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Effects of disturbance history and environmental factors on the diversity and productivity of understory vegetation in a cool-temperate forest in Japan

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Abstract

We assessed the species richness and aboveground productivity of understory plants in nine types of forest stand (116 plots in total) that had different disturbance histories that were combinations of the frequency of plantation (clear-cutting, site preparation, planting), typhoon damage, and selective cutting. We established two 1 × 1 m quadrats to measure species richness and productivity and one 1 × 30 m belt to measure species richness in each plot. Canopy leaf area index (LAI), soil NH_4^+, soil C/N ratio, slope angle, and slope aspect were measured as current environmental factors affecting each plot. The variance in species richness was better explained by disturbance history (69% in quadrats; 86% in the belt) than by current environmental factors. Species richness and the Simpson index decreased as the frequency of plantation increased. In contrast, the variance in productivity was better explained by current environmental factors (82%), especially canopy LAI (45%), than by disturbance history. The relations of species presence and productivity to the explanatory variables differed among species, although there were some common responses within life forms. The effects of disturbance on species diversity remained for 20–80 years. Forest management should therefore take into account the long-term effects of disturbance history to maintain understory plant diversity.

Key words: biodiversity, forest management, hierarchical partitioning, life form, plantation, typhoon.

Introduction

The determination of the mechanisms that control species diversity is a major issue in forest ecology. According to current theory, disturbance regime and resource availability are key factors in the structuring of plant communities (Denslow, 1980; McIntyre *et al.*, 1995). The availability of resources such as light and soil nutrients affects species richness through competition for resources. For example, high levels of resources decrease plant diversity because they enhance competitive exclusion (Tilman, 1984; Goldberg and Miller, 1990; Wedin and Tilman, 1993). In contrast, natural disturbances caused by strong winds, wildfires, and volcanic eruptions, and anthropogenic disturbances caused by forest management (e.g., plantation, harvesting) affect species richness by altering resource availability. For example, the removal of canopy trees increases light availability on the forest floor (Malcolm, 1994) and soil nutrient and water availability because of a decrease in uptake by disturbed canopy trees (e.g., Parsons *et al.*, 1994); these changes in resource availability can increase species richness via the immigration of early successional species (Brunet *et al.*, 1996; Decocq *et al.*, 2004).

Moreover, disturbance also affects species richness through habitat structure, e.g., coarse woody debris, litter layer, pits, and mounds (Beatty, 1984; Roberts and Zhu, 2002; Astrom *et al.*, 2005), and the availability of propagules (i.e., seed banks and seedlings; Meier *et al.*, 1995; Halpern *et al.*, 1999).

The diversity of plant species in most cool-temperate forest communities is much higher for understory forbs, ferns, and shrubs than for canopy trees (Halpern and Spies, 1995; Gilliam, 2007). Furthermore, the decomposition of understory plant litter is more rapid than that of canopy tree litter; the former accounts for only 10-15% of the annual total litter production in cool-temperate forests (Muller, 2003). Therefore, understory plants play important roles not only in maintaining species diversity but also in nutrient cycling in forest ecosystems (Siccama *et al.*, 1970; Fukuzawa *et al.*, 2006). Once the understory species composition is altered by disturbance, the changes may persist for many decades or centuries, and the understory species composition of old-growth forests may not recover for centuries after disturbance (Whitney and Foster, 1988; Halpern and Spies, 1995; Singleton *et al.*, 2001; Dupouey *et al.*, 2002). Two mechanisms explain the maintenance of species composition (Donohue *et al.*, 2000). First, limitations in dispersal and establishment can restrict recolonization at a site where species were previously removed by disturbance, even if the environmental conditions have recovered. We defined this mechanism as the effects of disturbance history. Second, current environmental conditions can restrict the establishment and growth of species that were formerly present at a site. Numerous studies have demonstrated the importance of the effects of disturbance history on diversity; however, few studies have quantitatively examined the relative importance of disturbance history and current environmental conditions.

The natural local flora corresponds to the local disturbance regime (Hiura, 1995). Anthropogenic disturbances caused by forest management greatly affect biodiversity; these effects differ from those caused by natural disturbance because anthropogenic disturbances differ from natural disturbances in severity and frequency (Halpern and Spies, 1995; Roberts and Gilliam, 1995b). The management of forests to sustain biodiversity and ecosystem functioning has become a major challenge for modern forestry (Bengtsson *et al.*, 2000; Lindenmayer *et al.*, 2000). Most cool-temperate forests have been managed for timber production. In Hokkaido, the northern island of Japan, plantation stands cover > 25% of the total forested area, and most of the remaining natural forests have experienced some kind of forest management (Hokkaido Government, 2005). The combination of natural and anthropogenic disturbance affects the diversity and functions of understory plants in these cool-temperate forests. Therefore, to understand the mechanisms underlying the maintenance of biodiversity for application to forest management, it is necessary to examine the effects of both natural and anthropogenic disturbances within a region (Roberts, 2004). However, most studies have only examined the effects of anthropogenic disturbance on understory plants by comparing anthropogenically disturbed forests and undisturbed old-growth forests (Duffy and Meier, 1992; Halpern and Spies, 1995; Singleton *et al.*, 2001), and the comparison of the effects of natural and anthropogenic disturbance is rarely made within a region (but see Reich *et al.*, 2001; Ramovs and Roberts, 2003).

