj	61	4.25	105	18.62		
<i>Aesculus turbinata</i>	At	91	6.34	46	8.16	18	3.08
<i>Acer mono</i>	Am	95	6.62	18	3.19	22	3.77
<i>Swida controversa</i>	Sc	30	2.09	4	0.71	1	0.17
<i>Zelkova serrata</i>	Zs	30	2.09				
<i>Fagus crenata</i>	Fe	16	1.11	8	1.42	22	3.77
<i>Salix bakko</i>	Sb	7	0.49	4	0.71		
<i>Magnolia obovata</i>	Mo	5	0.35	5	0.89	10	1.71
<i>Kalopanax pictus</i>	Kp	1	0.07	6	1.06	4	0.68
<i>Quercus crispula</i>	Qc	6	0.42			8	1.37
<i>Carpinus laxiflora</i>	Cl	1	0.07	4	0.71		
<i>Acer sieboldianum</i>	As	2	0.14			3	0.51
<i>Acer rufinerve</i>	Ar	2	0.14				
<i>Cornus kousa</i>	Ck	1	0.07			2	0.34
<i>Tilia japonica</i>	Tj			1	0.18		
<i>Salix udensis</i>	Su	1	0.07				
<i>Phellodendron amurense</i>	Pa			1	0.18		
<i>Cerasus sargentii</i>	Cs	1	0.07				
b) Subcanopy species							
<i>Acer amoenum</i>	Aa	28	1.95	19	3.37	51	8.73
<i>Fraxinus lanuginosa</i>	Fl	10	0.70	18	3.19	11	1.88
<i>Acer japonicum</i>	Aj	6	0.42	11	1.95	17	2.91
<i>Prunus grayana</i>	Pg	5	0.35				
<i>Rhus trichocarpa</i>	Rt			3	0.53		
<i>Acer nipponicum</i>	An			3	0.53		
<i>Acer distylum</i>	Ad			2	0.35		
<i>Acanthopanax sciadophylloides</i>	Ac			1	0.18	1	0.17
<i>Styrax obassia</i>	So	1	0.07				
<i>Ilex macropoda</i>	Im					2	0.34
<i>Sorbus alnifolia</i>	Sa					1	0.17

clear difference between fluvial deposits and canopy gaps (Figure 2).

#### EFFECT OF DISTURBANCE TYPE ON SAPLING OCCURRENCE

Comparison of sapling densities on fluvial deposits versus in gaps (Figure 3) revealed that 4 species, *U. laciniata*, *P. rhoifolia*, *A. mono*, and *Z. serrata*, were significantly biased to fluvial deposits ( $P < 0.05$ ), whereas 5 species, *C. japonicum*, *A. turbinata*, *A. amoenum*, *F. lanuginosa*, and *A. japonicum*, were significantly biased to canopy gaps. No site bias was detected in the other 4 species, although *S. controversa* was slightly biased to fluvial deposits ( $P = 0.09$ ). Many of the minor species (14 of 16 species)

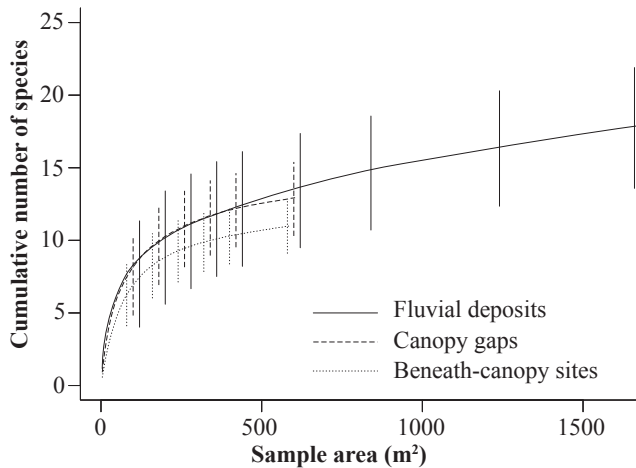


FIGURE 2. Species accumulation curves for canopy and subcanopy species against varying number of samples of 2- × 2-m quadrats. Vertical lines show 95% confidence intervals obtained by bootstrap resampling.

