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ORIGINAL ARTICLE

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Landslide-facilitated species diversity in a beech-dominant forest

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Abstract To evaluate the extent to which landslides affect community dynamics and consequent species diversity in a beech-dominated forest, differences in the composition and size structure of tree species were compared between landslide and adjacent stable (control) stands. Demography and changes in size were compared between the two stands over a 5-year period about 60 years after a landslide. In the control stand, replacement occurred even amongst late-successional species, with beech (*Fagus crenata*)—the most dominant species—increasing in relative abundance. In the landslide stand, very few large individuals of late-successional species occurred, whereas large individuals of early-successional species occurred only in the landslide stand. The traits indicate that the landslide strongly facilitated species diversity, not only by reducing the dominance of late-successional species, but also by promoting recruitment of early-successional species. However, new recruitment of early-successional species was inhibited in the landslide stand, although we observed succeeding regeneration and subsequent population growth of late-successional species there. As a result, the relative dominance of late-successional species increased with succession after the landslide, thus decreasing future species diversity. In beech-dominant forest landscapes in Japan that include communities with different developmental stages, the mosaic of serial stages may facilitate species diversity after a landslide.

Keywords Community dynamics · *Fagus crenata* · Regeneration · Replacement · Succession

Introduction

In forest communities, natural disturbances are important in determining structure, dynamics and species diversity (Runkle 1982; Pickett and White 1985; Whitmore 1989; Pollman and Veblen 2004; Reilly et al. 2006). Natural disturbances usually facilitate increased diversity of tree species by reducing the dominance of late-successional and shade-tolerant species and allowing the regeneration of early-successional species that require abundant light, thereby increasing overall richness (Connell 1978; Brokaw 1987; Denslow 1987; Bergeron et al. 1998; Chesson 2000; Seiwa 2007). Although the manner, intervals, spatial scale and causes of natural disturbances vary widely, research on the effects of natural disturbance has focused mainly on tree-fall gaps at single sites and relatively small spatial scales (≤ 100 m^2). A relatively small number of studies have looked at large disturbances caused by fire, big blowdowns, flooding or landslides. In particular, the ecological role of landslides in maintaining plant species diversity has been largely ignored, particularly in northern temperate forests (see references in Francescato et al. 2001; Fajardo and Alaback 2005; Geertsema and Pojar 2007).

Landslides differ from tree-fall gaps in several ways, as large mass movements remove not only canopy trees but also the understorey soil layer on a large scale (Pickett and White 1985; Guariguata 1990; Dalling and Tanner 1995). Thus, after landslides, both advance

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Nomenclature: Ohwi and Kitagawa (1983).

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regeneration and the soil seed bank are lacking (Guariguata 1990), soil nutrient status is low (Adams and Sidle 1987; Guariguata 1990; Shiels et al. 2008) and the substrate is unstable (Nakamura 1984; Shiels et al. 2008), although these conditions are spatially heterogeneous (Shiels et al. 2008; Velazquez and Gomez-Sal 2008). Although the lack of nutrients inhibits seedling growth (Dalling and Tanner 1995; Shiels et al. 2008), it usually promotes the establishment of light-demanding and early-successional species (Flaccus 1959; Guariguata 1990; Tanouchi and Yamamoto 1995; Francescato et al. 2001; Nishimura and Kohyama 2002; Geertsema and Pojar 2007; Velazquez and Gomez-Sal 2008). Thus, landslides are thought to play an important role in determining the regeneration of particular species or guilds and subsequent community structure (Flaccus 1959; Veblen and Ashton 1978; Veblen 1979; Stewart 1986; Guariguata 1990; Dalling and Tanner 1995; Yamamoto et al. 1995; Francescato et al. 2001; Restrepo and Vitousek 2001; Pollman and Veblen 2004; Fajardo and Alaback 2005; Velazquez and Gomez-Sal 2008).

Chronosequential analysis of landslide sites of different ages have shown successional replacement of early- by late-successional species (Flaccus 1959; Guariguata 1990; Francescato et al. 2001; Restrepo and Vitousek 2001), although some studies have indicated that late-successional species recruited promptly after landslide persist for long periods, even in the late-mature stages of succession (Nishimura and Kohyama 2002; Pollman and Veblen 2004; Elias and Dias 2009). Such differences are probably due to the inherent variability of abiotic and biotic environments within and amongst landslide sites. In mountains, aspect and slope influence the availability of water, nutrients and the extent of mass movement (Guariguata 1990; Walker et al. 1996; Enoki 2003; Geertsema and Pojar 2007; Shiels et al. 2008; Velazquez and Gomez-Sal 2008). These traits, together with climatic environmental conditions (e.g., precipitation and temperature) and the resultant floristic composition of the forests, strongly affect the replacement patterns of tree species after a landslide (e.g., Nishimura and Kohyama 2002; Pollman and Veblen 2004; Elias and Dias 2009). Thus, to clarify the role of landslides in determining forest communities, long-term investigations during long periods of forest succession, particularly in the late-successional stage, are needed in various forest communities.

In the northern temperate region of Japan, Japanese beech (*Fagus crenata*) is generally dominant in most forests, particularly on the Japan Sea side. The structure and dynamics of beech-dominated forests have been described in terms of gap dynamics; the forests consist of mosaic patches at different developmental stages caused by tree-fall gaps (Nakashizuka 1987; Yamamoto 1989). Beech seedlings established under the shaded canopy of beech trees are usually released by gap formation and grow into canopy trees (Cao and Ohkubo 1999). Furthermore, beech seedlings unfold their leaves earlier than the adults of most co-occurring tree species, thus promoting carbon acquisition prior to canopy closure (Tomita and Seiwa 2004). These traits, together with a lower light compensation point (Koike 1988), strongly enhance the persistence of beech in the forest understorey, generating a higher relative occurrence of beech-dominated old-growth forests (Nakashizuka and Iida 1995; Yamamoto and Nishimura 1999; Shimano 2002).

However, in forests on the Japan Sea side, landslides are common due to particular geologic (i.e., Tertiary) and climatic factors, such as heavy rain and deep snow (Miyagi 1992; National Research Institute for Earth Science and Disaster Prevention 1998; Nakamura 2002). Interactions amongst shallow, heavy-textured soils, weak rock types and highly dissected topography with steep slopes generate landslide-prone zones over a large area (Miyagi 1992; National Research Institute for Earth Science and Disaster Prevention 1998; Nakamura 2002). Although landslides are common in the area, few studies have evaluated the effects of landslides on forest structure and dynamics. Compared to tree-fall gaps, landslides may reduce the dominance of beech by involving a larger area of catastrophic disturbance. If so, species diversity would increase after the landslide because large disturbances usually enhance the recruitment of a large number of early-successional species.

In this study, we evaluated the effects of a landslide on the community structure and dynamics and subsequent species diversity of a *F. crenata*-dominant old-growth forest. We compared the floristic composition, size structure and demography (recruitment, mortality and growth rate) of dominant tree species in a landslide-affected and adjacent stable (control) stand in late succession. Our specific questions were the following. Does a landslide reduce the dominance of late-successional species and promote the recruitment of early-successional tree species? How and to what extent does community structure change after a landslide?