We addressed the following questions. Which has a stronger influence on the species diversity and productivity of understory plants: disturbance history or current environmental factors? How do natural and anthropogenic disturbances affect species diversity and productivity? In addition, because the response to disturbance history and current environmental factors is determined by both species characteristics and life form (Halpern, 1989; Roberts and Gilliam, 1995a; Oguchi *et al.*, 2006), we compared the responses of both species and life forms to disturbance history and current environmental factors.

Methods

Study site

This study was conducted in the Tomakomai Experimental Forest (TOEF), Hokkaido University, Japan (42°41′ N, 141°36′ E). A large part of TOEF is located on flat land with slope angle < 5°, and the forest covers 2715 ha. The mean monthly temperatures range from –3.2 to 19.1°C, and the annual precipitation is 1450 mm. Snow cover reaches a depth of 50 cm from December to March. Approximately 350 vascular plants have been recorded in the TOEF (Kudo and Yoshimi, 1916). The dominant canopy tree species in the natural stands are *Quercus crispula*, *Acer mono*, *Sorbus alnifolia*, and *Tilia japonica*, and the understory species include *Dryopteris crassirhizoma*, *Maianthemum dilatatum*, *Scisandra chinensis*, and *Sasa nipponica* (Hiura, 2001). The forest is formed on 2 m deep volcanogenous regosols that accumulated from the eruptions of Mt. Tarumae in 1669 and 1739; the depth of the A horizon is 0–6 cm (Shibata *et al.*, 1998). In a study, investigating the effects of anthropogenic disturbance due to forest management on diversity of understory plants, both disturbance and site-specific effects (e.g., due to topography and geology) were detected (Hannerz and Hanell, 1997). Thus, by using the sites where topographic and geologic factors are homogenous, it allows us to separate the effects of disturbance history from site-specific effects.

Disturbance history

There was no record of anthropogenic disturbance in TOEF until the early 20th century. Plantations in TOEF are created following clear-cutting and mechanical site preparation. Weeding and shrub clearing occur twice per plantation stand, and some stands are in their second rotation. The plantation stands are between 11 and 80 years old. The main planted tree species are *Larix kaempferi*, *Abies sachalinensis*, and *Picea glehnii*. Harvesting operations in TOEF are performed as selective cutting in plantation stands and natural forests. Although 3–56 years have passed since the last harvest, depending on the stand age, most harvesting occurred 10–25 years ago. The only major natural disturbance in TOEF since it was established in 1904 was a severe typhoon in 1954, although there have been some small disturbances caused by other typhoons. A secondary forest has developed in one-third of TOEF since the severe typhoon (Mishima *et al.*, 1958). TOEF has approximately 300 permanent forest plots (Hiura, 2005). The permanent plots have detailed disturbance history records and homogeneous forest structure within plots. These features are useful for the study of the effects of disturbance history on understory vegetation. We selected 116 square plots of 37 × 23 m to 50 × 60 m (mainly 40 × 50 m) from the permanent plots. To determine when plantation and harvesting (including salvage logging) occurred in the plots, we examined TOEF forest management records beginning in 1924. Damage from the severe typhoon in 1954 was estimated at four levels: undisturbed, low-severity disturbance with single canopy gaps, intermediate severity with patchy disturbed areas, and high severity with overall disturbance. Typhoon damage was determined using aerial photographs and maps created from field surveys of the damage (Mishima *et al.*, 1958). In the study plots, the relation between damage from the severe typhoon and harvesting or plantation frequency was not significant (likelihood ratio test, df = 112, harvesting: $\chi = 64.54$, $P = 0.38$, plantation: $\chi = 95.04$, $P = 0.35$). The study plots were divided into nine forest types based on disturbance history (Table 1).

Sampling design and data collection

Vegetation and environment surveys were conducted between 25 June and 23 July 2004. These data and data collected in July 2000 (Hiura, 2001) were combined (78 plots in 2004, 38 plots in 2000) and analyzed, with the assumption that the environmental conditions did not change between summer 2000 and summer 2004. The differences in current environmental factors were not significant between the two data sets in stands that had the same disturbance history (all $P > 0.09$). The 2000 data set had five quadrats within plots, and we randomly selected two quadrats from each plot for analysis with the 2004 data. To measure the diversity and productivity of understory plants, two 1 × 1 m quadrats were established randomly at least 5 m from the plot edges in each plot (232 quadrats in total). The plant species that appeared in each quadrat were recorded. To estimate aboveground productivity, we clipped the current-year product parts of understory plants, i.e. aboveground parts of forbs, ferns, monocots < 1 m tall, and current-year leaves and shoots for woody species < 1 m tall. In which the non-woody plants in this study area consisted mostly of current-year products. All samples were sorted by species, dried, and weighed. Data from the two quadrats in each plot were summed for analysis. Diversity was expressed using Simpson's index ($1/\Sigma P^2{}_i$), where p_i is the relative mass of species *i*. The relative mass was calculated as the mass of a single species divided by the total mass of vegetation from the plot for the two quadrats combined.

In addition to the quadrats, we used 1 × 30 m belt transects located at least 5 m from plot edges to detect species of low abundance. The species names were recorded for all vascular plants < 1 m tall that occurred in the belts.

