

Effect of fluvial and geomorphic disturbances on habitat segregation of trees species in a sedimentation-dominated riparian forest in warm-temperate mountainous region in southern Japan

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Abstract

We investigated habitat segregation and patterns of species diversity of trees in relation to variations in fluvial and geomorphic disturbances (erosion or sedimentation) along a longitudinal stream gradient from V-shaped valley to alluvial fan and between valley and adjacent hill slopes in a warm-temperate mountainous riparian forest in Kyushu, southwestern Japan. We divided the riparian area longitudinally into four geomorphic zones: V-shaped valley (VV-zone), upper fan (UF-zone), middle fan (MF-zone) and lower fan (LF-zone). We surveyed the distribution of tree species (DBH \geq 3cm) in the four riparian zones and in additional plots on hill slopes (SL-zone) representing the broader, non-riparian forest matrix. Detrended correspondence analysis (DCA) ordination demonstrated variations in species composition along the longitudinal stream gradient. Species guild analysis based on the detection of species' preferred zone by a bootstrap method revealed a guild structure corresponding to each geomorphic zone. The four riparian zones were differentiated from the SL-zone by having a low proportion of SL-guild species and high proportion of infrequent species that were characterized by deciduous leaf habit. The LF-zone was the most differentiated and was characterized by low tree density and specialist species established on the flat and unstable soil surface created by frequent deposition of sediment. The UF- and MF-zones were characterized by a high tree density and species richness (particularly of infrequent species) established on the stable ground surface of a high alluvial terrace. Micro-site heterogeneity produced by channel formation may also maintain a high species diversity in the riparian zones.

Keywords: *geomorphic guild, longitudinal stream gradient, micro-site heterogeneity, site stability, species diversity*

Introduction

Riparian forests maintain diverse vegetation structure through the influence of various types, intensities, and frequencies of disturbance promoted by fluvial and geomorphic processes (Nilsson et al. 1989; Baker 1990; Ito and Nakamura 1994; Sakio 1997; Suzuki et al. 2002). These fluvial and geomorphic disturbances vary longitudinally from headwater streams to low-gradient alluvial rivers and result in different types of plant communities according to longitudinal location (Johnson et al. 1976; Niiyama 1987, 1989; Ishikawa 1988; Hughes 1990; Duncan 1993; Aruga et al. 1996; Nakamura et al. 1997; Sakio 1997; Nakamura and Shin 2001; Suzuki et al. 2002; Nakamura and Inahara 2006). For each location, many studies have revealed the coexistence or habitat segregation of tree species, showing how tree life history is linked to variations in disturbance regime and heterogeneous micro-landforms (Johnson et al. 1976; White 1979; Kovalchik and Chitwood 1990; Swanson and Sparks 1990; Gregory et al. 1991; Malanson and Kupfer 1993; Stewart et al. 1993; Robertson and Augspurger 1999; Loehle 2000).

In Japan over the last decade, mountainous riparian forests have been receiving increasing attention from ecologists. Many studies on community structure and dynamics in riparian zones have been conducted, focusing particularly on the influence of riparian disturbances on community characteristics (Sato 1992, 1995; Kaneko 1995; Ann and Oshima 1996; Hara et al. 1996; Sakio 1997; Kaneko et al. 1999; Sakai et al. 1999; Sakio et al. 2002; Sakio and Yamamoto 2002; Suzuki et al. 2002). These studies reported unique structure and dynamics of riparian forests compared to those of forests situated on the ordinary slopes. They indicate the ecological importance of fluvial and geomorphic processes in the sedimentation-dominated areas, such as wide headwater streams or alluvial fans and terraces, for the maintenance of the regional plant diversity. However, most of these studies were conducted in cool-temperate central or northern Japan. In warm-temperate parts of the

country, the relationship between species distribution and micro-landform or disturbance regime has been reported for forest communities established on mountainous slopes or V-shaped valleys lacking floodplains and terraces (Hara et al. 1996; Sakai et al. 1999; Enoki 2003; Hattori et al. 2003; Enoki and Abe 2004; Ito et al. unpublished) or on the banks and gravel bars along low-gradient alluvial rivers (Ishikawa 1988; Sakio and Yamamoto 2002). However, much less information is available on tree species diversity patterns in mountainous riparian forests, including the sedimentation-dominated small alluvial fans in this region (Ito and Nogami 2005). Thus, there is a need to clarify the relationship between forest composition and the longitudinal stream gradient of fluvial and geomorphic disturbances from erosion-dominated to sedimentation-dominated areas, in order to evaluate whether or not and how these forests contribute to the maintenance of biodiversity at regional scale (Ito and Nogami 2005).

In this paper, we aimed to describe the pattern of tree distribution and diversity in relation to the geomorphic gradient in old-growth mountainous riparian forests in a warm-temperate Japan. For this objective, we examined 1) how the longitudinal stream gradient from V-shaped valley (erosion-dominated zone) to alluvial fan (sedimentation-dominated zone) promotes variations in site conditions and disturbance regimes, 2) how the tree distribution and diversity vary within the riparian zones in relation to microtopography and differ from the ordinary slope forest of the region, and 3) how the variations in site conditions and disturbance regime act to determine the tree distribution and diversity pattern. To assess address these questions, we investigated a small catchment consisting of a V-shaped valley and a small alluvial fan in the Kirishima Mountains, southern Kyushu, Japan. We measured physical site conditions and forest vegetation. We applied guild structure analysis, which has been adopted in previous studies (Sakai et al. 1999; Suzuki et al. 2002) to relate the diversity patterns to the site conditions and disturbance regimes. Based on these analyses, we discuss the influence of the geomorphic gradient, site conditions, and disturbance regime from slope to alluvial fan on tree distribution and tree species diversity.

Method

Study site

Figure 1

The study site was in Koike Lake caldera, which is a volcanic feature formed by the collapse of a crater of a volcano, in the Kirishima Mountains, southern Japan (130°57'E, 31°51'N) (Fig. 1). The study focused on an evergreen broadleaved riparian forest located in a V-shaped valley and associated alluvial fan at the bottom of the caldera, as well as the hill slopes above the riparian zone. The forest is situated at 330–400 m elevation. Annual mean temperature and precipitation are 15°C and 2260 mm, respectively. Surface soils consist of volcanic soils formed from pyroclastic and debris flow deposits. The climatic-vegetation zone of the forest is warm-temperate lucidophyllous (warm-temperate evergreen natural forest) dominated by *Quercus gilva* and *Machilus thunbergii* (Miyawaki 1981). Several deciduous species such as *Ulmus davidiana* var. *japonica*, *Sapindus mukurossi* and *Morus bombycis*, which are associated with the cool-temperate zone (Miyawaki 1981; Okuda 1997), were found at the site. This study site has been protected as part of the Kirishima Forest Reserve since 1934, and is covered with old-growth lucidophyllous forest with many trees exceeding 30 m height and 120 cm of diameter at breast height. There was no evidence of recent logging, and the forest seemed to have been maintained under natural disturbances for decades.

Figure 2

We divided the riparian area into four geomorphic zones and established contiguous survey plots with a width of 40 m placed end-to-end along the longitudinal direction of the slope: V-shaped valley zone (VV, 40 m × 60 m), Upper fan zone (UF, 40 m × 100 m), Middle fan zone (MF, 40 m ×

80 m) and Lower fan zone (LF, 40 m \times 80 m) (Fig. 2). Each geomorphic zone was distinguished from the adjacent zone by the differing longitudinal inclination and by observed variation in geomorphology and soil surface characteristics. The VV-zone was distinguished by narrow valley bottom and steep bank slope. The UF-zone had the steepest longitudinal slope, i.e., riverbed inclination (approximately 20-40%), and was distinguished by the large rocks covering the ground surface and deep channels. MF-zone was gentler (approximately 15-30%) than UF-zone with intermediate rock size and shallow channels. LF-zone had a relatively smaller riverbed inclination (approximately 5-15%) with no apparent surface rocks and channels.

In order to compare riparian vegetation with typical lucidophyllous vegetation in this region, we established another four quadrats (40 m \times 10 m each) in the hill slope forest (SL, 1600 m² in total). The stands of SL-zone were located in old-growth lucidophyllous forest on the upper slope of the caldera with relatively stable ground surface, i.e., with no evidence of recent disturbance related to earth surface processes such as landslides. The four quadrats were assumed to have been maintained by the gap dynamics owing to wind-blown disturbances by typhoons.