Methods

Study area

The study was carried out in an old-growth forest 580–620 m in altitude in the Ippitsuyama-Tashiro reserve area (38°49′2 N, 140°45′E), Miyagi, Japan (Fig. 1). The study area showed little evidence of human disturbance. Landslide characteristics in the Ippitsuyama-Tashiro Reserve area were measured via both topographical survey and aerial photographs (Miyagi 1992). On the southern slope of Mt. Ippitsu (718 m a.s.l.), the largest landslide (approximately 250 m in width) was observed from 695 m a.s.l. down to 580 m a.s.l., with an inclination of 18°. The soil is a well-drained Melanic Andosol (FAO-UNESCO 1998) that developed from Pliocene-Pleistocene sedimentary rock of unconsolidated or partially consolidated lake sediments, including sandstone, mudstone and conglomerate, with multiple

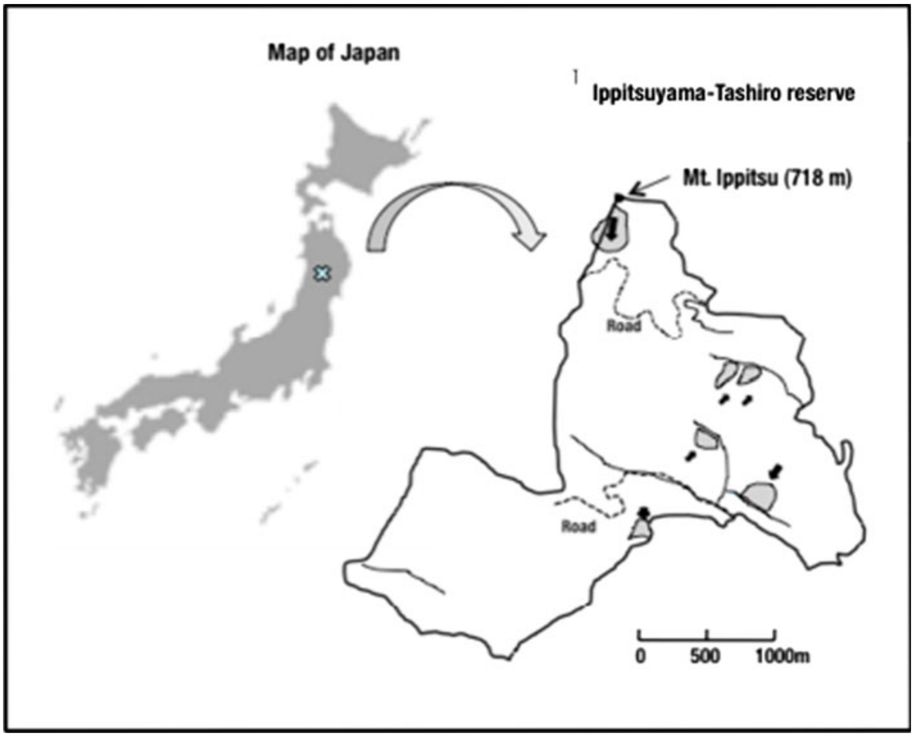

Fig. 1 Location of the Ippitsuyama-Tashiro reserve in Japan, showing the distribution of landslides (Miyagi 1992). *Arrows* show the direction of landslides. A study quadrat (100 × 100 m) was set in the largest landslide near Mt. Ippitsu

layers of deep volcanic ash (Miyagi 1992). Mean monthly temperature ranges from 23.0 °C in August to −1.8 °C in January. The mean annual precipitation measured at the nearest meteorological station (6 km west of the study site, 290 m altitude) was 2,140 mm, and the maximum snow depth was 165 cm (Hirabuki et al. 1992).

Field data

To compare the community dynamics between the landslide stand and neighboring stable stands, we established a 1-ha permanent plot (100 m × 100 m) in 1994 (Fig. 2). The plot included both a landslide stand (0.29 ha) and stable stand (control 0.71 ha), after dividing the site into 400 contiguous quadrats (5 m × 5 m). We re-measured the boundary between the landslide and control stands in 1994. The slope of the landslide was to some extent greater in the landslide (25°) than in the control stand (21°). The study area contained sparse dwarf bamboos (*Sasa kurilensis*) in the understorey.

To obtain demographic and spatial distribution data for all woody species (trees, shrubs and vines), we marked and mapped all stems with diameter at breast height (DBH) ≥3 cm in August 1994. In August 1999, we censused the DBH of all surviving stems, as well as newly recruited stems of DBH ≥3 cm. All recorded deaths were classified as standing dead, uprooted, stem breakage or disappeared.

To estimate when the landslide had occurred, we determined the ages of early-successional and small-seeded trees, using increment cores of four *Alnus hirsuta* individuals (19.9 cm ≤ DBH ≤ 35.6 cm) and five *Carpinus laxiflora* individuals (18.0 cm ≤ DBH ≤ 43.8 cm) in the landslide stand. In the control, we also determined the age of 11 randomly selected individuals of both the early-successional species *Castanea crenata* (27.9 cm ≤ DBH ≤ 41.6 cm) and the late-successional species *Aesculus turbinata* (6.7 cm ≤ DBH ≤ 74.0 cm). The stems were cored near the surface of the ground in 2008.

Data analyses

Tree species were divided into predetermined categories describing their successional status (i.e., early-, mid-, late-successional species), based on shade tolerance or environmental light availability in the common habitat of the species (Kikuzawa 1983; Seiwa and Kikuzawa 1991, 1996; Seiwa et al. 2006, 2009; Utsugi et al. 2006). An early-successional species is defined as a shade-intolerant pioneer species, found only in disturbed open areas created by landslide, flood, forest fire or severe typhoons. In contrast, a late-successional species is defined as a shade-tolerant, climax species that regenerates successfully in shaded forests. Mid-successional species display intermediate habits between early- and late-successional species, and their regeneration also usually requires gaps but of smaller area than that of