We collected environmental data on light availability, soil nutrients, and topography as factors that might explain species diversity and productivity in the plots. To estimate light availability, the leaf area index (LAI) at a height of 1 m was measured in each plot using an optical analyzer (LAI-2000; Li-Cor, Lincoln, NE, USA). Some previous study reported that the LAI-2000 analyzer may underestimate the actual LAI (Kussner and Mosandl, 2000; Law *et al.*, 2001). However, previous studies in this region found that the LAI-2000 produced reliable estimates that were not much smaller than direct measurements made in a secondary stand (LAI of around 4.0; Takahashi *et al.*, 1999) and a mature stand (LAI of 7.59; Fukushima *et al.*, 1998).

To measure soil nutrient availability, two soil samples were taken from a depth of 10 cm near the quadrats in each plot. Soil ammonium (NH_4^+) was extracted in water and analyzed using ion chromatography (DX500; Dionex Corp., Sunnyvale, CA, USA). The soil C/N ratio was measured using a C/N analyzer (Sumitomo NC-900, Osaka, Japan).

Although the canopy tree composition and density indirectly affect understory plants via light and soil nutrient availability, we did not use canopy tree composition and density as explanatory variables because we measured light and soil nutrient availability directly. For topography, slope aspect and slope angle were analyzed in ArcGIS 9.0 (ESRI Inc., Redlands, CA, USA) using a digital elevation model.

Data analysis

The coefficient of each explanatory variable (i.e., LAI, NH_4^+, slope angle, slope aspect, plantation frequency, harvesting, typhoon damage, and lack of damage) for the dependent variables of species richness, Simpson index, productivity, and species presence/absence was estimated using a generalized linear model (GLM). The likelihood ratio test was used to determine whether the data supported a full model over a null model. The effect of disturbance history on species richness and productivity was examined using a likelihood ratio test. The effect of the number of years since the last anthropogenic disturbance on species richness was also examined using a likelihood ratio test. To compare species richness in quadrats and belts, and Simpson index in quadrats among stands with different plantation frequency, we carried out multiple comparisons general linear hypothesis tests in the MULTCOMP library version 1.0-2 (Hothorn *et al.*, 2008) in R statistical software.

Hierarchical partitioning alleviates problems of multicollinearity among variables (MacNally, 2000, 2002) and has been used in numerous studies (e.g., Heikkinen *et al.*, 2004; Banks *et al.*, 2005). Disturbance history and environmental factors are closely related. For example, LAI (Kashian *et al.*, 2005) and soil N (Zimmerman *et al.*, 1995) both change with the number of years since the last disturbance. Thus, we used hierarchical partitioning to examine the contribution of each explanatory variable to species richness, Simpson index, productivity, and species presence/absence by examining each explanatory variable separately. The significance of the independent contribution of each explanatory variable was tested using randomizations (MacNally, 2002). Hierarchical partitioning examines all model combinations jointly to identify the average influence of parameters, rather than just the single best model, and then estimates the percentage independent contribution of each parameter to the total explained variation in the dependent variable. This analysis was performed for life form richness and productivity, as well as for all understory species. To asses the contributions of the explanatory variables to the presence of each species, we analyzed the presence/absence of individual understory species in the plots using the belt transect survey data. We show the results for species presence/absence for species that occurred in more than five plots and for which the full model was significant ($P < 0.05$). Because the productivity of all understory plants can be affected by the dominant species, we estimated the contributions of the explanatory variables to the productivity of each species using hierarchical partitioning. We show the results for species productivity for species that occurred in more than five plots and for which the full model was significant ($P < 0.05$). All statistical analyses were conducted using R version 2.6.0 (R Development Core Team 2006).

Results

We detected 207 species in the survey. The total dry mass of understory plants was 20–50 g/m^2, which corresponded to approximately 10–20% of the canopy tree litter of 300–400 g/m^2 (Shibata *et al.*, 2005) in this forest. The results corresponded with the average total aboveground dry mass of 41 g/m^2 and 15.9 % of the canopy litter in North American forests (Muller, 2003).

Effects of disturbance history on understory plants

The type of disturbance history had a significant effect on species richness (in quadrats: $\chi^2 = 46.838$, df = 8, $P < 0.001$, in belts: $\chi^2 = 72.794$, df = 8, $P < 0.001$). However, the number of years since the last anthropogenic disturbance did not significantly affect species richness or the Simpson index (all $P > 0.24$), except for plantation species richness in the belt surveys ($P < 0.001$). The sum of the variance explained by disturbance history variables (i.e., plantation frequency, harvesting, and typhoon severity) composed a large portion of the variation in species richness (69% in quadrats; 77% in belts; Fig. 1A, B). In particular, plantation frequency explained 34.6% of the variation in species richness, and species richness decreased as plantation frequency increased (Fig. 2). In contrast, species richness tended to be higher in harvested stands than in unharvested stands (Table 2).

Furthermore, the 1954 typhoon influenced a single peak model of species richness; namely, low-severity typhoon-disturbed stands had higher species richness than undisturbed stands and high-severity disturbed stands, although the effect was significant only in the quadrat survey ($P < 0.05$).

For productivity, the sum of the variance explained by parameters representing disturbance history (18.4%) was lower than that of environmental factors. The disturbance history parameters were not statistically significant, although the type of disturbance history had a significant effect on productivity ($F = 2.573$, df = 8, 107, $P = 0.013$). For the Simpson index, disturbance history and current environmental factors explained similar amounts of variance (disturbance history: 46.8%, current environmental factors: 46.2%).