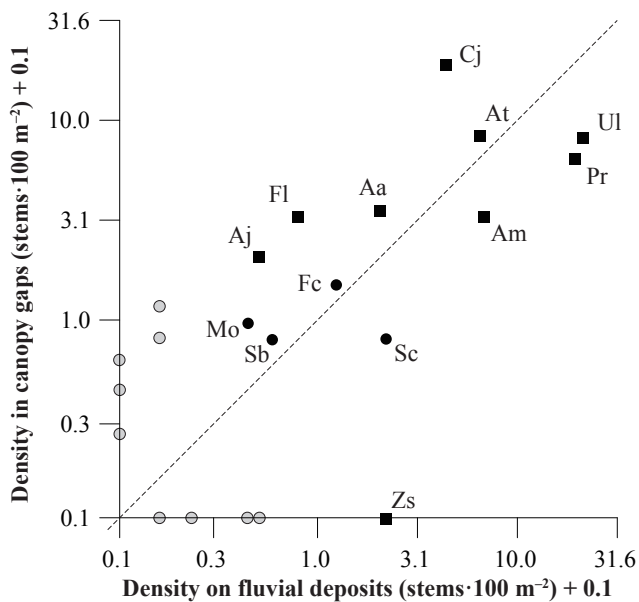


FIGURE 3. Sapling densities on fluvial deposits and in canopy gaps. Major species are shown with black symbols accompanied by their code (see Table II). Squared species had densities significantly biased to either fluvial deposits or canopy gaps. The dotted line shows the 1:1 line representing an absence of bias between sites. Both axes are log-scaled, and species with extremely small sample sizes are omitted.

had no saplings either on fluvial deposits or in gaps (Table II).

#### EFFECT OF LIGHT CONDITIONS

The density of species along light levels varied among the 13 major species (Figure 4). Saplings of *U. laciniata*, *P. rhoifolia*, *A. turbinata*, *A. mono*, and *A. amoenum* occurred in a wide range of light conditions, being relatively common at lower light levels (I and II, although at level III for *P. rhoifolia*). A similar tendency was observed for *F. crenata*, *F. lanuginosa*, and *M. obovata*, but these species lacked saplings in areas with light level I. In contrast, *C. japonicum* and *S. bakko* became common as the light level increased (Figure 4).

Cluster analysis confirmed the distributional trend along light conditions and detected 4 groups (A–D) (Figure 5). Groups A and B were characterized as moderately shade-tolerant species, because saplings belonging to these 2 groups were common at light levels II and III (Figure 4); Group A appeared to be slightly more shade-tolerant because there were no saplings of these species at light levels IV and V. In contrast, Group C consisted of light-demanding species, as indicated by higher densities under high-light conditions (light levels IV and V). Group D species were generalists in terms of light, with an abundance of saplings across the range of light levels (Figure 4).

#### CLASSIFICATION OF DISTRIBUTION PATTERNS

The microhabitat preferences of the species were classified in a disturbance type × light requirement matrix. The 13 major species were projected into 11 of the 12 possible combinations of environments (“cells”) (Table III). Nine species were the sole species present in the cell they occupied; 5 of these species (*Z. serrata*, *A. mono*, *A. japonicum*, *F. lanuginosa*, and *C. japonicum*) showed very specific habitat preferences (Table III). The other species were found to compete in shared environments, but no more than 3 species shared a single preferred environment.

## Discussion

In the study forest, the majority of saplings were found on disturbed sites, and species richness was also higher at these sites than in the undisturbed beneath-canopy sites. Therefore, disturbances provide important regeneration sites for many species in this forest. The relative densities of saplings in canopy gaps and on fluvial deposits (Figure 3) suggest that major species possess a preference for regeneration sites provided by canopy disturbance (e.g., *C. japonicum*, *F. lanuginosa*) or fluvial disturbance (e.g., *Z. serrata*, *P. rhoifolia*). There also appear to be some disturbance-generalist species (e.g., *F. crenata*). These preferences appear to be consistent with seedling ecology found in previous studies. For example, bare-soil substrates and increased light in gaps enhance seedling emergence and survival in *C. japonicum* (Kubo *et al.*, 2000; 2004; Masaki *et al.*, 2007). With regard to species that prefer fluvial deposit sites, seedling emergence is enhanced for *P. rhoifolia* (Masaki *et al.*, 2007). Thus, the observed preferences for disturbance type

appear to reflect microenvironmental preferences in the seedling stage.