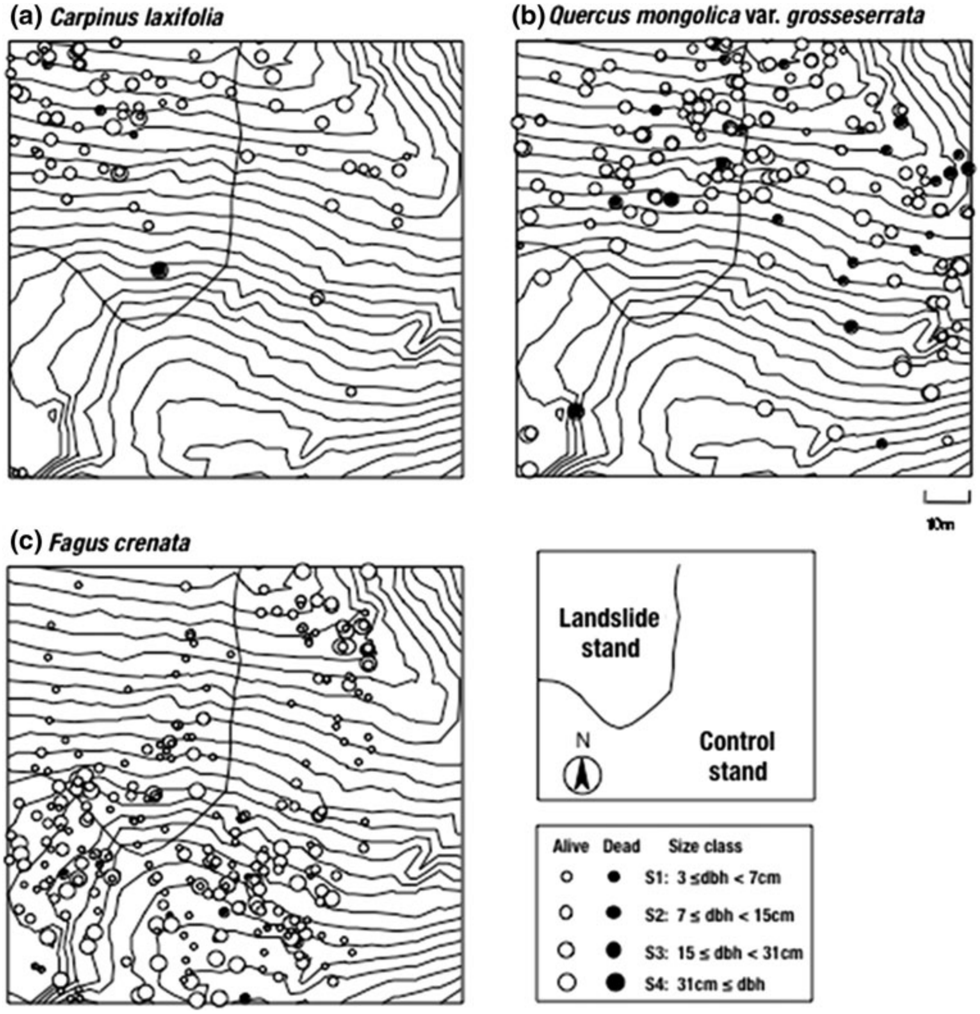

Fig. 2 Spatial distribution of individual trees of early- (**a** *Carpinus laxifolia*), mid- (**b** *Quercus mongolica* var. *grosseserrata*) and late-successional tree species (**c** *Fagus crenata*). *Open* and *filled circles* show individuals alive in 1999, and those that died between 1994 and 1999, respectively. *Contour lines* are 2-m intervals

early-successional species. Species diversity and richness were quantified using Shannon's species diversity index (H'; Margurran, 1988) and the number of species in each stand.

Basal area (BA) and density of species i in the landslide stand ("$\mathrm{BA}_{\mathrm{landslide},i}$" and "$\mathrm{density}_{\mathrm{landslide},i}$") were evaluated with a generalized linear model (GLM) subject to BA and density of species i in the control stand ("$\mathrm{BA}_{\mathrm{cont},i}$" and "$\mathrm{density}_{\mathrm{cont},i}$") and the successional status of each species ("status"). "Status" is the categorical variable for the successional status of each species with values of "early successional", "mid successional" or "late successional" (see Table 1). Actual BA and density were used in the analysis (per 0.71 ha for control stand and 0.29 ha for landslide stand). A Gaussian distribution for $\mathrm{BA}_{\mathrm{landslide},i}$ was assumed. A Poisson distribution for $\mathrm{density}_{\mathrm{landslide},i}$ was assumed, and log-link function was used in the analysis. Akaike's information criterion (AIC), which balances the fit of the model against the number of parameters, was used to select the best-fit model (Anderson and Burnham 2001). The full model includes both two variables and the interaction of these variables, and to select the best-fit model, we will delete explanatory variable(s) successively from the full model. But the model composed of the interaction only was intentionally avoided. Then the model with the lowest AIC was accepted as best for the data (Crawley 2005; McCarthy 2007). We used R version 2.9.1 (R Development Core Team 2007) for the analyses (cf. Zuur et al. 2009).

To evaluate the effect of the landslide on size structure, we compared DBH frequency distributions in 1994 at the landslide and control stands using Kolmogorov–Smirnov two-sample goodness-of-fit tests for the 11 major tree species. The 1994 and 1999 survey data were also used to calculate mortality and recruitment rates and rates of gain and loss in BA for each tree species using the following equations:

Table 1 Basal area and density of tree species in control and landslide stands in 1994

Species	Abr.	Successional status[a]	Basal area				Density			
			Control		Landslide		Control		Landslide	
			m^2 ha^{-1}	%	m^2 ha^{-1}	%	ha^{-1}	%	ha^{-1}	%
Tall trees										
Fagus crenata	Fc	L	13.44	30.6	4.45	14.3	301	23.6	169	9.9
Quercus mongolica var. grosseserrata	Qm	M	10.34	23.5	8.27	26.5	130	10.2	314	18.4
Castanea crenata	Cc	E	7.85	17.9	4.96	15.9	76	6.0	62	3.6
Acer mono	Am	L	2.29	5.2	0.42	1.3	56	4.4	62	3.6
Aesculus turbinata	At	L	2.02	4.6	0.18	0.6	62	4.9	48	2.8
Magnolia obovata	Mo	M	1.29	2.9	0.51	1.6	23	1.8	55	3.2
Acanthopanax sciadopylloides	Ac	L	0.74	1.7	0.26	0.8	52	4.1	45	2.6
Carpinus laxifolia	Cl	E	0.65	1.5	5.97	19.1	27	2.1	204	11.9
Acer sielboldianum	As	L	0.64	1.4	0.52	1.7	142	11.1	141	8.3
Sorbus alnifolia	Sa	L	0.64	1.4	1.21	3.9	79	6.2	114	6.7
Alnus hirsuta	Ah	E	0.33	0.7	1.44	4.6	6	0.4	31	1.8
Other[b]			3.57	8.1	2.93	9.4	249	19.5	414	24.3
Shrubs[c]			0.08	0.2	0.08	0.2	48	3.8	21	1.2
Vines[d]			0.10	0.2	0.03	0.1	25	2.0	24	1.4
Total			43.95	100.0	31.22	100.0	1276	100.0	1704	100.0

[a] successional status: *E* early successional, *M* mid successional, *L* late successional. Letters in parentheses in footnotes b–d also show successional status

[b] Others include *Kalopanax pictus* (L), *Prunus sargentii* (L), *Acer distylum* (L), *Stylax obassia* (L), *Cornus controversa* (L), *Fraxinus lanuginosa* (L), *Prunus grayana* (L), *Acer micranthum* (L), all of which were observed in both control and landslide stands. *Acer rufinerve* (M), *Cornus kousa* (L), *Maackia amurensis* var. *buergeri* (L), and *Ulmus daviniana* var. *japonica* (M), were observed only in control, whereas *Populous sieboldii* (E), *Clethra barbinervis* (E) and *Crytomeria japonica* (L) were observed only in landslide

[c] Shrubs include *Enkianthus campanulatus* (L) and *Viburnum furcatum* (L), both of which were observed in both stands. *Callicarpa japonica* (L), *Eunymus oxyphyllus* (L), *Hydrangea paniculata* (M) and *Hamamelis japonica* (L) were observed only in the control stand

[d] Vines include *Vitis coignetiae* (L), *Hydrangea retiolaris* (L) and *Rhus ambigua* (M), all of which were observed in both the stands. *Schizophragma*

$$\text{Mortality rate}\ \left(\text{year}^{-5}\right) = N_{\text{d}}/N_{\text{l}}$$

$$\text{Recruitment rate}\ \left(\text{year}^{-5}\right) = N_{\text{r}}/N_{\text{l}}$$

$$\text{Rate of loss in BA}\ \left(\text{year}^{-5}\right) = \text{BA}_{\text{d}}/\text{BA}_{\text{l}}$$

$$\text{Rate of gain in BA}\ \left(\text{year}^{-5}\right) = (\text{BA}_{\text{S}} + \text{BA}_{\text{r}})/\text{BA}_{\text{l}},$$

where N_{d} and N_{r} are the numbers of dead and recruited stems during the 5-year period, respectively, and N_{l} is the number of living stems recorded in 1994. BA_{d} is the BA in 1994 of stems that died during the 5-year period, and BA_{l} is the BA of stems alive in 1994. BA_{S} is the increase in BA of stems surviving the 5-year period, and BA_{r} is the BA of stems recruited during the period, as recorded in 1999.