Geomorphology and soil survey of riparian zone

To quantify physical characteristics of each riparian zone, and interpret disturbance history, we surveyed the geomorphology and soil survey of each zone. First, we mapped micro-landform (channels and alluvial terraces produced by debris flow deposits) in and around the plots of the riparian zones (VV-, UF-, MF- and LF-zones) to grasp the heterogeneity of soil surface conditions. Then we measured slope inclination, which might interact with flow or sedimentation intensity (Nakamura and Inahara 2006), in the longitudinal direction along the center line of the plots at 10 m intervals. For each riparian zone, we also undertook a geomorphic survey of the transverse sections of each plot with one transect running perpendicular to the valley at each 20 m interval to identify

ground surface undulation, that is, the heterogeneity of micro-site conditions, formed by channels and sediment. We measured the elevation along these transects at ca 50 cm interval to represent the distribution of channels and sediments.

In order to estimate the difference in the disturbance intensity of sedimentation, surface rock size distribution was estimated using photographs of the soil surface. Rock size was assumed to reflect the disturbance intensity (degree of destruction) of sedimentation, and thus effect of the site conditions for established trees. Photos were taken of quadrats (1 m \times 1 m in area) at three to five points at 20 m intervals along the center line of each plot of the riparian zones. A scale was included in each photograph and we counted the number of rocks on the soil surface according to the following rock diameter ranges: 2-5 cm, 5-10 cm, 10-20 cm, 20-50 cm and >50 cm.

We also described soil profiles to directly observe the evidence of past disturbances related to sedimentation. Eighteen points were randomly selected in and around the plots of the riparian zones (six points for each of UF-, MF- and LF-zone; none for VV-zone) to describe the soil profile. Two points in UF-zone, which were located outside the plot (c. 5m apart from the plot line) were included because we could easily observe the naturally exposed soil profile on the deep channel wall. We described soil layers by color, texture, grain size, hardness, and thickness, which reflect the frequency and intensity of sedimentation, to 1-2 m depth depending on the depth to bedrock. From these observations, we identified layer characteristics as pyroclastic flow deposits (presumably relating to very intensive disturbances), debris flow deposits consisting of rocks (intensive disturbances), or tractive deposits and others (less intensive disturbances). According to the description in the literatures (Machida et al. 1981, Saito 1988, Licker 2003), pyroclastic flow deposits consist of the products of volcanic explosions, characterized by sharp-shaped rock fragments. Debris flow deposits consist of coarse rock with a wide range of sizes. Tractive deposits consist of sandy soil and small-size rocks.

Vegetation survey

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| Table 1 |
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We recorded positions and diameter at breast height (1.3 m; referred to hereafter as DBH) of all living individual trees (DBH \geq 3 cm) in all zones including the hill slope (SL) zone (68 species and 2146 individuals in total), and calculated their basal area (BA). For multi-stemmed individuals, the BA was taken as the BA of largest stem within the clump. A summary of the tree cover in the surveyed plots is shown in Table 1. Nomenclature followed Ohwi and Kitagawa (1992).

Data analysis

In order to characterize the site condition and estimate the disturbance regimes of the four riparian zones, we calculated average values of longitudinal slope, mean diameter of surface rocks, number of coarse rocks (diameter > 20 cm) per 1 m², ground surface undulation, and percentage depth of sediments (pyroclastic flow deposits, debris flow deposits, tractive deposits and others) in the soil profile. Ground surface undulation of each transverse section was calculated as the standard deviation of elevation. The mean diameter of surface rock was calculated by assuming that the diameter of rocks in a given diameter range was equal to the mid point of the range (e.g., for all rocks within the diameter range of 2-5 cm, a diameter of 3.5 cm was applied). The size of rocks exceeding 50 cm was set at 75 cm to represent an upper extreme of rock size.

In order to analyze the degree of dominance of each species in each of the geomorphic zones, summed dominance ratio (SDR) was evaluated for each species as the mean of relative basal area and relative tree density, according to Numata and Yoda (1957).

Vegetation analyses compared vegetation among 400 m² (20 m \times 20 m) grids (10 m \times 40 m quadrats for SL) to analyze the differentiation of species composition at the community level in relation to the geomorphic zones. We applied detrended correspondence analysis (DCA; Hill and Gauch 1980) to

ordinate the grids and quadrats by using a matrix of the absolute number of trees as dominance values for each species in each grid or quadrat (36 grids and quadrats in total). DCA was performed using PC-ORD Version 4 (McCune and Mefford 1999), a personal computer-based software package. Guild structure was determined for each geomorphic zone based on zone preference of species (VV, UF, MF, LF or SL) to determine the degree of habitat segregation among zones. The zone preference (distributional bias to a particular zone) of each species was determined using the bootstrap method (Manly 1997) taking into account the number of individuals and BA of each species in each geomorphic zone; this analysis is based on the assumption that the expected number of individuals or BA of a given species in a given geomorphic zone is proportional to that of the total pooled population of all species. For each species, 100,000 random selections were made from the total tree population of the zones (2146 individuals) to produce a sample size equivalent to the number of trees of the target species, and the number of selected trees within each of the five geomorphic zones for each random sample was then counted. The result was compared with the observed value of individual trees of the target species to obtain the probability that the number of trees within a particular geomorphic zone exceeded the value that would be expected if the distribution was completely random throughout the area. Similar probabilities were calculated for BA measurements, but using 1,000,000 random selections for each species in order to address large fluctuations within samples. For a given species, the preferred geomorphic zone was designated where a probability exceeding 0.95 was obtained. Species guilds were assigned as VV-, UF-, MF-, LF- or SL-guild according to their preferred geomorphic zone, except when there was no preference (generalist or GEN). Species that had a minimum expected value of less than 10 occurrences were treated as infrequent species (INF).

The proportion of individuals or basal area belonging to each guild occurring in each geomorphic zone was compared among zones to determine the degree of habitat segregation. Multiple comparisons using the resampling method were made by calculating bootstrap probabilities

(Westfall and Young 1993). Resampling was performed 10,000 times.

Furthermore, composition of the infrequent species (INF), which made up a high proportion of all species (44 out of 68 species) in this study, were examined in detail to characterize the vegetation of each geomorphic zone with respect to the species characteristics (leaf habits and characteristic habitats). As most pioneer tree species of the region have a deciduous leaf habit, we compared the composition of deciduous infrequent species among the geomorphic zones. The characteristic habitat was determined for 1) lucidophyllous natural forest (warm-temperate evergreen forest) containing the most species in the region, 2) aestatilignosa natural forest (cool-temperate, summer-green forest) which contain fewer species in the region, and 3) coppice woodlands species which are strongly related to severe disturbance (Ohwi and Kitagawa 1992; Okuda 1997; Mogi et al. 2000). Species not described in the literature were labeled ‘others’.

In order to evaluate the species diversity of the five geomorphic zones, we also compared the species-area curves of each geomorphic zone from the cumulative number of species with addition of 100 m² (10 m × 10 m) subdivisions making up 400 m² quadrats.

Results

Site condition at each geomorphic zone

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| Table 2 |
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The geomorphic and soil characteristics of the riparian geomorphic zones are summarized in Table 2. Longitudinal slope was steepest in the upper fan (UF-zone, 28.0%), followed by the middle fan (MF-zone, 21.1%), V-shaped valley (VV-zone, 15.8%), and the lower fan (LF-zone, 9.7%). Ground surface undulation across the slope was greatest in the VV-zone (1.06 m) because of its steep bank

slope. In the three fan zones, the relatively high ground surface undulation in the UF-zone (0.68 m) reflected the elevation difference between the relatively high terraces (debris flow sediments) and deep channels; undulation values decreased in the longitudinal direction to the MF- and LF-zones resulting in the flattest ground surface in the LF-zone. The average size of rocks exposed on the soil surface was largest in the VV-zone and UF-zone, and decreased downstream from there. The number of large rocks (diameter > 20cm) demonstrated a similar trend to that of average rock size.

The average thickness of each sediment layer in the soil profile progressively decreased from the UF-zone toward the LF-zone. The type of sediment in the soil profile was dominated by debris flow deposits in the UF-zone and by tractive deposits in the LF-zone. The MF-zone had a sediment composition that was intermediate between the UF- and LF-zones.