Effects of current environmental factors on understory plants

The sum of the variance explained by current environmental factors constituted a large part of the variation in productivity (81.6%): LAI explained 45.3% and NH_4^+ explained 15.0% (Fig. 1D, Table 2). However, these parameters explained only a small part of the variation in species richness. LAI and NH_4^+ had significant negative effects on productivity and species richness (Table 2). The topographic variables were not significant in explaining the variation in species richness, the Simpson index, or productivity.

Life form and species differences

The response of species richness and productivity to disturbance history and current environmental factors differed among life forms. For example, in the belt survey, LAI explained 0.0% of the variation in the species richness of forbs, but 5.4% in that for trees. The sum of the variance explained by current environmental factors was higher for the productivity of vines (98.4%) that for that of other life forms.

There were various responses of species presence/absence and productivity to disturbance history and current environmental factors, although there were some common responses within life forms (Appendices A, B). For example, the presence of *Phryma leptostachya* var. *asiatica* was significantly positively related to LAI, but this pattern was not reflected by all forbs in the belt survey.

Discussion

Our results clearly illustrate that disturbance history has a stronger influence on the species richness of understory plants than do current environmental factors. In particular, as the plantation frequency increased, species richness decreased. In contrast, current environmental factors had a stronger influence on the productivity of understory plants than did disturbance history. The responses of presence and productivity to disturbance history and current environmental factors varied among the species, although there were some common responses within life forms.

Species richness is more strongly affected by disturbance history than current environmental factors

Disturbance history affects species richness by altering propagule availability and habitat structure (Meier *et al.*, 1995; Buckley *et al.*, 1997; Halpern *et al.*, 1999; Astrom *et al.*, 2005). In contrast, environmental factors affect species richness through resource competition (Tilman, 1984; Goldberg and Miller, 1990; Wedin and Tilman, 1993). We found that disturbance history explained more of the variation in species richness (69% in quadrats; 86% in belts) than did current environmental factors, even long after the disturbance had occurred (50 years after the typhoon, an average of 58 years since plantation, and an average of 16 years since harvesting). Therefore, for local flora in this area, the effects of propagule availability and habitat structure on species richness were most likely greater than the effects of resource competition. These results agree with previous studies that indicated that species that are lost from the understory might not reappear even by one century after severe disturbance (Whitney and Foster, 1988; Singleton *et al.*, 2001; Dupouey *et al.*, 2002) because of dispersal and establishment limitations (Donohue *et al.*, 2000). There are two possible explanations for these results. First, the number of forb species, which are particularly sensitive to disturbance, composed approximately half of the total species in our study. The dispersal ability of forbs is generally low (Cain *et al.*, 1998); thus, forbs tend to retain disturbance effects longer than other life forms. Second, species that are adapted to the predisturbance canopy tree phenology might have difficulty persisting in highly disturbed stands. The seasonality of light resource availability for understory plants is greatly affected by canopy tree phenology (Uemura, 1994). If most canopy trees are removed from stands by clear-cutting in preparation for plantation establishment or by a severe typhoon, the forest floor receives abundant light throughout the year.

Effects of anthropogenic and natural disturbance on species richness

Species richness and the Simpson index decreased as the plantation frequency increased (Fig. 2). There are two possible explanations for these results. First, the creation of a plantation is a very severe form of disturbance that involves clear-cutting and mechanical site preparation (Roberts and Zhu, 2002). Thus, species that prefer a stable habitat in the forest may be extirpated. Second, the establishment of a plantation usually creates a homogenous environment (microtopography, coarse woody debris, light distribution, and litter content), in contrast to the environment of an old-growth forest. Machinery preparation with plantation obliterates heterogeneity in microtopography (e.g. mound, pit), which allows coexistence and higher richness in stands (Beatty, 1984). Several studies reported that diversity of understory plants in clear cutting stands recover more quickly than our plantation stands (Reiners, 1992; Ford *et al.*, 2000; Gilliam, 2002). One of the reason why diversity of understory plants recover more slowly in plantation stands, the heterogeneity in microtopography would not recover in long-term (Beatty, 2003). Clear-cutting and site preparation eliminate coarse woody debris, which is related to heterogeneity on the forest floor (Goodburn and Lorimer, 1998; Roberts and Zhu, 2002; Ramovs and Roberts, 2003), and reduce plant species diversity (Thomas *et al.*, 1999; Miller *et al.*, 2002). Furthermore, because plantations are usually even aged and have only one or several canopy species, the understory light distribution and litter content are homogeneous. The conversion of a stand from deciduous broadleaf tree species to one or several coniferous tree species changes the seasonality of resource availability on the forest floor via leaf phenology of canopy, thus decreasing species that are adapted to the seasonality of resource availability (Sparks *et al.*, 1996; Amezaga and Onaindia, 1997). This type of forest conversion also changes the litter quality on the forest floor because coniferous leaf litter has lower pH (Binkley and Valentine, 1991; Brandtberg *et al.*, 2000) and greater accumulation because of slower decomposition (Klemmedson, 1992; Cornelissen, 1996) than does broadleaf leaf litter. This may also affect the understory species composition. The replanting of stands through rotations may increase the negative effects on species richness over those of a single plantation.