We also compared the relative growth rate of the DBH (RGR_{D}) of the 11 dominant tree species between the landslide and control stands using the Mann–Whitney *U* test. RGR_{D} was calculated as follows:

$$\text{RGR}_{\text{D}} = [\ln(\text{DBH}_{1999}) - \ln(\text{DBH}_{1995})]/5$$

DBH sizes were classified into four size classes of nearly equal intervals after log transformation (S1: 3 cm ≤ DBH < 7 cm; S2: 7 cm ≤ DBH < 15 cm; S3: 15 cm ≤ DBH < 31 cm; S4: 31 cm ≤ DBH). In each size class, we compared the RGR_{D} of the 11 tree species between the landslide and control stands using the Mann–Whitney *U* test.

Results

Ages of tree species

In the landslide stand, the mean age (in years) in 2008 of the two early-successional species was 74.1 ± 1.1 (mean ± SE, range 69–77, $n = 9$), with that of *Alnus hirsuta* 78.3 ± 0.5 ($n = 4$) and *Carpinus laxiflora* 74.8 ± 1.9 ($n = 5$; Fig. 3). The small variance despite variable stem sizes (18.0 cm ≤ DBH ≤ 43.8 cm), together with the maximum age (77 years old), suggest that the landslide occurred around 1931 (i.e., 77 years before the 2008 core sampling and 63 years before the first monitoring of the stands in 1994). This estimate is based on the assumption that early-successional and small-seeded species were recruited promptly after the landslide (see “Discussion”).

In the control stand, the mean age in 2008 of the early-successional species *Castanea crenata* and the late-successional species *Aesculus turbinata* was 96.1 ± 4.4 years (mean ± SE; $n = 11$) and 102.2 ± 22.7 years (mean ± SE; $n = 11$), respectively. In *A. turbinata*, age varied widely (35–270 years) and was positively correlated with DBH ($\text{age} = 3.18 \times \text{DBH} + 13.5$, $r^2 = 0.960$); the age of *C. crenata* showed less variance (80–131 years) and was not correlated with DBH (Fig. 3).

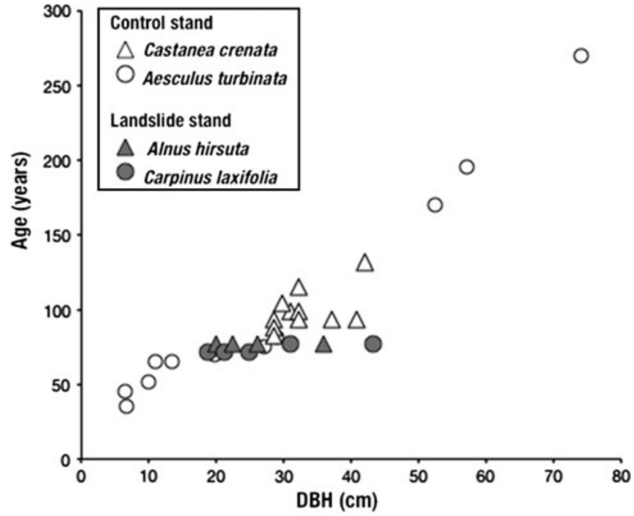

Fig. 3 Relationships between tree diameter and tree age for two early-successional species (*Alnus hirsuta, Carpinus laxifolia*) in the landslide stand and one early- (*Castanea crenata*) and one late-successional species (*Aesculus turbinata*) in the control stand

Species composition

The total number of woody perennial species (trees, shrubs and vines; DBH ≥3 cm) was 39, 33 and 42 in the control stand (0.71 ha), landslide stand (0.29 ha) and in the whole plot (1.0 ha), respectively, in both 1994 and 1999 (Table 1). Shannon's diversity index (H') was 2.67, 2.77 and 2.80 for the control stand, landslide stand and the whole plot, respectively. Two early-successional species, *Populus maximowicziana* and *Clethra barbinervis*, were observed only in the landslide stand, whereas six late-successional species (*Acer rufinerve*, *Cornus kousa*, *Maackia amurensis* var. *buergeri*, *Euonymus oxyphyllus*, *Hamamelis japonica* and *Schizophragma hydrangeoides*) and two mid-successional species (*Hydrangea paniculata* and *Ulmus davidiana* var. *japonica*) were observed only in the control stand. As a result, the proportion of early-successional species to the total number of species was greater in the landslide (18.2 %) than the control stand (10.3 %).

In 1994, the total BA of all woody plants (DBH ≥3 cm) pooled across all species was greater in the control (44.0 $\text{m}^2\ \text{ha}^{-1}$) than in the landslide stand (31.2 $\text{m}^2\ \text{ha}^{-1}$; Table 1). In the landslide stand, the rank of relative BA percentages was highest for the late-successional species *F. crenata* (30.6 %), but the relative BA was greatly reduced in the landslide stand (14.3 %). Similarly, a large reduction in relative BA percentage in the landslide compared to the control stand was also observed for most of the dominant late-successional species: *Acer mono* (5.2–1.3 %), *Aesculus turbinata* (4.6–0.6 %) and *Acanthopanax sciadopylloides* (1.7–0.8 %; Fig. 4a). In contrast, the relative BA percentage of the two early-successional species *Carpinus laxiflora* and *Alnus hirsuta* was greater in the landslide (19.1, 4.6 %) than in the control stand (1.5, 0.7 %), respectively, although the early-successional species *Castanea crenata* showed little difference between the two stands. In the two mid-successional species *Quercus mongolica* var. *grosseserrata* and *Magnolia obovata*, the relative BA percentage differed little between the two stands (Fig. 4a). As a result, the relative BA percentage of *Q. m. grosseserrata* was greatest, followed by the early-successional species *C. laxiflora* and *C. crenata*, and then *F. crenata* in the landslide stand. These results were also confirmed by the generalized linear models (GLMs) for the abundance (BA and density) of the tree species in the landslide stand, which clearly revealed that the full model showed the lowest AIC both in BA and density (Tables 2, 4). AIC value increased if the interaction (Status × $\text{BA}_{\text{cont},i}$ and Status × $\text{Density}_{\text{cont},i}$) was deleted from the full model. The full model was selected, since we avoided selecting the model composed of the

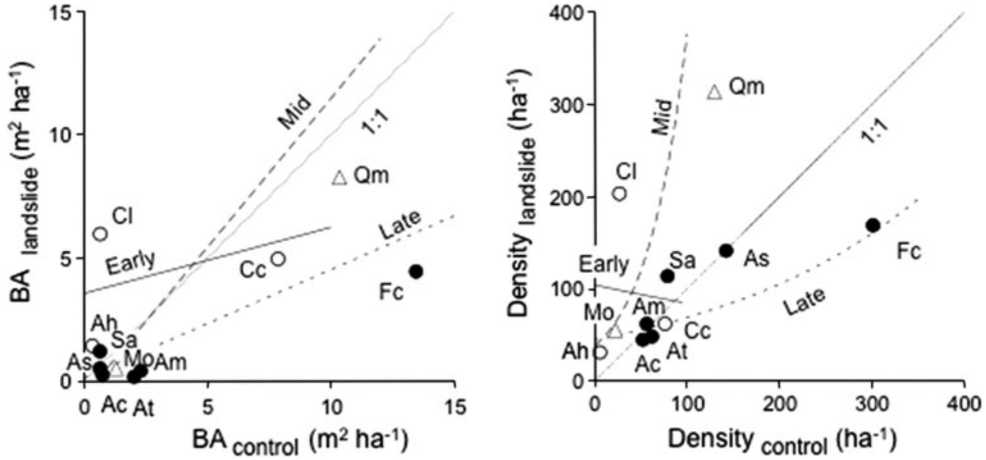

Fig. 4 Comparisons of basal area (BA) and density between control and landslide stands in 1994 for three early-successional specie, *Castanea crenata* (Cc)*, Carpinus laxifolia* (Cl)*, Alnus hirsuta* (Ah), two mid-successional species, *Quercus mongolica var. grosseserrata* (Qm)*, Magnolia obovata* (Mo) and five late-successional species, *Fagus crenata* (Fc), *Acer mono* (Am), *Aesculus turbinata* (At), *Acanthopanax sciadopylloides* (Ac), *Acer sieboldianum* (As), *Sorbus alnifolia* (Sa)