Stand structure and ordination of vegetation

Table 3

Sixty-eight tree species (DBH \geq 3 cm) were recorded from the zones. Tree density was high in the SL-, UF- and MF-zones and extremely low in the LF-zone (Table 1). A summary of the floristic composition in the study plots is shown in Table 3. The maximum DBH in the UF- and MF-zones was higher than the SL-, the VV- and the LF-zones. The species composition in the SL-zone was characterized by high dominance of *Machilus thunbergii* (SDR of 18.4%; summed dominance ratio) and *Distylium racemosum* (SDR of 16.7%). The VV-zone was dominated by *M. thunbergii* (SDR of 21.8%), followed by *M. japonica* (SDR of 10.4%) and *Quercus gilva* (SDR of 9.7%). Vegetation on the fan zones (UF-, MF- and LF-zones) was dominated by *Q. gilva*, which had a SDR of 16.5% to 25.0%, associated with *M. japonica*, *M. thunbergii* and *Camellia sasanqua*. Coniferous species such as *Cephalofaxus harringtonia* and deciduous species such as *Morus bombycis* and *Sapindus mukoross* were the component species in LF-zone but were uncommon in the UF- or MF-zones (see

Appendix).

Figure 3

The DCA ordination of the 36 grids and quadrats (Fig. 3) showed a clear differentiation of species composition between the LF-zone and other zones along the first axis (Eigenvalue = 0.389); however, the grids in the UF-zone and the MF- zones were not so clearly separated from each other. Quadrats in the SL-zone and grids in the VV-zone received lower scores for the first axis, contrasting with the higher scores of VV-zone of the second axis (Eigenvalue = 0.144). Grids in the UF- and MF-zone were equally scattered on the second axis in an intermediate position along the first axis between the LF-zone and the SL- and VV-zones.

Species guild analysis

Appendix

Forty-four of the 68 species were infrequent (INF-type species), i.e., there were less than 10 individuals across all zones. The other 24 species were sufficiently common to perform an analysis of site preference on their occurrence data. As a result of the bootstrap analysis, six species showed no bias towards any geomorphic zone and were classified as generalist species (GEN-type). The remaining 18 species showed a preference to at least one of the five geomorphic zones (Appendix). As a result, five species guilds were identified, and one for each of the five geomorphic zones. There were five species in the SL-guild, two species in the VV-guild, five species in the UF-guild, two species in the MF-guild and four species in the LF-guild. Most component species of the guilds were evergreen species usually found in lucidophyllous forest (after Okuda 1997), with the only exceptions being *Cornus controversa* in the MF-guild (deciduous coppice woodland species), *Ficus erecta* in the LF-guild (deciduous lucidophyllous species), and *Celtis sinensis* and *Styrax japonica* in the generalist group (deciduous coppice woodland species).

Figure 4

The proportion of species in each of the seven species groups (five geomorphic guilds, generalists [GEN], and infrequent species [INF]) within each geomorphic zone is shown in Fig 4. According to multiple comparison by the bootstrap method, there were no significant differences in the species composition between any of the geomorphic zones ($p>0.05$), although the absolute number of infrequent species tended to be higher in the UF- and MF-zones (23 and 28 species, respectively) than in other zones (4, 9 and 12 species for SL-, VV-, and LF-zones, respectively). The proportion of SL-guild species tended to decrease down the longitudinal gradient and was lowest in the LF-zone (1 species).

Figure 5

The proportion of individuals in each species guild within each geomorphic zone is shown in Figure 5. These proportions varied significantly between every pair of geomorphic zones (Multiple comparison, $p<0.05$). Each guild was most strongly represented in its geomorphic zone, e.g., a high proportion of species belonging to the UF guild occurred in the UF-zone. The LF-zone showed a higher proportion of infrequent species than the other zones.

Table 4

With respect to the distribution of the types of INF species by geomorphic zone (Table 4), the fan zones (UF-, MF- and LF-zones) had a higher proportion of ‘aestatilignosa species’ (after Okuda, 1997) and ‘coppice species’ than the SL-zone, contrasting with the higher proportion of ‘lucidophyllous species’ in the SL-zone. Similarly, all geomorphic zones on the fan had a higher proportion of ‘deciduous species’ than the SL-zone.

Species-area curves

Figure 6

Overall, the cumulative increase in species number in the UF- and MF-zones was steeper and continued to increase with area compared to the more gradual increase of the SL-, VV- and LF-zones (Fig. 6). These patterns reflected the large number of infrequent species recorded in the UF- and MF-zones. The MF-zone showed the steepest increase and the highest maximum number (Table 1). The UF-zone showed a trend similar to the MF-zone, but with slightly lower species number. The species number in the SL-zone was higher than VV- or LF-zones at smaller scales ($<500\text{m}^2$), but lower species number at larger areas. The VV- and LF-zones showed patterns of increase and maximum values similar to each other, which exceeded the species number of the SL-zone at 1000 m^2 and 1800 m^2 , respectively.

Discussion

Site condition of riparian area

Table 5

This study site shows a clear gradient in disturbance regime and site conditions in relation to fluvial and geomorphic processes. Based on ground surface undulation (indicating the heterogeneity of micro-site conditions), rock size of the sediment (indicating intensity of disturbance), and sediment composition and thickness (representing intensity and frequency of disturbance) (see Table 2), we estimated disturbance type (predominance of erosion or sedimentation), disturbance regimes and site conditions in the geomorphic zone in the riparian area (Table 5).

The soil surface undulations in the LF-zone were not strongly developed, (i.e., unclear channel

formation) compared with the UF- and MF-zones (Table 2). This result is attributable to the LF-zone being one of sedimentation rather than erosion, as in the case the upper zones with clearer channels. In the LF-zone, the relatively flat surface was presumably caused by underflow of LF-zone due to its low riverbed inclination and sandy sediments with high water permeability, resulting in a homogeneous micro-site condition combined with flat sediments with low elevation. While the thick sediment layers in the UF-zone were formed by debris flow deposits, the thin layer in the LF-zone was characterized by tractive deposits comprising fine rocks and sands (Table 2). Thus, within the sedimentation-dominated riparian zones (UF-, MF- and LF-zones), we suggest that intensity of disturbance decreased but the frequency increased to downstream along the longitudinal stream gradient from the UF- to LF-zone. As well as the case of our study site, the same trend of disturbance intensity and frequency was reported in the alluvial fan in a temperate riparian forest in central Japan (Ito and Marutani 1993). Sakio (1997) also reported that the frequency of disturbance by the sedimentation of sands and fine rocks was higher compared to infrequent disturbance by debris flows in a cool-temperate *Fraxinus platypoda* – *Pterocarya rhoifolia* forest of central Japan. The distribution of fine rocks and sands, flat ground surface, and inferred high sedimentation frequency of the LF-zone (Table 5) suggests that it had the most differentiated habitat condition compared to the other riparian zones and the hill slope.

The soil surface of the UF- and MF-zones could be considered more stable than the VV- and LF-zones due to the relatively high elevation of the terraces produced by rocky debris flow deposits (Table 5). Generally, once a high terrace is formed by sedimentation of a debris flow, the formed terraces could be stable for a long time (Ito and Nakamura 1994). In the same site as the previous study of Sakio (1997), Kawanishi et al. (2004) reported that the terraces formed by debris flows were relatively stable for a certain period. With regard to the intensity of disturbance, Nakamura & Inahara (2006) suggest that disturbance intensity decreases along an elevation gradient from the active channel to higher terraces in a braided river on an alluvial fan in northern Japan. Considering

the presence of both stable deposits and frequently disturbed channels, the UF- and MF-zones represented more heterogeneous habitats than the VV- and LF-zones.

Habitat segregation and species diversity pattern

This study revealed the habitat segregation for tree species along the longitudinal stream gradient in the warm-temperate riparian forests. The five geomorphic species guilds distinguished in the study (Appendix) indicated a certain level of habitat segregation producing the distribution bias of tree species between the geomorphic zones. The number of individuals in each geomorphic guild was dominant in its defining geomorphic zone (Fig. 5), suggesting that the distinguished guilds significantly affected the differentiation of species composition among the geomorphic zones. Furthermore, DCA ordination of 36 grids and quadrats (Fig. 3) indicated the species composition varying along the longitudinal stream gradient, which might reflect the significant habitat segregation detected by the guild analysis.

In a cool-temperate region in northern Japan, Suzuki et al. (2002) reported clear differences in species composition between the slope and riparian zone in terms of the guild composition analyzed by difference in presence or absence of species. In our study site in the warm-temperate region, although geomorphic guilds were distinguished and showed the differences in their composition between geomorphic zones on the individual-number basis (Fig. 5), the differences in their composition of species number were not clear (Fig. 4) compared to the case reported by Suzuki et al. (2002). This suggested an overlapping distribution of the guilds in our case, suggesting a relatively high capacity for the species present to establish on sub-optimal zones compared with those in the cool-temperate region.