The present analysis also suggests that light requirements of saplings differ among major species. Interspecific separation of light resources for plant regeneration has been assumed and frequently reported for the sapling stage in many studies (e.g., Kobe, 1999; Gasser *et al.*, 2010), but not

in other studies (Arii & Lechowicz, 2002; Gravel, Beaudet & Messier, 2008). In the present study, 8 of the 13 major species showed different distribution ranges depending on light levels (Figures 4 and 5; Group A–C). Group C consisted of *C. japonicum* and *S. bakko*, which are known as shade-intolerant, light-demanding species (Kubo *et al.*, 2004; Nakamura & Inahara, 2007). *Fraxinus lanuginosa*

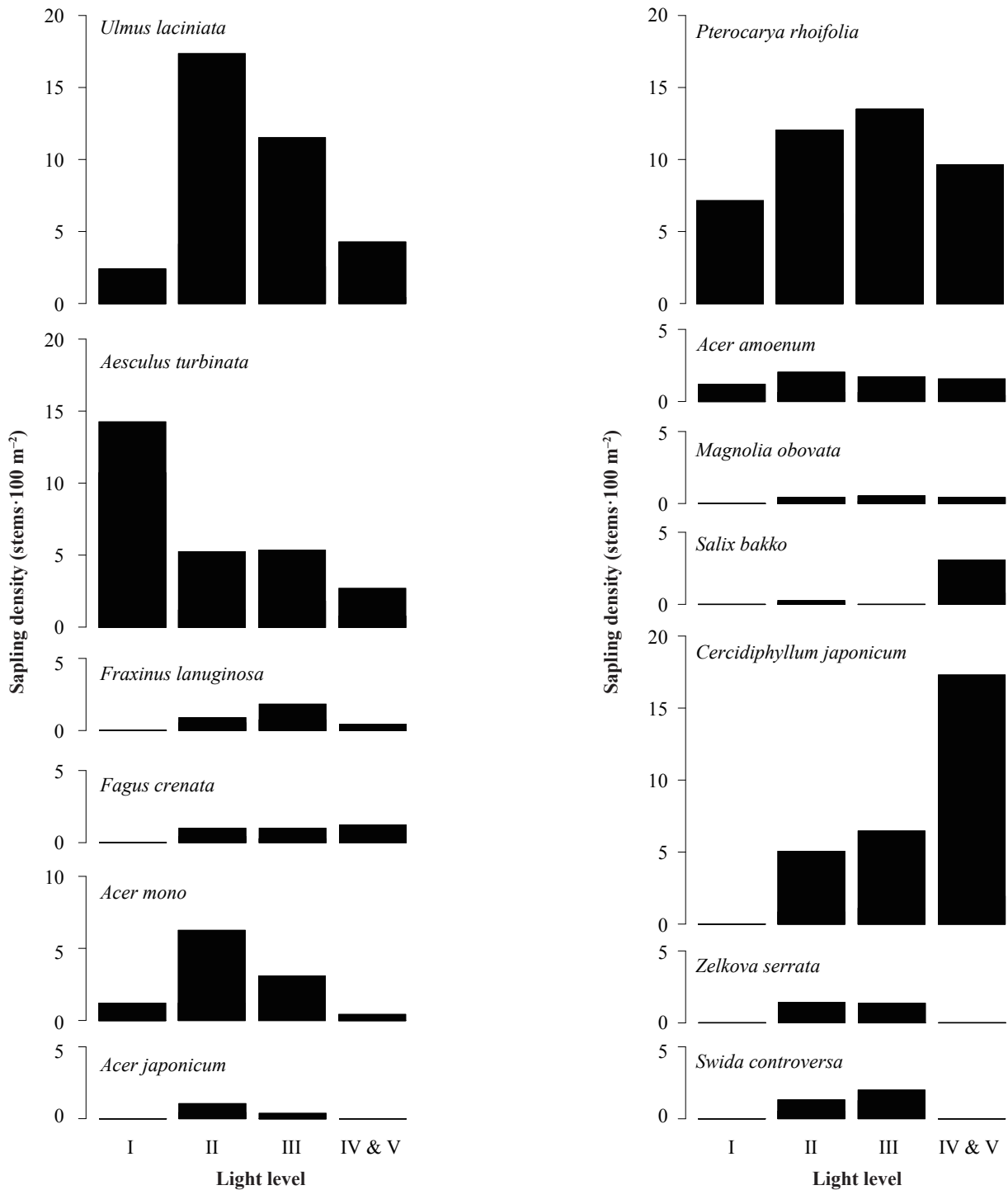


FIGURE 4. Stem densities for the 13 major species along light levels in disturbed sites. The calculated openness was converted into 5 light levels (levels IV and V were pooled to improve appearance).