Table 2 Comparison of Akaike's information criterion (AIC) of the model selection in the generalized linear model (GLM) for the basal area (BA) of species *i* in the landslide stand

Model[a]	AIC[b]	ΔAIC[c]
1. Status + Status × $BA_{cont,i}$	18.331	–
2. Status	29.682	11.351

[a] Model 1 is the full model

[b] AIC value of '$BA_{cont,i}$ + Status + Status × $BA_{cont,i}$' model is the same with that of model 1 indicating that the effect of $BA_{cont,i}$ in this model is included by the interaction in the model 1

[c] Difference of AIC value with the smallest AIC value

Table 3 Results of GLM analysis of the best model for BA of species *i* in landslide stand with respect to the BA of species *i* in control stand ($BA_{cont,i}$) and the successional status (Status)

Variable	Coeff.
Intercept	1.033
Status[a]	
Mid successional	−1.206
Late successional	−0.990
Status × $BA_{cont,i}$	
Early successional	0.078
Mid successional	0.350
Late successional	0.127

Coeff. Estimated coefficient

[a] Reference category is 'early successional'

Table 4 Comparison of AICs of the model selection in the GLM for the densities of species *i* in landslide stand

Model[a]	AIC[b]	ΔAIC[c]
1. Status + Status × $Density_{cont,i}$	130.608	–
2. Status	209.260	78.653

[a] Model 1 is the full model

[b] AIC value of '$Density_{cont,i}$ + Status + Status × $Density_{cont,i}$' model is the same with that of model 1 indicating that the effect of $Density_{cont,i}$ in this model is included by the interaction in the model 1

[c] Difference of AIC value with the smallest AIC value

interaction only. The estimated coefficient of interaction for mid- and late successional species both in BA and density was positive, implying that the species with high abundance in the control stand showed high abundance in the landslide stand (Tables 3, 5). Intercept of the early successional species was greater than that of the mid- and late successional species. The abundance of the late successional species in the landslide stand was lower than that of the early successional species.

Size structure

When all woody plants (DBH ≥3 cm) were pooled across all species, we found a greater number of small size class (3 cm ≤ DBH < 33 cm) individuals in the landslide than in the control stand, whereas the reverse was true in the large size class (DBH ≥33 cm; Fig. 5a), resulting in a higher overall density in the landslide (1,704 ha^{-1}) than in the control stand (1,276 ha^{-1}; Table 1).

Table 5 Results of GLM analysis of the best model for the densities of species *i* in landslide stand with respect to the densities of species *i* in control stand ($Density_{cont,\ i}$) and the successional status (Status)

Variable	Coeff.
Intercept	3.409
Status[a]	
Mid successional	−1.002
Late successional	−0.599
Status × $Density_{cont,i}$	
Early successional	−0.002
Mid successional	0.006
Late successional	0.023

[a] Reference category is 'early successional'

In most early- and mid-successional species, the frequency distribution of DBH was bell-shaped (*Castanea crenata*, *Alnus hirsute*, *Q. m. grosseserrata*) or hump-shaped (*Carpinus laxifolia*) in both the control and landslide stands (Fig. 5b, c). One exception was *Magnolia obovata*, which showed an inverse J-shaped distribution in the landslide stand. In contrast, most of the late-successional species showed an inverse J-shaped distribution in both of the stands (Fig. 5d).

The number of stems of the two early-successional species *C. laxiflora* and *A. hirsuta* was smaller in the control than in the landslide stand in all size classes (Fig. 5b), and the large size class (DBH ≥28 cm) of these two species was scarce or absent in the control stand, resulting in a significantly lower density of the two trees in the control than in the landslide stand (Fig. 4b). In contrast, the number of stems in the larger size classes was smaller in the landslide than in the control stand for most of the late-successional species (Fig. 5d). In particular, *F. crenata* had a smaller number of stems in all size classes in the landslide than in the control stand (Figs. 2c, 5d), resulting in a lower overall density in the landslide stand (Fig. 4b). In contrast, the number of stems of both mid-successional species, *Q. m. grosseserrata* and *M. obovata* in smaller size classes was higher in the landslide than in the control stand (Figs. 2b, 5c), resulting in a higher overall density of these trees in the landslide compared to the control stand (Fig. 4).

Recruitment, mortality and growth

The mortality rate of all woody plants (DBH ≥3 cm) pooled across all species was greater than the recruitment rate in the control stand (Fig. 6a). However, the total BA (43.8 m^2) of trees in the control stand did not change during the 5-year period (Fig. 6c), most likely because the greater gain than loss rates of the most dominant species (*F. crenata*) far exceeded the greater