The habitat for trees of the riparian zones (VV-, UF-, MF- and LF-zones) were obviously differentiated from that of the hill slope (SL-zone) because they commonly had a low proportion of

SL-guild individuals and a high proportion of infrequent species (Fig. 5). The composition of infrequent species in the riparian zones was characterized by the presence of *aestatilignosa* (cool-temperate summer-green natural forest) species and coppice woodland species compared to the SL-zone represented by *lucidophyllous* (warm-temperate evergreen natural forest) species (Table 4). Thus, we suggest that the hill slope and riparian zones were basically segregated as different habitats by different disturbance regimes, as reported for cool-temperate mountainous forests (Sakio 1997; Sakio et al. 2002; Suzuki et al. 2002). Our results also indicate that the mountainous riparian zone in warm-temperate evergreen forests provides habitat for the *aestatilignosa* species.

The habitat of the LF-zone was shown to be the most segregated from the SL-zone of the four riparian zones as reflected by differences in guild composition (Fig. 5). This differentiation could be attributed to the disturbance regime in this zone which produces a flat but unstable soil surface resulting from frequent sedimentation of fine rocks and sands (Table 5). We suggest that this disturbance regime also promotes the low tree density of this zone (Table 1). The species distinguished as LF-guild or infrequent species which were intensively observed in the LF-zone could be expected to have life histories that are well adapted to less intensive but frequent disturbances rather than to intensive disturbances such as the destruction of canopy trees by debris flows (c.f., Sakio 1997; Nakamura & Inahara 2006). These species typical of the LF-zone were uncommon in the other zones. The species richness of this zone was low compared with the UF and MF-zones (Fig. 6), presumably because of the homogenous micro-site conditions. However, the disturbance regime and resulting site condition of the LF-zone would contribute toward maintaining the regional flora by providing habitat for certain rare species.

The UF-zone and MF-zone were dominated by *Quercus gilva* (Table 3). These zones consisted of the stable ground surface of alluvial terraces (Table 5), which presumably have a better soil moisture condition than that of upper slopes because of the location close to the channel (c.f., Nagamatsu and Miura 1997; Kikuchi 2001). Thus, the moist soil conditions in these zones would provide suitable

habitats for *Q. gilva*, which have been described to prefer flat and moist sites with fertile soil (Miyawaki 1981). The relatively stable sediment surfaces would also partly explain the dominance of *Q. gilva*, which have been known as a typical climax species preferring to stable habitats (Miyawaki 1981). In contrast, frequent and less intensive disturbances along the channel or LF-zone might be less advantageous for *Q. gilva*, even if the soil moisture condition of these site are same or better than that on the terraces in UF-or MF-zones. In addition to *Q. gilva*, the stable and moist site condition of these zones presumably explains the occurrence of *Abies filma* with large DBH (but low frequency) on the debris flow deposits. *Abies filma* was also reported to have a preference for moist sites such as foot-slopes (Nakao 1985). The species of the UF-guild were common in the other zones (Appendix), suggesting that they had a high capacity to become established on any stable surface in all the habitats examined. The existing of many trees with large DBH in the UF- and MF- zones (Table 3) would also reflect the stability for a long period on the alluvial terraces.

The UF- and MF-zones were characterized by high tree density and species richness (particularly of infrequent species). These characteristics would also be related to the stable ground surface of these higher elevation deposits (Table 5). On the other hand, the formation of clear (relatively deep) channels could contribute to the establishment of infrequent species that are dependent on frequent disturbance. These site characteristics of partial stability and heterogeneity in the UF- and MF- zones were thought to be a major factor in determining the high species diversity of these zones.

In conclusion, this study clarified the pattern of site conditions, fluvial and geomorphic disturbance regimes, and habitat segregation of tree species along the longitudinal stream gradient in a warm-temperate riparian forest. Our results suggested the importance of sedimentation-dominated disturbance regimes resulting in conspicuous site condition and forest structure. These conditions promoted by sedimentation-dominated disturbance regimes appear to contribute to the maintenance of the regional flora by supporting many infrequent species, including several species of the *aestatilignosa* tree group, which are hardly maintained on the ordinary slopes of the region.

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Captions

Figure 1. Location of the study plots of riparian and slope forests.

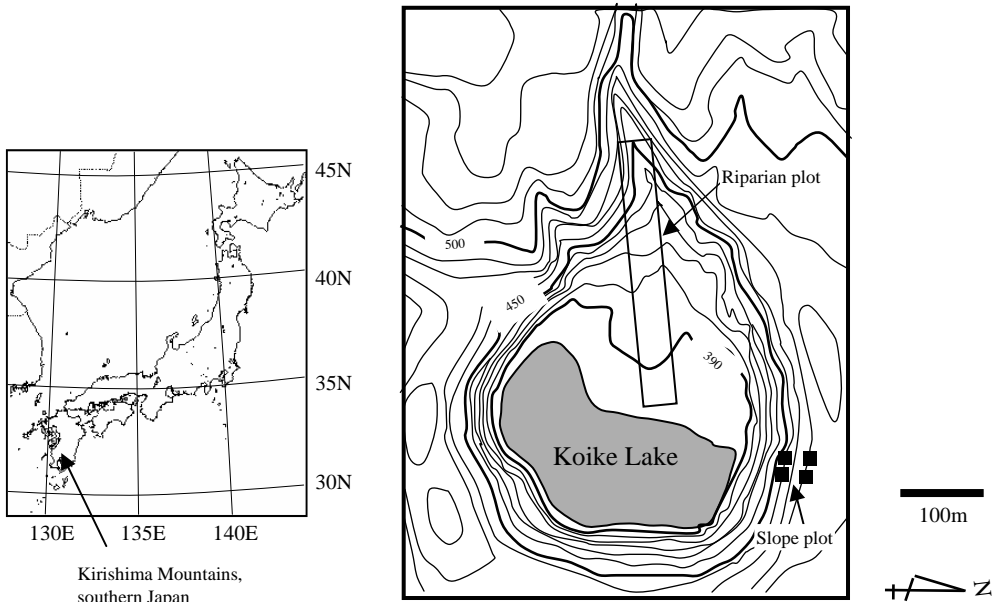
Figure 2. Arrangement of the riparian zone plots and distribution of micro-landform.

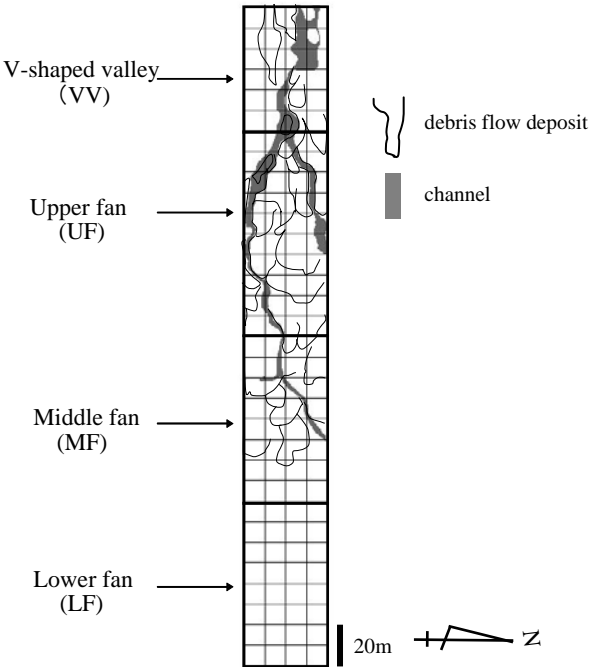
Figure 3. Scatter plot of 36 grids and quadrats for the first two axes of the detrended correspondence analysis (DCA) ordination showing differences in tree species composition among zones.

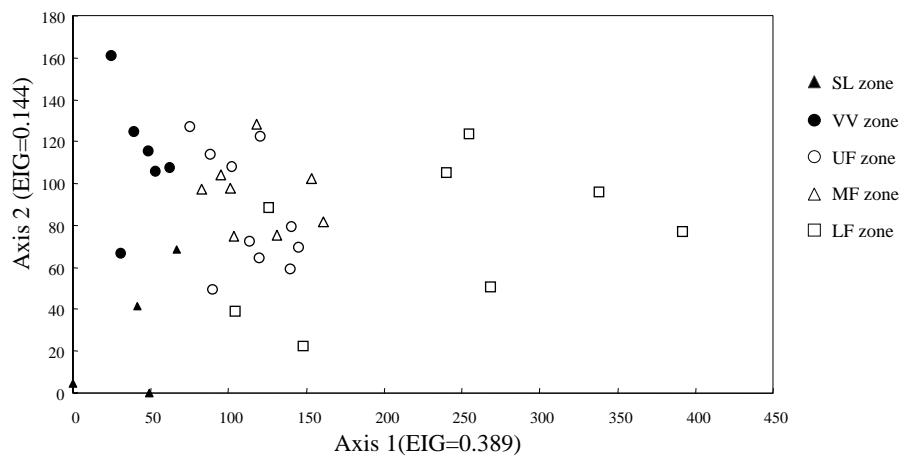
Figure 4. Proportion of the number of species by guild type on the five different geomorphic zones.