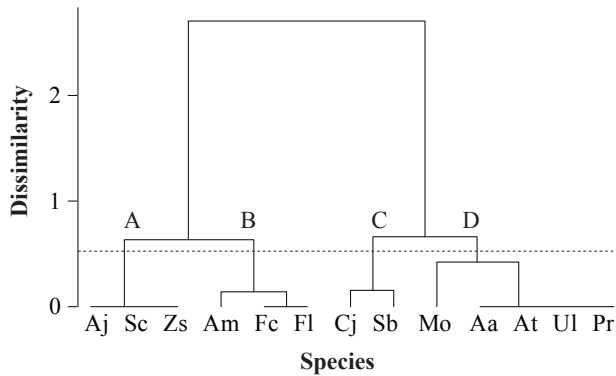


FIGURE 5. Dendrogram showing sapling light requirements for the 13 major species divided into 4 groups (A, B, C, and D) at a level indicated by the dotted line. The dendrogram was drawn via Ward linkage. See Table II for species codes.

TABLE III. Classification of 13 major species by favourable microhabitats, as defined by disturbance type  $\times$  light requirement. For disturbance type, species are sorted to the habitat for which their sapling distribution showed significant bias or to the “unbiased” row (see also Figure 3). For the light requirement group, species are sorted to the preferred light habitat detected via cluster analysis (Figure 5). See Table II for species codes.

Disturbance type	Light requirement group*			
	A	B	C	D
Fluvial deposits	Zs	Am	-	Ul, Pr
Canopy gaps	Aj	Fl	Cj	At, Aa
Unbiased	Sc	Fc	Sb	Mo

\* A, shade tolerant; B, slightly shade tolerant; C, light demanding; D, generalist. See text for details.

and *A. japonicum*, members of Group B and Group A respectively, preferred canopy gaps (Figure 3). The light-density relationship (Figure 4) for these 2 species shows that they can utilize relatively low light, e.g., small gaps. This is consistent with the fact that in the present forest, *F. lanuginosa* and *A. japonicum* are not riparian-specialists (Suzuki *et al.*, 2002). A similar inference would yield the prediction that *C. japonicum* requires higher light, which is provided by larger gaps (Sakio *et al.*, 2002; Masaki *et al.*, 2007). On the other hand, *A. turbinata* showed no preference for light conditions. This is mainly because this species has large (>5 g in dry weight) seeds, which enables seedlings to survive in deep shade (Hoshizaki, Suzuki & Sasaki, 1997). Thus, the range of light conditions in the present riparian stand appears to be sufficiently large for a variety of species to exhibit substantially different preferences for light-habitats, which can lead to an enriched sapling species composition.

In the simulation of species-area curves, the sapling community showed similar patterns on fluvial deposits and in gaps (but consistently showed a greater number of species in these locations than in beneath-canopy quadrats). This result suggests that the 2 types of disturbance may have equivalent effects on species diversity, in contrast to previous notions that emphasized the role of fluvial disturbances (e.g., Suzuki *et al.*, 2002; Sakio *et al.*, 2002). In the list of sapling habitat preferences expressed in the matrix of disturbance type  $\times$  light requirements, most species

were “scattered” over the environmental combinations (Table III). These results suggest that a single disturbance regime, *i.e.*, fluvial disturbance or canopy gap creation *per se*, would not produce the diversity of sapling species composition in the present riparian forest. This may be firstly because the microsite conditions provided by canopy gaps also involve some alterations of the forest floor: not only increased light but also access to mineral soils on uprooted mounds. Both of these conditions are critical in the establishment of *C. japonica* seedlings (Kubo *et al.*, 2004; Masaki *et al.*, 2007). Second, it might be because canopy gaps are scattered spatially compared with fluvial deposit sites (Figure 1), enabling many species to encounter the gaps. This possibility can be discounted, however, because even in *A. turbinata*, the largest-seeded species in temperate forests, seed dispersal distance is sufficiently great to reach a nearby canopy gap and is effective for distributing seeds over the plot (Hoshizaki, Suzuki & Nakashizuka, 1999).