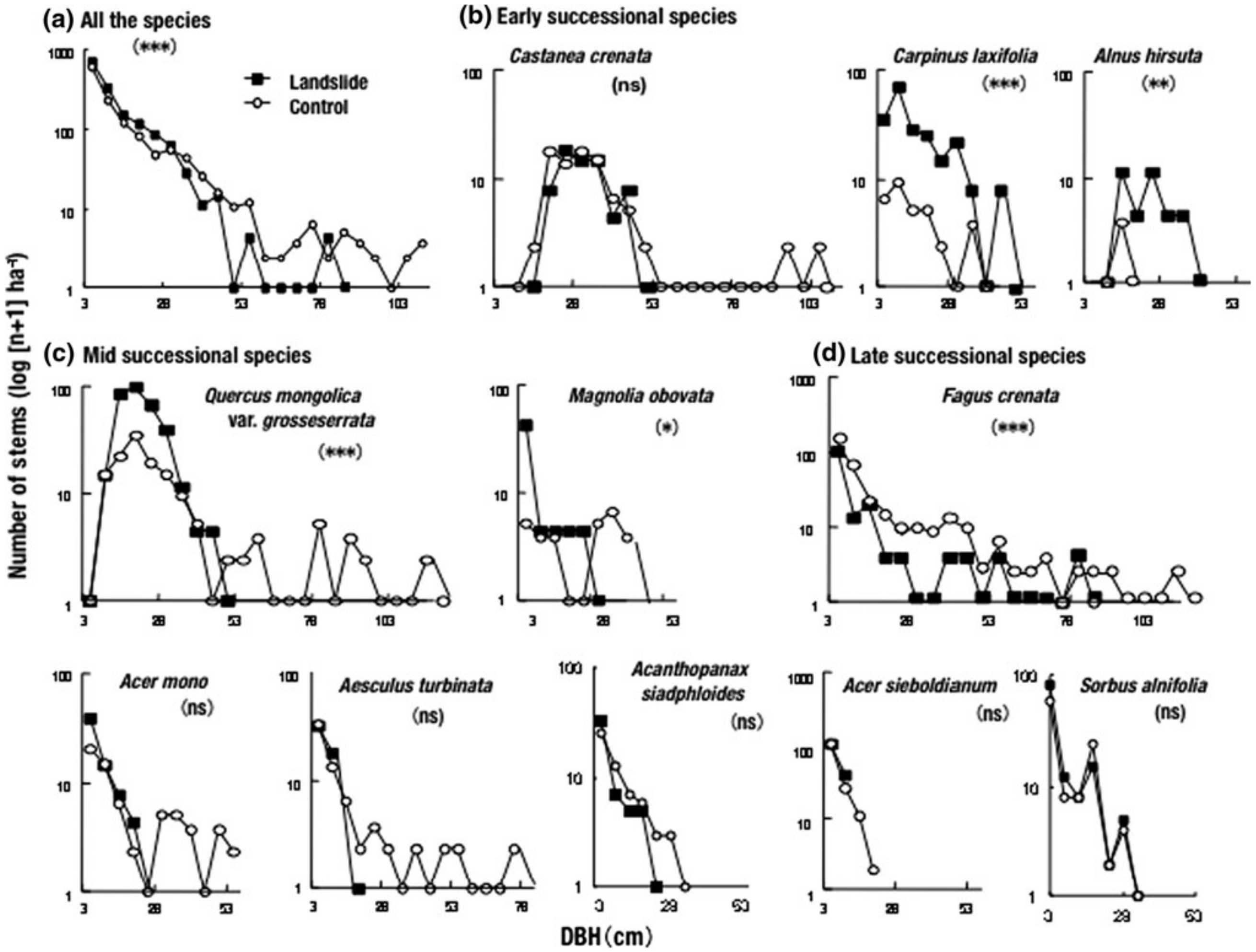

Fig. 5 Comparison of diameter at breast height (DBH) frequency distributions between the landslide and control stands of all stems pooled across **a** all 11 investigated species, **b** 3 early-successional species, **c** 2 mid-successional species, and **d** 6 late-successional species in a beech-dominated forest. *Asterisks* show significant differences between the two stands based on the Kolmogorov–Smirnov test (*ns* not significant; $*P < 0.05$; $**P < 0.01$; $***P < 0.001$)

loss compared to gain rates of both the second most dominant species (*Q. m. grosseserrata*) and third most dominant species (*Castanea crenata*; Fig. 6c). In the landslide stand, most of the late-successional species showed greater BA gain than loss rates over the 5-year period, although the reverse was true for two early-successional species (*C. laxiflora* and *A. hirsuta*) and a late-successional species (*Acanthopanax sciadophylloides*). As a result, the total BA increased slightly from 31.1 to 32.0 m^2 during the 5 years (Fig. 6d).

In both the control and landslide stands, the $\mathrm{RGR_D}$ of most species decreased with increasing DBH, regardless of successional status, resulting in a size-dependent decrease in $\mathrm{RGR_D}$ when all woody plants (DBH ≥3 cm) were pooled across all species (Fig. 7a). Several exceptions were also observed, particularly in the landslide stand, in which $\mathrm{RGR_D}$ increased with increasing DBH in the mid-successional species *Q. m. grosseserrata*, whereas $\mathrm{RGR_D}$ was greatest in the S2 size class, showing a unimodal (rise and fall) pattern within a range of DBH in early- (*C. laxifolia*), mid- (*M. obovata*) and late-successional species (*A. mono*). $\mathrm{RGR_D}$ was usually higher in the landslide stand than in the control stand, but the difference was statistically significant for the three most dominant species (*C. crenata*, *Q. m. grosseserrata* and *F. crenata*; Fig. 7b–d).

Mortality agents

In the control stand, the mortality rate of the smallest-size DBH class was highest (S1), and decreased with increasing DBH (Fig. 8a). In contrast, the mortality rate increased with increasing DBH, in the order S1, S2, S3, in the landslide stand, although the lowest mortality was observed in the largest DBH class (S4).

Standing dead trees accounted for the greatest proportion of dead trees in both the control and landslide stands (Fig. 8b, c). The second greatest cause of mortality was stem breakage in the control stand, and uprooting in the landslide stand. Total BA loss caused by uprooting was greater in the landslide stand (20 %)

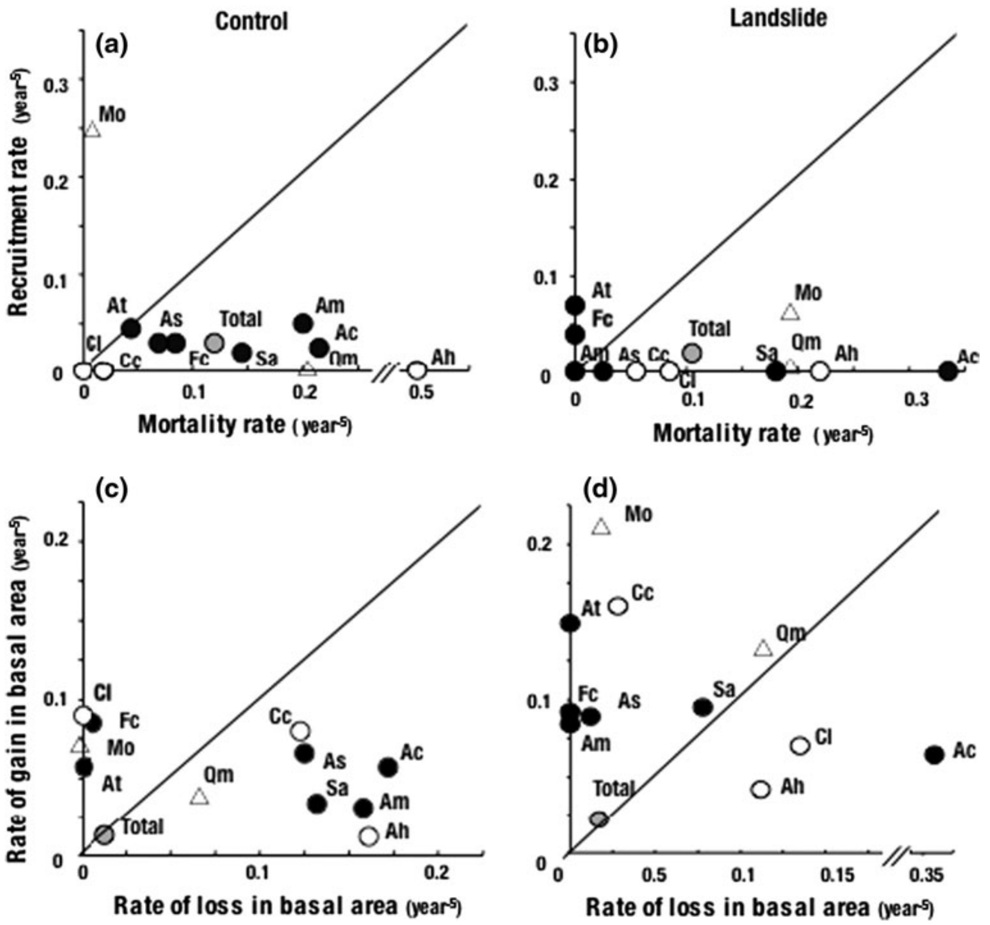

Fig. 6 Relationships between the recruitment and mortality rate in **a** control and **b** landslide stands. Relationships between basal area rates of gain and loss in **c** control and **d** landslide stands of the 11 dominant tree species in a beech-dominated forest. Abbreviations of species names as in Fig. 4

compared to the control stand (3 %). In the landslide stand, the proportion of mortality caused by uprooting increased with increasing DBH, in the order S1, S2, S3 (Fig. 8c). There was no uprooting in S4, because there were very few individuals of the largest DBH class in the landslide stand (see Fig. 5). In the landslide stand, uprooting was most frequent for *Q. m. grosseserrata* (64 %), followed by *Acanthopanax sciadopylloides* (12 %), *Acer palmatum* var. *matsumurae* (12 %) and *Sorbus alnifolia* (12 %), while there was little difference in the death rate between the two stands, probably due to the uprooting that occurred in the control stand in several species including *Euonymus oxyphyllus* (30 %), *Q. m. grosseserrata* (14 %), *Acanthopanax sciadopylloides* (14 %), *Fraxinus lanuginose* (14 %), *Acer distylum* (14 %) and *Prunus grayana* (14 %).