Harvesting had a positive effect on species richness (Table 2). Previous studies in broadleaf forest suggest that understory species richness increases after selective tree harvesting because these species are tolerant to intermediate canopy disturbance and some early successional species favor such disturbance (Brunet *et al.*, 1996; Gotmark *et al.*, 2005). The presence of *Potentilla freyniana*, *Hypericum erectum*, *Rubus crataegifolius*, *Rubus idaeus* var. *aculeatissimus*, and *Aralia elata* was positively related to harvesting (Appendix A). These species prefer relatively open stands (Satake *et al.*, 1981, 1989) and their immigration would increase the total species richness.

In terms of natural disturbance, the species richness of quadrats indicated a single peak model related to the 1954 typhoon: species richness was high in stands in which only single trees were disturbed. Typhoons create canopy gaps that increase light and soil nutrient availability in the understory (Liechty *et al.*, 1997; Carlton and Bazzaz, 1998), promoting the immigration of early successional species (Peterson and Pickett, 1995). Furthermore, typhoons can create microenvironmental heterogeneity (e.g., pit and mound topography), allowing species with various ecological characteristics to coexist in a stand. Nevertheless, stands that received severe typhoon disturbance had lower species richness than undisturbed stands. Severe typhoon disturbance might result in excess irradiance and dry soils, negatively affecting species that prefer dark and humid environments. Moreover, if a poor disturbance-tolerant species becomes extirpated from a stand because of high-severity disturbance, it may be difficult for the species to reestablish if the available seed sources are located far from the center of the disturbed area.

Productivity is more strongly affected by current environmental factors than disturbance history

Current environmental factors, particularly LAI and NH_4^+, explained much of the variation in productivity (Fig. 1D). These results agree with the theory that light and soil nutrients explain most of the variation in productivity when water availability is high (Tilman, 1988). Furthermore, the predominance of LAI in explaining productivity was consistent with previous findings that understory plant productivity is closely related to the size of the canopy opening (Malcolm, 1994; Stone and Wolfe, 1996).

Management implications

Our results demonstrate that the effects of disturbance can remain for 50-80 years. The plantation frequency explained most of the variation in species richness (Fig. 1A, B). Thus, understory plants in this area are much more sensitive to plantation than to selective harvesting and typhoon disturbance. Therefore, plantations should not be created over large areas and should have rotations of > 50-80 years so that stand-level species diversity can be maintained. Future research should clarify whether plantations have a permanent negative effect on species diversity and how much time is needed for recovery to a pre-plantation state. When examining the effects of disturbance and environmental factors on understory plants, it is necessary to account for the influence of dominant life forms and species characteristics. If this is not considered, the response of rare species to disturbance and current environmental factors can be overlooked, even though it is important to the maintenance of species diversity.

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Table 1. Environmental variables, species richness, Simpson index, and productivity in nine stand types.

Disturbance history	Plantated frequency	Harvested	Typhoon	Replication	LAI (m^2/m^2)	NH_4^+ (mg/100g dry soil)	CN ratio	Slope (degree)	Species richness in quadrats	Species richness in belt transects	Simpson index	Productivity (dry g/m^2)
PPHT	2	Harvested	Disturbed	5	3.27 ± 0.54	1.79 ± 0.19	13.90 ± 0.59	3.10 ± 1.04	18.80 ± 3.97	38.80 ± 3.87	4.22 ± 1.02	46.33 ± 11.98
PPH	2	Harvested	-	3	3.29 ± 0.33	1.81 ± 0.27	14.59 ± 0.46	4.75 ± 1.26	21.00 ± 4.58	35.67 ± 3.84	4.25 ± 1.31	49.48 ± 17.09
PHT	1	Harvested	Disturbed	4	4.25 ± 0.43	1.93 ± 0.02	13.55 ± 0.49	1.75 ± 0.87	27.75 ± 7.11	40.75 ± 6.73	2.56 ± 0.85	44.51 ± 18.53
PH	1	Harvested	-	35	4.08 ± 0.09	1.97 ± 0.13	13.01 ± 0.38	2.45 ± 0.37	25.53 ± 1.26	49.74 ± 1.41	5.30 ± 0.45	26.71 ± 1.55
P	1	-	-	9	3.78 ± 0.09	2.37 ± 0.16	15.06 ± 0.72	2.89 ± 0.69	26.33 ± 2.36	50.33 ± 3.54	5.73 ± 0.75	38.93 ± 5.40
HT	-	Harvested	Disturbed	7	4.07 ± 0.15	2.20 ± 0.38	13.45 ± 0.23	2.61 ± 0.92	32.71 ± 2.45	58.43 ± 3.94	8.63 ± 0.68	23.64 ± 2.67
H	-	Harvested	-	19	4.21 ± 0.13	1.98 ± 0.14	13.20 ± 0.49	3.81 ± 0.77	27.05 ± 1.49	56.56 ± 1.41	5.83 ± 0.64	34.99 ± 4.32
T	-	-	Disturbed	18	3.99 ± 0.09	2.16 ± 0.15	13.93 ± 1.74	2.99 ± 0.54	31.67 ± 1.44	51.42 ± 1.22	6.57 ± 0.55	33.09 ± 3.99
N	-	-	-	16	3.87 ± 0.10	2.07 ± 0.13	15.00 ± 0.36	5.80 ± 0.77	29.56 ± 1.28	57.94 ± 1.36	6.06 ± 0.63	35.75 ± 5.04
Total				116	3.99 ± 0.05	2.06 ± 0.06	13.87 ± 0.17	3.32 ± 0.25	27.66 ± 0.70	51.63 ± 0.87	5.75 ± 0.25	33.04 ± 1.64

PPHT: First plantation (clear cutting and planted), subsequently second plantation, and then, harvesting (selective cutting). Experienced some kind of damage by typhoon in 1954.