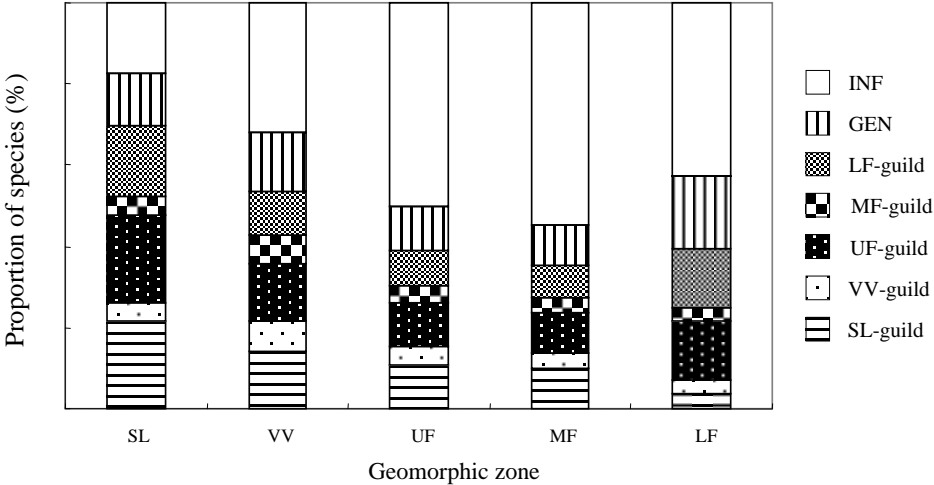
Figure 5. Proportion of the number of individuals by guild types on the five different geomorphic zones.

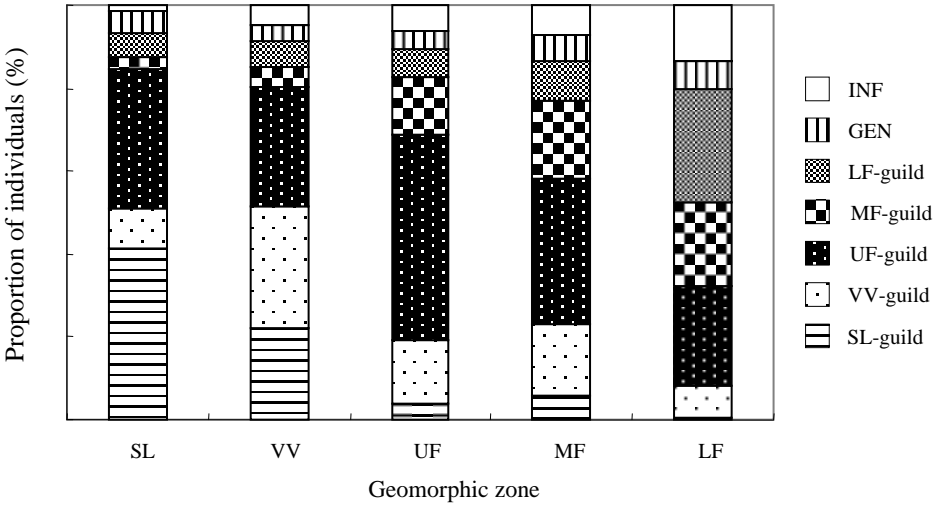
Figure 6. Species-area curves for the five different geomorphic zones.











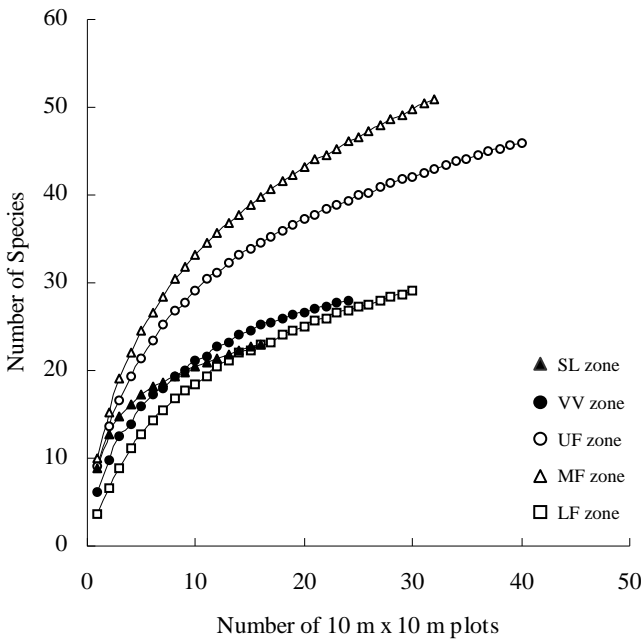


Table 1. Plot size, number of species, number of individuals and tree density in five different geomorphic zones.

| Geomorphic zones | Plot size (m ²) | Number of species | Number of individuals | Tree density (No./ha) |
|----------------------|--------------------------------|----------------------|--------------------------|--------------------------|
| Slope (SL) | 1600 | 23 | 330 | 2062 |
| V-shaped valley (VV) | 2400 | 28 | 271 | 1129 |
| Upper fan (UF) | 4000 | 46 | 754 | 1885 |
| Middle fan (MF) | 3200 | 51 | 618 | 1931 |
| Lower fan (LF) | 3200 | 28 | 173 | 541 |
| Total | 14400 | 68 | 2146 | 1490 |

Table 2. Soil surface conditions and soil profiles in the riparian zone.

| | Geomorphic zone | | | |
|---|----------------------|----------------|-----------------|----------------|
| | V-shaped valley (VV) | Upper fan (UF) | Middle fan (MF) | Lower fan (LF) |
| Longitudinal slope inclination (%) | 15.8 | 28.0 | 21.1 | 9.7 |
| Ground surface undulation (m) ¹⁾ | 1.06 | 0.68 | 0.27 | 0.11 |
| Surface rock size ²⁾ | | | | |
| Average rock diameter (cm) | 12.88 | 13.06 | 7.67 | 5.80 |
| Number of coarse rock (>20cm) | 6.33 | 6.2 | 1.5 | 0.25 |
| Average thickness of each sediment | - | 50.3 | 13.2 | 11.6 |
| Proportion of sediments (%) | | | | |
| Pyroclastic flow deposits | - | 17.1 | 35.0 | 10.9 |
| Debris flow deposits | - | 79.5 | 16.0 | 0 |
| Tractive deposits | - | 3.4 | 45.4 | 85.2 |
| Others (fall deposits) | - | 0 | 3.5 | 3.8 |

¹⁾ Ground surface undulation was calculated as a standard deviation of elevations measured on the traverse grid line (20m interval) of each plot.

²⁾ Rock size was measured for those have diameter more then 2cm.