Discussion

Predominance of beech in a stable stand

In the control stand, the rate of gain of total BA was identical to the loss rate, resulting in little difference in total BA during the 5-year study period, suggesting that an undisturbed stand may attain equilibrium in forest dynamics. However, two dominant late-successional species (*F. crenata*, *A. turbinata*) and one mid-successional species (*M. obovata*) with inverse J-shaped DBH distributions showed greater BA gain than loss rates. This trait, together with the fact that *A. turbinata* showed a wide age range dependent on tree size, suggests that these three species successfully regenerated and increased their dominance in a stable stand of old-growth forest. In contrast, the BA decreased for most of the other species, irrespective of their successional status. This, together with the bell-shaped DBH distribution of most of the early- and mid-successional species suggests that these species were limited in population growth and new recruitment. This contrast in population dynamics suggests that species replacement may occur even within late-successional stages without large disturbances, such as landslides or forest fires (Woods 1979; Lorimer et al. 1994; Seiwa 1998; Montgomery et al. 2010).

In temperate hardwood forests in northern Japan, *F. crenata* successfully regenerates even under the canopy of several late-successional species (Tomita and Seiwa

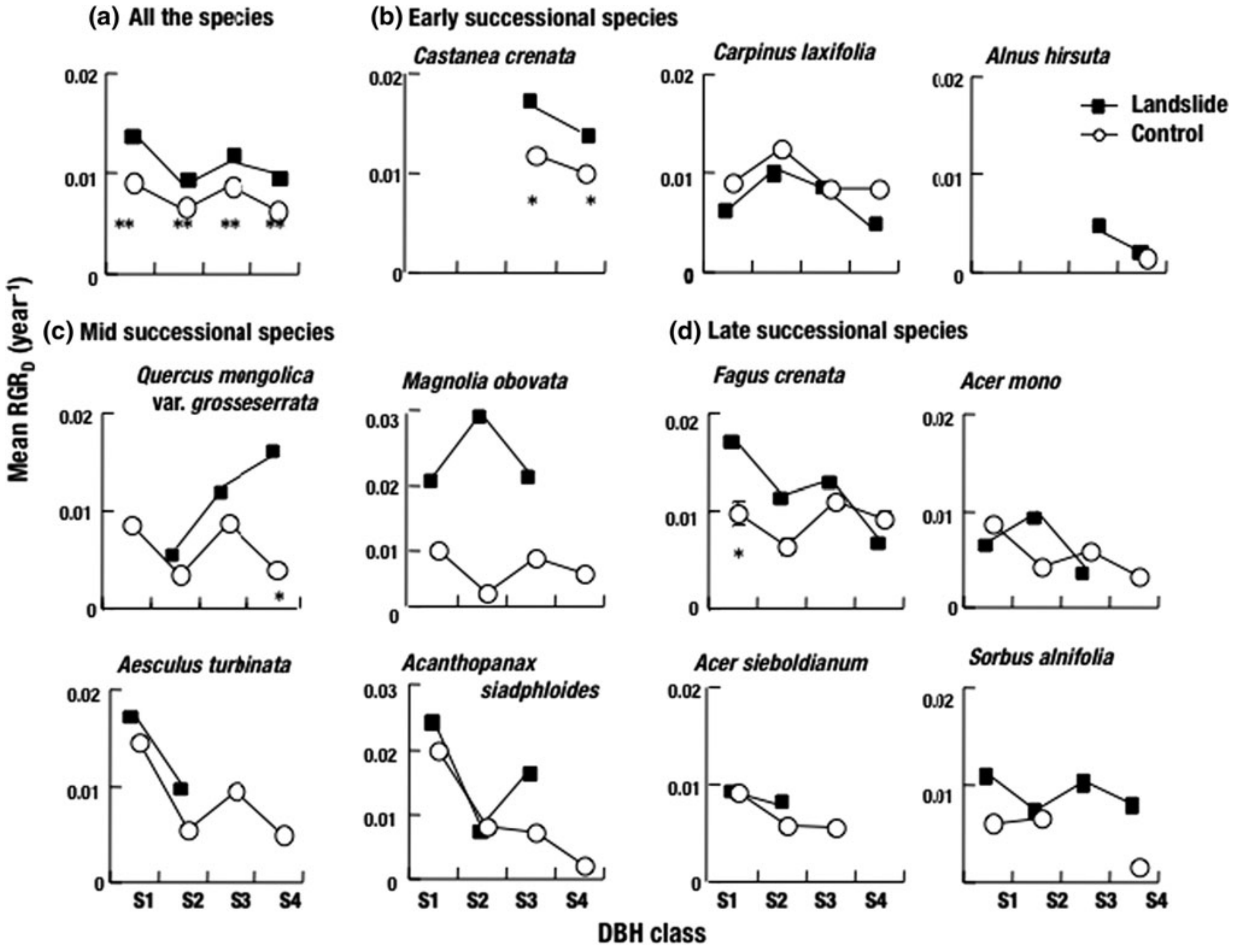

Fig. 7 Comparison of the relative growth rates in diameter (RGR$_D$) between landslide and control stands of all stems pooled across **a** all 11 species, **b** 3 early-successional species, **c** 2 mid-successional species and **d** 6 late-successional species in a beech-dominated forest. DBH sizes were classified into four size classes of nearly equal intervals after log-transformation (S1: 3 cm ≤ DBH < 7 cm; S2: 7 cm ≤ DBH < 15 cm; S3: 15 cm ≤ DBH < 31 cm; S4: 31 cm ≤ DBH). In each size class, RGR$_D$ was compared between the two stands using the Mann–Whitney *U* test. *Asterisks* indicate significant differences between the landslide and control stands based on the Mann–Whitney *U* test (*$P < 0.05$, **$P < 0.01$)

2004; Koyama et al. 2007). Because *F. crenata* juveniles usually unfold their leaves about 3 weeks earlier than other co-occurring hardwood species, the carbon gain of *F. crenata* is greatly enhanced prior to canopy closure in spring, thus promoting their establishment even in the absence of canopy disturbance (Tomita and Seiwa 2004; Koyama et al. 2007). Yamamoto and Nishimura (1999) also showed that the relative abundance of *F. crenata* increases with stand development in an old-growth forest, even though small tree-fall gaps occurred frequently. These findings suggest that the relative dominance of *F. crenata* tends to increase in old-growth forests, unless a large disturbance occurs. This situation is similar to that of the “climax microsuccession” documented by Forcier (1975) and Poulson and Platt (1996), who described the effects of wind disturbance on North American hardwood forests. Climax microsuccession for mid- and late-successional species (*F. crenata, A. turbinata*) may occur as an integral part of the forest cycle.