PPH: First plantation, subsequently second plantation, and then, harvesting.

PHT: Plantation and then, harvesting. Experienced some kind of damage by typhoon in 1954.

PH: Plantation and then, harvesting.

P: Plantation. H: Harvesting. T: Experienced some kind of damage by typhoon in 1954. N: not disturbed.

Table2. Independent Explained ratio and coefficients of variables in species richness, Simpson index, and productivity for each of life forms.

	Life form (Dominance)	Intercepts	Environment factor																
			LAI (m^2/m^2)			NH_4^+ (mg/100g dry soil)			CN ratio			Slope (degree)			Aspect				
			Explained (%)	Coefficient	*P*	Explained (%)	Coefficient	*P*	Explained (%)	Coefficient	*P*	Explained (%)	Coefficient	*P*	Explained (%)	Coefficient			*P*
																W	S	E	
Species richness in quadrats	All species	4.44	4.3	-0.15	**	3.1	-	n.s.	18.8	-0.04	***	0.0	-	n.s.	5.3	-	-	-	n.s.
	Forbs(47%)	4.04	4.9	-0.25	**	5.5	-	n.s.	10.0	-0.04	**	1.0	-	n.s.	1.8	-	-	-	n.s.
	Trees (27%)	3.17	5.5	-	n.s.	0.2	-	n.s.	29.2	-0.04	***	1.3	-	n.s.	1.3	-	-	-	n.s.
	Ferns (12%)	0.49	19.4	-	n.s.	2.4	-	n.s.	0.1	-	n.s.	43.9	-	n.s.	24.4	-	-	-	n.s.
	Monocotyledons (9%)	2.85	24.5	-0.25	**	0.0	-	n.s.	53.1	-0.06	***	1.4	-	n.s.	10.6	-	-	-	n.s.
	Vines (5%)	0.95	3.9	-	n.s.	9.8	-	n.s.	10.5	-	n.s.	31.5	-	n.s.	0.5	-0.01	-0.02	-0.05	*
Species richness in belts	All species	4.63	0.7	-	n.s.	1.4	-	n.s.	8.0	-0.02	**	1.3	-	n.s.	2.4	-	-	-	n.s.
	Forbs(44%)	3.77	0.0	-	n.s.	0.6	-	n.s.	3.2	-	n.s.	3.3	-	n.s.	0.1	-	-	-	n.s.
	Trees (31%)	3.55	5.4	-0.12	*	0.3	-	n.s.	17.6	-	n.s.	4.9	-	n.s.	0.1	-	-	-	n.s.
	Ferns (10%)	2.11	0.5	-	n.s.	0.1	-	n.s.	0.5	-	n.s.	21.6	-0.19	***	39.8	-0.02	-0.07	-0.24	*
	Monocotyledons (9%)	2.35	10.3	-	n.s.	8.0	-	n.s.	11.3	-	n.s.	6.5	-	n.s.	1.0	-	-	-	n.s.
	Vines (6%)	1.60	7.8	-	n.s.	12.5	-	n.s.	36.6	-	n.s.	29.0	-	n.s.	10.0	-	-	-	n.s.
Simpson index	All species	13.29	0.0	-	n.s.	14.4	0.51	*	33.5	-0.51	***	0.0	-	n.s.	11.8	-	-	-	n.s.
Productivity	All species	5.65	45.3	-0.39	***	15.0	-0.17	***	4.5	-	n.s.	10.6	-	n.s.	6.3	-	-	-	n.s.
	Forbs (24%)	4.23	27.1	-	n.s.	13.9	-	n.s.	0.2	-	n.s.	30.7	-	n.s.	3.8	-	-	-	n.s.
	Trees (14%)	6.43	58.0	-0.59	***	0.1	-	n.s.	8.4	-0.11	**	5.1	-	n.s.	1.7	-	-	-	n.s.
	Ferns (33%)	2.54	3.9	-	n.s.	43.4	-0.65	***	9.5	-	n.s.	2.1	-	n.s.	22.9	-	-	-	n.s.
	Monocotyledons (15%)	7.12	26.1	-0.95	***	2.1	-	n.s.	8.4	-	n.s.	16.5	-	n.s.	3.6	-	-	-	n.s.
	Vines (14%)	5.62	37.7	-0.60	***	8.6	-	n.s.	44.0	-0.15	***	0.0	-	n.s.	7.9	-	-	-	n.s.

Explained (%): Proportions of variance explained by the parameter. Given as the percentage of the total explained variance (Total = independent + joint).

Each categories' coefficients were estimated based on following categories. Aspect: north, Harvested:unharvested, Plantation: unplanted, Typhoon: undisturbed.

P : Significance of independent contoribution of a certain parameter. Values of *P* shown are the results of the randomization test. ***: $P < 0.001$, **: $P < 0.01$, *: $P < 0.05$, n.s.: not significant.

Full model χ or *F* : Chi-square statistics (d.f. = 103) used for species richness, F-statistics (d.f. = 13, 103) used for productivity and Simpson-index.

Full model *P* -value: The likelihood-ratio test was used for the difference in deviance between the full model and the null model from GLM (species richness: poisson distribution, Simpson index: Gamma distribution, productivity: log-normal distribution) with dependent variable.

Table 2. (*continued*).