Table 3. Species composition in the five different geomorphic zones. Species are ordered by number of individuals on each zone to the fifth most abundant species.

| Family | Species | Number of individuals (No. per plot) | Mean DBH (cm) | Max DBH (cm) | Relati BA (%) | Relati densit (%) | SDR (%) |
|----------------------------------|------------------------------|--|---------------------|--------------------|---------------------|-------------------------|------------|
| Slope (SL-zone) | | | | | | | |
| Lauraceae | <i>Machilus thunbergii</i> | 31 | 20.5 | 89.3 | 9.4 | 27.3 | 18.4 |
| Hamamelidaceae | <i>Distylium racemosum</i> | 30 | 21.2 | 71.7 | 9.1 | 24.4 | 16.7 |
| Lauraceae | <i>Machilus japonica</i> | 41 | 12.1 | 55.6 | 12.4 | 11.3 | 11.9 |
| Fagaceae | <i>Castanopsis cuspidata</i> | 16 | 23.0 | 89.0 | 4.8 | 16.7 | 10.8 |
| Theaceae | <i>Camellia japonica</i> | 55 | 6.3 | 23.4 | 16.7 | 2.8 | 9.7 |
| | Others | 173 | 7.3 | 89.3 | 47.6 | 17.4 | 32.5 |
| | Total | 330 | 11.3 | 89.3 | 100 | 100 | 100 |
| V-shaped valley (VV-zone) | | | | | | | |
| Lauraceae | <i>Machilus thunbergii</i> | 57 | 15.0 | 41.5 | 22.5 | 21.0 | 21.8 |
| Lauraceae | <i>Machilus japonica</i> | 35 | 11.6 | 28.5 | 7.9 | 12.9 | 10.4 |
| Fagaceae | <i>Quercus gilva</i> | 8 | 32.0 | 85.8 | 16.4 | 3.0 | 9.7 |
| Hamamelidaceae | <i>Distylium racemosum</i> | 28 | 9.6 | 58.9 | 8.8 | 10.3 | 9.6 |
| Theaceae | <i>Cleyera japonica</i> | 25 | 8.1 | 29.4 | 3.3 | 9.2 | 6.2 |
| | Others | 153 | 8.9 | 66.2 | 41.1 | 43.5 | 42.3 |
| | Total | 271 | 12.4 | 85.8 | 100 | 100 | 100 |
| Upper fan (UF-zone) | | | | | | | |
| Fagaceae | <i>Quercus gilva</i> | 92 | 10.9 | 142.7 | 20.8 | 12.2 | 16.5 |
| Lauraceae | <i>Machilus japonica</i> | 106 | 9.9 | 41.9 | 9.7 | 14.1 | 11.9 |
| Lauraceae | <i>Machilus thunbergii</i> | 95 | 9.3 | 38.7 | 7.4 | 12.6 | 10.0 |
| Theaceae | <i>Camellia sasanqua</i> | 112 | 5.8 | 18.2 | 2.8 | 14.9 | 8.8 |
| Lauraceae | <i>Litsea acuminata</i> | 63 | 11.1 | 39.4 | 6.6 | 8.4 | 7.5 |
| | Others | 468 | 6.9 | 117.2 | 52.6 | 37.9 | 45.3 |
| | Total | 754 | 9.9 | 142.7 | 100 | 100 | 100 |
| Middle fan (MF-zone) | | | | | | | |
| Fagaceae | <i>Quercus gilva</i> | 101 | 11.0 | 107.4 | 25.9 | 16.3 | 21.1 |
| Lauraceae | <i>Machilus thunbergii</i> | 98 | 9.6 | 39.5 | 9.7 | 15.9 | 12.8 |
| Theaceae | <i>Camellia sasanqua</i> | 77 | 5.3 | 11.0 | 1.9 | 12.5 | 7.2 |
| Theaceae | <i>Cleyera japonica</i> | 54 | 7.4 | 14.4 | 2.5 | 8.7 | 5.6 |
| Lauraceae | <i>Machilus japonica</i> | 51 | 11.5 | 29.1 | 6.7 | 8.3 | 7.5 |
| | Others | 381 | 6.8 | 146.3 | 53.4 | 38.3 | 45.9 |
| | Total | 618 | 9.8 | 146.3 | 100 | 100 | 100 |
| Lower fan (LF-zone) | | | | | | | |
| Fagaceae | <i>Quercus gilva</i> | 35 | 12.8 | 99.7 | 29.7 | 20.2 | 25.0 |
| Lauraceae | <i>Machilus japonica</i> | 16 | 13.6 | 32.2 | 7.3 | 9.2 | 8.3 |
| Lauraceae | <i>Machilus thunbergii</i> | 13 | 15.3 | 42.3 | 8.3 | 7.5 | 7.9 |
| Lauraceae | <i>Neolitsea aciculata</i> | 21 | 5.9 | 13.3 | 1.6 | 12.1 | 6.9 |
| Moraceae | <i>Morus bombycis</i> | 5 | 26.7 | 56.2 | 9.2 | 2.9 | 6.1 |
| | Others | 90 | 10.6 | 83.1 | 43.9 | 48.0 | 45.9 |
| | Total | 173 | 12.0 | 99.7 | 100 | 100 | 100 |

¹⁾ SDR; Summed dominance ratio calculated as the mean of relative BA and relative density.

Table 4. Distribution of infrequent species by habitat preference and leaf habit. Figures are the number of species and proportion of the total number for the geomorphic zone as a percent (in brackets).

| | | Geomorphic zone | | | | | | | | | |
|------------------------|--|-----------------|-------|----|------|----|------|----|------|----|------|
| | | SL | | VV | | UF | | MF | | LF | |
| Characteristic habitat | | | | | | | | | | | |
| Aestatilignosa forest | | 0 | (0) | 0 | (0) | 2 | (9) | 1 | (3) | 1 | (8) |
| Coppice forest | | 0 | (0) | 5 | (56) | 9 | (39) | 12 | (43) | 5 | (42) |
| Lucidophyllous forest | | 4 | (100) | 3 | (33) | 1 | (48) | 14 | (50) | 5 | (42) |
| Unknown | | 0 | (0) | 1 | (11) | 1 | (4) | 1 | (3) | 1 | (8) |
| Leaf habit | | | | | | | | | | | |
| Evergreen | | 3 | (75) | 3 | (33) | 8 | (35) | 13 | (46) | 4 | (33) |
| Deciduous | | 1 | (25) | 6 | (67) | 1 | (65) | 15 | (54) | 8 | (67) |

Table 5. Summary of fluvial and geomorphic disturbance types and site condition in the geomorphic zones in the riparian area.

| Geomorphic zone | Disturbance type | Stability of soil | Heterogeneity of micro-site |
|------------------------------------|---------------------------|-------------------|-----------------------------|
| V-shaped valley (VV) | erosion | low | high |
| Middle fan (MF) and Upper fan (UF) | erosion and sedimentation | high | very high |
| Lower fan (LF) | sedimentation | low | low |

Appendix. Summary of bootstrap probability analysis for preferred geomorphic zones of each species.