Landslides facilitate species richness

The control stand had great numbers of large individuals of most of the late-successional species, but very few large early-successional individuals. In contrast, the landslide stand had large numbers of large individuals of early-successional species, but very few large individuals of late-successional species compared to the adjacent control stand. Furthermore, two small-seeded early-successional species, *P. maximowicziana* and *C. barbinervis*, were observed only in the landslide stand, whereas seven late-successional species were seen only in the control stand. These findings suggest strongly that most dominant late-successional species in the old-growth

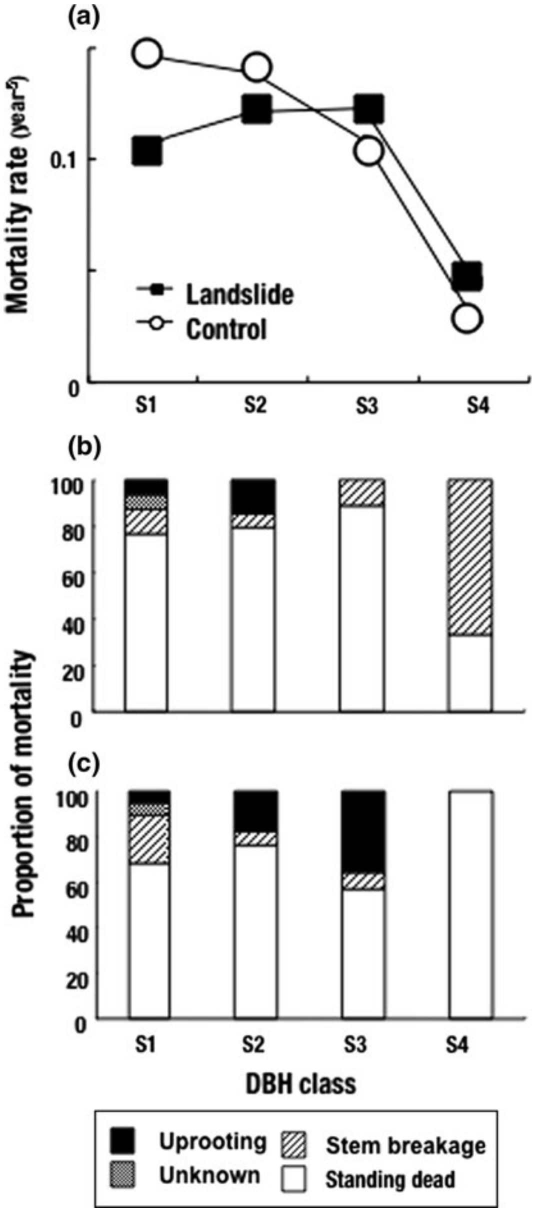

Fig. 8 **a** Comparison of mortality rates between landslide and control stands for the four DBH size classes (S1: 3 cm ≤ DBH < 7 cm; S2: 7 cm ≤ DBH < 15 cm; S3: 15 cm ≤ DBH < 31 cm; S4: 31 cm ≤ DBH). Proportion of the different causes of tree death during the 5-year period from 1994 to 1999 in **b** control and **c** landslide stands for the four DBH size classes. Data of all stems across all species were pooled

forest were killed by the catastrophic disturbance of the landslide and that early-successional trees initiated recruitment.

A landslide usually removes not only canopy foliage, but also a wide area of litter accumulation via catastrophic mass flow (e.g., Guariguata 1990; Geertsema and Pojar 2007), thus altering environmental signals for seed germination. In addition to greater irradiance of the forest floor, the nature of the light is altered by an increase in red to far-red wavelengths (R:FR; Vazquez-Yanes et al. 1990; Daws et al. 2002; Seiwa et al. 2009). Greater irradiance also results in warmer soil during the day, causing greater fluctuations in soil temperatures (Seiwa et al. 2009). These increased environmental signals resulting from a landslide would strongly enhance seed germination of photoblastic species such as the early-successional trees alder (*Alnus* spp.), birch (*Betula* spp.) and aspen (*Populus* spp.; Haeussler and Tappeiner 1993; Baskin and Baskin 2001; Seiwa et al. 2009). In the landslide stand, absence of litter accumulation also appears to promote seedling emergence of small-seeded species originating from fallen seeds (Flaccus 1959; Yamamoto et al. 1995; Lewis 1998; Francescato et al. 2001), owing to physical barrier removal (Seiwa and Kikuzawa 1996; Kanno and Seiwa 2004). Thus, the occurrence of a greater number of early-successional species in the landslide compared to the control stand may result from improved environmental conditions for seed germination and seedling emergence due to the catastrophic disturbance of the landslide.

Colonization by woody species on debris plains has been thought to occur promptly after a disturbance (Hupp 1983; Garwood 1985), most likely because litter accumulation and/or recovery of understorey plants (e.g., herbs, shrubs) soon after a landslide strongly inhibits seed germination and/or seedling emergence of early-successional species. At this study site, our analysis of increment cores of early-successional species (*C. laxiflora* and *A. hirsuta*) also indicated that same-cohort trees colonised promptly after the landslide.

Our findings clearly suggest that the landslide strongly facilitated species diversity in this beech-dominated old-growth forest in northern temperate Japan, not only by promoting the recruitment of early- and mid-successional tree species, but also by reducing the dominance of late-successional species, particularly the most dominant species, *F. crenata*. We found that the relative dominance of *F. crenata* increases with time in the absence of a large disturbance, such as a landslide, as shown in the control stand. On the Japan Sea side, the relative abundance of Japanese beech (*F. crenata*) is usually high, and most of the area overlaps with an active landslide zone (National Research Institute for Earth Science and Disaster Prevention 1998; Nakamura 2002). Furthermore, our study showed that a steep slope facilitates the landslide, particularly in regions with unstable sediments from the Tertiary. These traits suggest that landslides are one of the most important factors facilitating species diversity in forests of this region.

Late-stage forest succession after a landslide

In 1994, approximately 60 years after the landslide, DBH distribution was bell-shaped for two early-successional species (*C. crenata* and *A. hirsuta*) and one mid-successional species (*Q. m. grosseserrata*), and hump-shaped for one early-successional species (*C. laxifolia*) in the landslide stand, with no recruitment but high mortality rates during the 1994–1999 period. *Alnus* *hirsuta* and *C. laxifolia* also showed lower BA gain than loss rates. In contrast, most of the late-successional species showed higher BA gain than loss rates, as well as inverse J-shaped DBH distributions. These contrasting demographic characters indicate that new recruitment of early- and mid-successional species was inhibited, and population sizes gradually decreased, whereas late-successional species underwent succeeding regeneration and subsequent population growth. In addition, our findings suggest that tree replacement from early- to late-successional species continued at later stages of forest succession, approximately 60 years after the landslide. In turn, this continuing replacement will likely result in a decrease in species diversity in the near future.

Although standing dead trunks are the most important cause of death in both landslide and control stands, uprooting remains a major cause of death, particularly for large individuals in the landslide stand. This trait suggests that the landslide has continued to affect tree death 60 years after the catastrophic event. The slow speed of the mass movement may cut the root systems of standing trees, creating canopy gaps in the landslide stand. However, uprooting may facilitate the regeneration only of late-successional tree species, probably because an uprooting disturbance is insufficient to promote regeneration of early-successional species. Even though soil disturbances by uprooting might promote seed germination and/or seedling emergence of small-seeded early-successional species (Seiwa and Kikuzawa 1996; Pickett and White 1985), rapid recovery of canopy foliage of neighbouring trees might rapidly affect the environmental conditions (e.g., light, litter accumulation), inhibiting the regeneration of early-successional species.

In conclusion, this comparison of community properties between landslide and adjacent stable stands clearly revealed the important roles of a landslide in maintaining species diversity through changing species composition and abundance. In general, the importance of landslides as a natural disturbance agent in temperate hardwood forests has long been overlooked or underestimated. At the landscape level, landslides may occur at a variety of scales and intervals. Even though the effects of mass movement may continue for a long time (> 50–100 years), if the landscape of a beech-dominated forest includes communities at different developmental stages, the mosaic of serial stages may also facilitate species diversity by engendering habitat diversity.

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