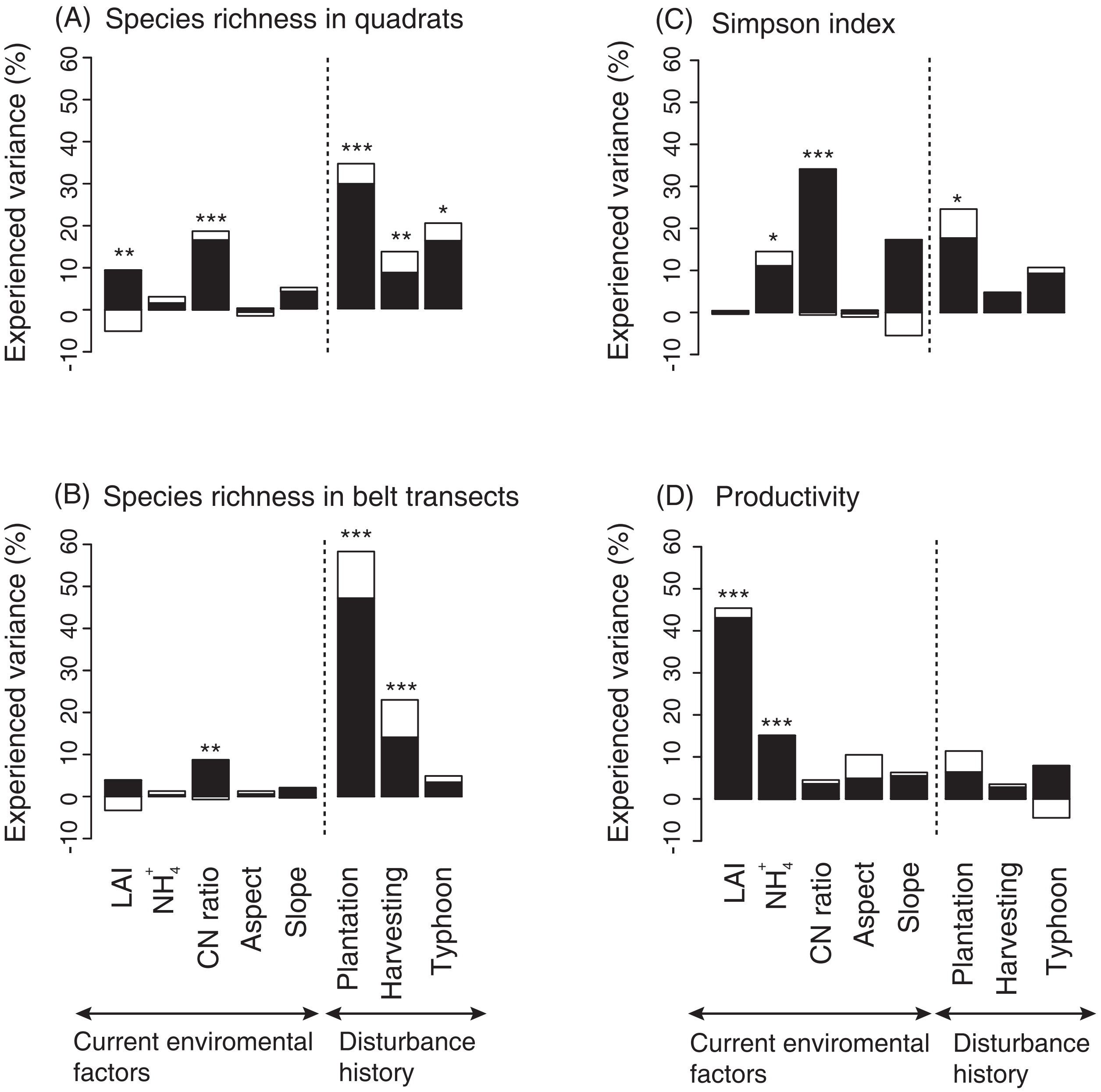
Disturbance factor												Full model χ or *F*	Full model *P*-value
Plantation				Harvesting			Typhoon						
Explained (%)	Coefficient		*P*	Explained (%)	Coefficient	*P*	Explained (%)	Coefficient			*P*		
	One time	Two times						Low	Middle	High			
34.6	-0.10	-0.47	***	13.6	0.21	**	20.4	0.06	-0.03	-0.07	*	92.74	**<0.001**
55.0	-0.26	-1.00	***	21.3	0.20	***	0.5	-	-	-	n.s.	107.49	**<0.001**
43.4	-0.11	-0.25	**	19.0	0.07	*	0.0	-	-	-	n.s.	20.48	0.08
7.5	0.35	-0.32	***	0.8	-	n.s.	1.5	0.43	0.09	0.02	**	13.60	0.40
1.0	-	-	n.s.	1.1	-	n.s.	8.2	-	-	-	n.s.	21.46	0.06
28.5	0.30	0.16	***	13.9	-	n.s.	1.5	0.30	0.09	0.08	***	16.51	0.22
58.2	-0.10	-0.38	***	23.0	0.03	***	5.0	-	-	-	n.s.	78.52	**<0.001**
65.7	-0.21	-0.70	***	24.8	0.00	***	2.3	-	-	-	n.s.	89.59	**<0.001**
36.8	-0.03	-0.41	***	4.3	-	n.s.	30.8	-	-	-	n.s.	25.72	**0.02**
0.1	-	-	n.s.	21.8	0.20	***	15.6	-	-	-	n.s.	17.47	0.18
35.0	-0.20	-0.05	*	26.4	-	n.s.	1.5	-	-	-	n.s.	11.28	0.59
2.1	-	-	n.s.	0.0	-	n.s.	1.9	-	-	-	n.s.	4.69	0.98
24.7	-0.71	-1.57	*	4.8	-	n.s.	10.8	-	-	-	n.s.	3.38	**<0.001**
11.4	-	-	n.s.	3.5	-	n.s.	3.5	-	-	-	n.s.	3.42	**<0.001**
1.6	-	-	n.s.	22.7	-	n.s.	0.1	-	-	-	n.s.	1.44	0.16
6.1	-0.46	0.23	***	19.6	-0.01	***	1.0	-	-	-	n.s.	3.63	**<0.001**
0.7	-	-	n.s.	0.0	-	n.s.	17.4	-	-	-	n.s.	1.52	0.12
14.9	-	-	n.s.	15.6	-	n.s.	13.0	-	-	-	n.s.	1.89	**0.04**
0.7	-	-	n.s.	1.0	-	n.s.	0.1	-	-	-	n.s.	2.54	**0.01**