| Species | Number of individuals | Guild ¹⁾ type | Geomorphic zone | | | | | | | | | | | | | | | | | | | |
|----------------------------------|-----------------------|-----------------------------|-------------------|----------|-----|----------|-----|----------|-----|----------|-----|----------|-----|----------|-----|----------|----|----------|-----|----------|-----|----------|
| | | | SL | | | | VV | | | | UF | | | | MF | | | | LF | | | |
| | | | No. | <i>p</i> | BA | <i>p</i> | No. | <i>p</i> | BA | <i>p</i> | No. | <i>p</i> | BA | <i>p</i> | No. | <i>p</i> | BA | <i>p</i> | No. | <i>p</i> | BA | <i>p</i> |
| <i>Camellia japonica</i> | 99 | SL | +++ ²⁾ | 0.00 | ++ | 0.04 | +++ | 0.00 | + | 0.11 | --- | 0.00 | - | 0.15 | --- | 0.00 | -- | 0.02 | --- | 0.00 | --- | 0.00 |
| <i>Distylium racemosum</i> | 76 | SL | +++ | 0.00 | +++ | 0.00 | +++ | 0.00 | + | 0.31 | --- | 0.00 | --- | 0.00 | --- | 0.00 | -- | 0.03 | --- | 0.00 | --- | 0.00 |
| <i>Cinnamomum japonicum</i> | 39 | SL | +++ | 0.00 | + | 0.08 | - | 0.26 | - | 0.13 | --- | 0.00 | - | 0.19 | --- | 0.01 | - | 0.56 | - | 0.17 | + | 0.24 |
| <i>Castanopsis sieboldii</i> | 32 | SL | +++ | 0.00 | ++ | 0.02 | + | 0.38 | - | 0.58 | -- | 0.04 | - | 0.06 | - | 0.07 | - | 0.25 | - | 0.07 | - | 0.07 |
| <i>Castanopsis cuspidata</i> | 17 | SL | +++ | 0.00 | + | 0.30 | - | 0.10 | - | 0.10 | -- | 0.01 | -- | 0.01 | + | 0.19 | ++ | 0.03 | - | 0.24 | - | 0.24 |
| <i>Machilus thunbergii</i> | 294 | VV | -- | 0.01 | ++ | 0.03 | +++ | 0.00 | + | 0.11 | - | 0.17 | - | 0.06 | + | 0.05 | - | 0.31 | --- | 0.01 | - | 0.31 |
| <i>Aucuba japonica</i> | 50 | VV | --- | 0.00 | --- | 0.00 | +++ | 0.00 | + | 0.07 | + | 0.39 | + | 0.25 | - | 0.06 | - | 0.41 | -- | 0.02 | -- | 0.02 |
| <i>Machilus japonica</i> | 249 | UF | + | 0.34 | + | 0.27 | + | 0.27 | - | 0.44 | +++ | 0.01 | + | 0.34 | --- | 0.00 | - | 0.41 | - | 0.21 | - | 0.52 |
| <i>Camellia sasanqua</i> | 218 | UF | --- | 0.00 | -- | 0.03 | --- | 0.00 | --- | 0.00 | +++ | 0.00 | ++ | 0.05 | ++ | 0.02 | + | 0.30 | - | 0.15 | + | 0.35 |
| <i>Cleyera japonica</i> | 194 | UF | + | 0.44 | - | 0.29 | + | 0.49 | + | 0.29 | ++ | 0.03 | + | 0.18 | - | 0.42 | + | 0.39 | --- | 0.00 | --- | 0.00 |
| <i>Litsea acuminata</i> | 141 | UF | + | 0.51 | + | 0.32 | - | 0.38 | + | 0.41 | ++ | 0.01 | + | 0.18 | -- | 0.03 | - | 0.19 | - | 0.41 | - | 0.17 |
| <i>Illicium anisatum</i> | 23 | UF | + | 0.48 | - | 0.46 | -- | 0.05 | -- | 0.05 | ++ | 0.01 | ++ | 0.05 | - | 0.31 | - | 0.44 | - | 0.15 | - | 0.15 |
| <i>Quercus gilva</i> | 245 | MF | --- | 0.00 | --- | 0.00 | --- | 0.00 | - | 0.44 | + | 0.23 | + | 0.32 | +++ | 0.00 | + | 0.19 | +++ | 0.00 | + | 0.18 |
| <i>Cornus controversa</i> | 34 | MF | -- | 0.00 | --- | 0.00 | + | 0.43 | + | 0.24 | + | 0.42 | + | 0.29 | ++ | 0.02 | + | 0.22 | - | 0.06 | - | 0.06 |
| <i>Neolitsea aciculata</i> | 85 | LF | - | 0.57 | - | 0.53 | + | 0.39 | - | 0.36 | - | 0.22 | + | 0.37 | - | 0.24 | - | 0.62 | ++ | 0.02 | + | 0.18 |
| <i>Cephalotaxus harringtonia</i> | 58 | LF | --- | 0.00 | - | 0.05 | - | 0.06 | - | 0.37 | --- | 0.01 | - | 0.22 | + | 0.14 | + | 0.33 | +++ | 0.00 | ++ | 0.02 |
| <i>Ficus erecta</i> | 29 | LF | - | 0.16 | + | 0.25 | -- | 0.02 | -- | 0.02 | --- | 0.01 | - | 0.06 | +++ | 0.01 | + | 0.20 | +++ | 0.00 | + | 0.09 |
| <i>Ilex rotunda</i> | 20 | LF | - | 0.39 | - | 0.57 | - | 0.26 | - | 0.23 | + | 0.24 | - | 0.24 | - | 0.13 | + | 0.20 | ++ | 0.02 | + | 0.07 |

| | | | | | | | | | | | | | | | | | | | | | | |
|--|----|-----|----|------|----|------|----|------|-----|------|-----|------|-----|------|-----|------|-----|------|-----|------|-----|------|
| <i>Eurya japonica</i> | 35 | GEN | + | 0.16 | + | 0.27 | - | 0.34 | - | 0.24 | - | 0.27 | - | 0.50 | - | 0.57 | + | 0.32 | + | 0.31 | + | 0.19 |
| <i>Quercus salicina</i> | 23 | GEN | + | 0.27 | - | 0.60 | + | 0.57 | + | 0.11 | - | 0.41 | - | 0.16 | + | 0.33 | + | 0.24 | - | 0.14 | - | 0.15 |
| <i>Neolitsea sericea</i> | 20 | GEN | + | 0.07 | + | 0.28 | - | 0.07 | - | 0.07 | - | 0.41 | + | 0.13 | - | 0.28 | - | 0.21 | + | 0.07 | - | 0.67 |
| <i>Celtis sinensis</i> | 19 | GEN | -- | 0.04 | -- | 0.04 | + | 0.44 | + | 0.15 | + | 0.52 | - | 0.43 | + | 0.15 | + | 0.20 | - | 0.54 | - | 0.22 |
| <i>Styrax japonica</i> | 13 | GEN | - | 0.11 | - | 0.11 | + | 0.50 | + | 0.30 | - | 0.27 | + | 0.38 | + | 0.14 | + | 0.24 | + | 0.28 | - | 0.70 |
| <i>Ternstroemia gymnanthera</i> | 11 | GEN | - | 0.48 | - | 0.85 | - | 0.23 | - | 0.87 | + | 0.34 | - | 0.65 | - | 0.61 | - | 0.71 | + | 0.22 | + | 0.08 |
| <i>Acer palmatum</i> | 9 | INF | - | 0.22 | - | 0.22 | + | 0.32 | - | 0.60 | + | 0.06 | ++ | 0.03 | -- | 0.05 | -- | 0.05 | + | 0.53 | - | 0.48 |
| <i>Ligustrum japonicum</i> | 9 | INF | - | 0.22 | - | 0.22 | + | 0.32 | + | 0.08 | - | 0.61 | - | 0.53 | + | 0.51 | - | 0.32 | + | 0.53 | - | 0.61 |
| <i>Sapindus mukorossi</i> | 8 | INF | - | 0.26 | - | 0.26 | - | 0.34 | - | 0.34 | + | 0.58 | - | 0.57 | - | 0.28 | + | 0.35 | ++ | 0.00 | + | 0.08 |
| <i>Morus bombycis</i> | 8 | INF | - | 0.26 | - | 0.26 | - | 0.34 | - | 0.34 | -- | 0.03 | -- | 0.03 | + | 0.42 | - | 0.47 | +++ | 0.00 | +++ | 0.01 |
| <i>Premna microphylla</i> | 7 | INF | - | 0.31 | - | 0.31 | + | 0.22 | + | 0.16 | - | 0.23 | - | 0.26 | + | 0.11 | + | 0.19 | - | 0.56 | - | 0.56 |
| <i>Celtis jessoensis</i> | 5 | INF | - | 0.43 | - | 0.43 | - | 0.51 | - | 0.51 | +++ | 0.01 | +++ | 0.01 | - | 0.18 | - | 0.18 | - | 0.66 | - | 0.66 |
| <i>Sambucus racemosa ssp. sieboldiana</i> | 5 | INF | - | 0.43 | - | 0.43 | - | 0.51 | - | 0.51 | - | 0.12 | - | 0.12 | +++ | 0.00 | +++ | 0.00 | - | 0.66 | - | 0.66 |
| <i>Abies firma</i> | 5 | INF | - | 0.43 | - | 0.43 | - | 0.51 | - | 0.51 | + | 0.24 | + | 0.27 | - | 0.55 | + | 0.25 | + | 0.34 | - | 0.66 |
| <i>Torreya nucifera</i> | 4 | INF | + | 0.49 | + | 0.08 | - | 0.58 | - | 0.58 | - | 0.56 | - | 0.38 | + | 0.33 | - | 0.54 | - | 0.71 | - | 0.72 |
| <i>Symplocos kuroki</i> | 4 | INF | + | 0.49 | + | 0.16 | - | 0.58 | - | 0.58 | + | 0.44 | + | 0.36 | - | 0.67 | - | 0.56 | - | 0.71 | - | 0.72 |
| <i>Daphniphyllum macropodum</i> | 4 | INF | - | 0.51 | - | 0.51 | - | 0.58 | - | 0.58 | + | 0.44 | + | 0.28 | + | 0.33 | + | 0.27 | - | 0.72 | - | 0.71 |
| <i>Carpinus tschonoskii</i> | 3 | INF | - | 0.61 | - | 0.61 | - | 0.67 | - | 0.67 | - | 0.72 | + | 0.07 | + | 0.64 | - | 0.38 | + | 0.22 | - | 0.79 |
| <i>Litsea coreana</i> | 3 | INF | - | 0.61 | - | 0.61 | - | 0.67 | - | 0.67 | + | 0.28 | - | 0.58 | + | 0.64 | + | 0.18 | - | 0.78 | - | 0.78 |
| <i>Phellodendron amurense</i> | 3 | INF | - | 0.61 | - | 0.61 | - | 0.67 | - | 0.67 | - | 0.72 | + | 0.26 | + | 0.20 | + | 0.32 | - | 0.78 | - | 0.78 |
| <i>Zelkova serrata</i> | 3 | INF | - | 0.61 | - | 0.61 | - | 0.67 | - | 0.67 | - | 0.72 | - | 0.56 | + | 0.64 | - | 0.56 | + | 0.22 | + | 0.08 |
| <i>Viburnum odoratissimum var. awabuki</i> | 3 | INF | - | 0.61 | - | 0.61 | - | 0.67 | - | 0.67 | - | 0.27 | - | 0.27 | + | 0.64 | + | 0.34 | ++ | 0.02 | + | 0.06 |
| <i>Quercus myrsinaefolia</i> | 3 | INF | - | 0.61 | - | 0.61 | ++ | 0.04 | +++ | 0.00 | - | 0.27 | - | 0.27 | + | 0.64 | - | 0.37 | - | 0.78 | - | 0.78 |