The combination of canopy and ground-surface disturbances may be significant. In light-requirement terms, groups A and B include several competing species. Thus, the niche segregation hypothesis suggests that other means of partitioning the habitat or resources should be necessary (e.g., differential preferences for soil nutrients at the seedling stage; Gravel, Beaudet & Messier, 2008). As fluvial deposits in KRRF contain a variety of grain sizes, they provide diverse conditions during seedling establishment. Variation in light availability may have additive effects on stage transition from seedling to sapling. Thus, we propose that the combination of multiple types of disturbances increases the likelihood of sapling habitat partitioning among species (and ultimately species coexistence) in species-rich riparian habitats.

To date, only a few studies have examined the effect of multiple factors (such as light  $\times$  soil conditions) on the distribution patterns of saplings in two-species (*Acer–Fagus* or *Betula–Fagus*) systems (Arii & Lechowicz, 2002; Gravel, Beaudet & Messier, 2008; Gasser *et al.*, 2010). Among these, only Gravel, Beaudet, and Messier (2008) argue that the factors affecting distribution of regenerated individuals should be considered in terms of ontogeny (*i.e.*, life-stage transition). Our present results may be valuable because they suggest that multiple factors limit sapling distribution in a highly species-rich system in a different forest type.

The present analysis, however, had several limitations for the complete understanding of niche segregation. For example, the space represented by fluvial disturbance and high light conditions (*i.e.*, Group C) was vacant. This combination may be preferred by *Salix* spp. (Niiyama, 1990; Karrenberg, Edwards & Kollmann, 2002; Nakamura & Inahara, 2007), but in KRRF, samples of this genus may have been insufficient for meaningful results (“unbiased” in this study). In addition, the most abundant canopy species, such as *P. rhoifolia* and *U. laciniata*, were not segregated (Table III). In these species, resource requirements should be evaluated more critically, based on ecophysiological and/or manipulative studies (*i.e.*, fundamental niches), although such studies are limited in number (Villagra *et al.*, 2013).

Alternatively, different analyses of the key processes affecting sapling bank dynamics, *e.g.*, long-term performance of saplings (Mann *et al.*, 2008), may be effective in testing niche segregation in species-rich systems.

In summary, our analyses show that the tendency for sapling occurrence differed among species. Riparian habitats for saplings appeared to be partitioned, to some extent, between species under multiple disturbance regimes in response to disturbance type and light gradient, although this was not evident in all species. To fully test the apparent segregation of sapling regeneration niches in this species-rich forest, future analyses of long-term sapling dynamics that incorporate multiple environmental factors will be essential.

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## Appendix I

APPENDIX I, TABLE I. Detailed descriptions and the history of canopy and fluvial disturbances in the study site, Kanumazawa Riparian Research Forest (KRRF). Gap ID is assigned according to the year of gap formation.

Site ID	Season/month and year of disturbance	Affected area (m <sup>2</sup> )	Type of disturbance
Canopy gap formation			
G1	1989, 1990 (seasons unknown)	113	Multiple trees, stem broken
G2	October 1991	43	Single tree, uprooting
G3	October 1991	196	Single tree, uprooting
G4	Early spring 1993	155	Single tree, uprooting
G5	Early spring 1993	207	Multiple trees, stem broken
G6	Early spring 1995, early spring 1999	413	Multiple trees, stem broken
G7	Summer 1998	43	Single tree, standing dead
G8	Early spring 2000	385	Single tree, stem broken
G9	Early spring 2000	40	Single tree, stem broken
G10	October 2002	159	Single tree, uprooting
G11	Early spring 2003	24	Single tree, uprooting
Fluvial sediment transport			
F1	August 1988	680	Sedimentation
F2	August 1988	615	Sedimentation
F2	August 1998	125	Erosion (site separated)
F2	September 2007	340	Sedimentation (re-loaded)
F3	September 2007	144	Sedimentation

## Appendix II

a) Sedimentation in site F1



b) Erosion in site F2



c) Woody debris in site F2



d) Reloaded sediments in site F2



e) Sedimentation in site F3



APPENDIX II, FIGURE 1. Photographic records of fluvial disturbances in Kanumazawa Riparian Research Forest (KRRF). a) Fluvial deposits, including large amounts of boulders and small amounts of woody debris, in site F1, which was created by a heavy-rain-induced fluvial sediment transport event on 28–29 August 1988. b, c) Severe erosion (b) and accompanying woody debris (c) in site F2 after intermittent heavy rains during 26–31 August 1998. d, e) Boulder–gravel mixture of fluvial deposits in sites F2 (d) and F3 (e), both of which were created by typhoon-induced heavy rains on 7 September 2007. Photos by W. Suzuki (a), K. Hoshizaki (b, c, e), and S. Oki (d).