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|--|---|-----|---|------|---|------|---|------|---|------|---|------|---|------|---|------|---|------|-----|------|-----|------|
| <i>Ulmus davidiana</i> var. <i>japonica</i> | 3 | INF | - | 0.61 | - | 0.61 | - | 0.67 | - | 0.67 | - | 0.27 | - | 0.27 | - | 0.36 | - | 0.36 | +++ | 0.00 | +++ | 0.00 |
| <i>Mallotus japonicus</i> | 2 | INF | - | 0.72 | - | 0.72 | - | 0.76 | - | 0.76 | - | 0.42 | - | 0.42 | + | 0.08 | + | 0.08 | - | 0.85 | - | 0.85 |
| <i>Idesia polycarpa</i> | 2 | INF | - | 0.72 | - | 0.72 | - | 0.76 | - | 0.76 | - | 0.42 | - | 0.42 | + | 0.08 | + | 0.08 | - | 0.85 | - | 0.85 |
| <i>Elaeocarpus japonicus</i> | 2 | INF | + | 0.28 | + | 0.06 | - | 0.76 | - | 0.76 | + | 0.58 | - | 0.48 | - | 0.51 | - | 0.51 | - | 0.85 | - | 0.85 |
| <i>Ilex latifolia</i> | 2 | INF | - | 0.72 | - | 0.72 | - | 0.76 | - | 0.76 | + | 0.58 | + | 0.33 | + | 0.49 | + | 0.30 | - | 0.85 | - | 0.85 |
| <i>Ehretia acuminata</i> var. <i>obovata</i> | 2 | INF | - | 0.72 | - | 0.72 | - | 0.76 | - | 0.76 | + | 0.58 | + | 0.23 | + | 0.49 | - | 0.62 | - | 0.85 | - | 0.85 |
| <i>Ficus erecta</i> f. <i>sieboldii</i> | 2 | INF | - | 0.72 | - | 0.72 | - | 0.76 | - | 0.76 | + | 0.58 | - | 0.54 | - | 0.51 | - | 0.51 | + | 0.16 | ++ | 0.05 |
| <i>Aphananthe aspera</i> | 2 | INF | - | 0.72 | - | 0.72 | - | 0.76 | - | 0.76 | + | 0.12 | + | 0.12 | - | 0.51 | - | 0.51 | - | 0.85 | - | 0.85 |
| <i>Quercus glauca</i> | 1 | INF | - | 0.85 | - | 0.85 | - | 0.87 | - | 0.87 | - | 0.65 | - | 0.65 | + | 0.29 | + | 0.29 | - | 0.92 | - | 0.92 |
| <i>Prunus buergeriana</i> | 1 | INF | - | 0.85 | - | 0.85 | - | 0.87 | - | 0.87 | + | 0.35 | + | 0.35 | - | 0.71 | - | 0.71 | - | 0.92 | - | 0.92 |
| <i>Villebrunea frutescens</i> | 1 | INF | - | 0.85 | - | 0.85 | + | 0.13 | + | 0.13 | - | 0.65 | - | 0.65 | - | 0.71 | - | 0.71 | - | 0.92 | - | 0.92 |
| <i>Michelia compressa</i> | 1 | INF | - | 0.85 | - | 0.85 | + | 0.13 | + | 0.13 | - | 0.65 | - | 0.65 | - | 0.71 | - | 0.71 | - | 0.92 | - | 0.92 |
| <i>Viburnum phlebotrichum</i> | 1 | INF | - | 0.85 | - | 0.85 | - | 0.87 | - | 0.87 | - | 0.65 | - | 0.65 | + | 0.29 | + | 0.29 | - | 0.92 | - | 0.92 |
| <i>Dendropanax trifidus</i> | 1 | INF | - | 0.85 | - | 0.85 | - | 0.87 | - | 0.87 | - | 0.65 | - | 0.65 | + | 0.29 | + | 0.29 | - | 0.92 | - | 0.92 |
| <i>Zanthoxylum ailanthoides</i> | 1 | INF | - | 0.85 | - | 0.85 | - | 0.87 | - | 0.87 | - | 0.65 | - | 0.65 | + | 0.29 | + | 0.29 | - | 0.92 | - | 0.92 |
| <i>Stachyurus praecox</i> | 1 | INF | - | 0.85 | - | 0.85 | - | 0.87 | - | 0.87 | - | 0.65 | - | 0.65 | + | 0.29 | + | 0.29 | - | 0.92 | - | 0.92 |
| <i>Clerodendrum trichotomum</i> | 1 | INF | - | 0.85 | - | 0.85 | - | 0.87 | - | 0.87 | + | 0.35 | + | 0.35 | - | 0.71 | - | 0.71 | - | 0.92 | - | 0.92 |
| <i>Cornus macrophylla</i> | 1 | INF | - | 0.85 | - | 0.85 | + | 0.13 | + | 0.13 | - | 0.65 | - | 0.65 | - | 0.71 | - | 0.71 | - | 0.92 | - | 0.92 |
| <i>Euonymus alatus</i> f. <i>striatus</i> | 1 | INF | - | 0.85 | - | 0.85 | - | 0.87 | - | 0.87 | - | 0.65 | - | 0.65 | + | 0.29 | + | 0.29 | - | 0.92 | - | 0.92 |
| <i>Diospyros lotus</i> | 1 | INF | - | 0.85 | - | 0.85 | - | 0.87 | - | 0.87 | - | 0.65 | - | 0.65 | - | 0.71 | - | 0.71 | + | 0.08 | + | 0.08 |
| <i>Ilex chinensis</i> | 1 | INF | - | 0.85 | - | 0.85 | - | 0.87 | - | 0.87 | - | 0.65 | - | 0.65 | + | 0.29 | + | 0.29 | - | 0.92 | - | 0.92 |
| <i>Stewartia monadelpha</i> | 1 | INF | - | 0.85 | - | 0.85 | - | 0.87 | - | 0.87 | + | 0.35 | + | 0.35 | - | 0.71 | - | 0.71 | - | 0.92 | - | 0.92 |
| <i>Magnolia hypoleuca</i> | 1 | INF | - | 0.85 | - | 0.85 | + | 0.13 | + | 0.13 | - | 0.65 | - | 0.65 | - | 0.71 | - | 0.71 | - | 0.92 | - | 0.92 |

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|----------------------------|---|-----|---|------|---|------|---|------|---|------|---|------|---|------|---|------|---|------|---|------|---|------|
| <i>Callicarpa japonica</i> | 1 | INF | - | 0.85 | - | 0.85 | + | 0.13 | + | 0.13 | - | 0.65 | - | 0.65 | - | 0.71 | - | 0.71 | - | 0.92 | - | 0.92 |
| <i>Ilex integra</i> | 1 | INF | - | 0.85 | - | 0.48 | - | 0.87 | - | 0.23 | - | 0.65 | - | 0.54 | - | 0.71 | + | 0.29 | + | 0.08 | + | 0.09 |
| <i>Rhus sylvestris</i> | 1 | INF | - | 0.85 | - | 0.85 | - | 0.87 | - | 0.87 | - | 0.65 | - | 0.65 | + | 0.29 | + | 0.29 | - | 0.92 | - | 0.92 |
| <i>Diospyros japonica</i> | 1 | INF | - | 0.85 | - | 0.85 | - | 0.87 | - | 0.87 | + | 0.35 | + | 0.35 | - | 0.71 | - | 0.71 | - | 0.92 | - | 0.92 |

¹⁾ LF, Lower fan; MF, Middle fan; UF, Upper fan; VV, V-shaped valley; SL, Slope; GEN, GENERALIST; INF, Infrequent species, which had minimum expected value of tree number less than 10.

²⁾ "+" and "-" mean more and less than the expected values, respectively. +++ and ---, p<0.001; ++ and --, p<0.01; + and -, p<0.05; (+) and (-), not significant.