Figure captions

Figure 1. The effects of the explanatory variables on species richness, the Simpson index, and productivity. Solid and open bars indicate independent and joint explained variance, respectively. Asterisks indicate the significance of independently explained variance: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$.

Figure 2. The effect of plantation frequency on (A) species richness in quadrats (2 m^2), (B) species richness in belts (30 m^2), and (C) the Simpson index. Vertical bars indicate standard error. Lower case letters represent results of multiple comparisons ($P < 0.05$).

Takafumi and Hiura Figure.1

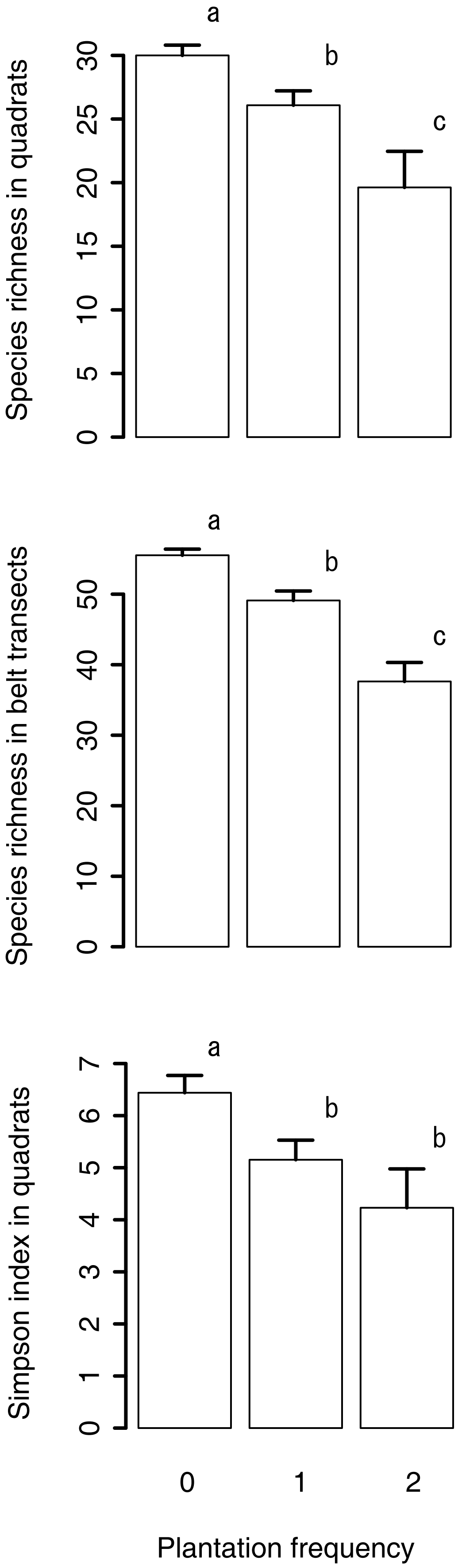


(A) Species richness in quadrats

(B) Species richness in belt transects

(C) Simpson index

(D) Productivity


a
b
c
Species richness in quadrats
0
5
10
15
20
25
30
a
b
c
Species richness in belt transects
0
10
20
30
40
50
a
b
b
Simpson index in quadrats
0
1
2
3
4
5
6
7
0
1
2
Plantation frequency

Appendix A. Explained ratio and coefficients of variables of the presence/absence for species with significant full model (p<0.05).

Species name	Life form	Intercepts	Environment factor																
			LAI (m^2/m^2)			NH_4^+ (mg/100g dry soil)			CN ratio			Slope (degree)			Aspect				
			Explained (%)	Coefficient	*P*	Explained (%)	Coefficient	*P*	Explained (%)	Coefficient	*P*	Explained (%)	Coefficient	*P*	Explained (%)	Coefficient			*P*
																W	S	E	
Aralia cordata	Fo	-42.88	25.5	-	n.s.	3.0	-	n.s.	0.5	-	n.s.	-	-	n.s.	9.0	-	-	-	n.s.
Agrimonia japonica	Fo	2.77	15.6	-1.04	*	3.6	-	n.s.	6.0	-	n.s.	-	-	n.s.	36.8	1.34	1.36	1.57	*
Angelica genuflexa	Fo	-4.56	0.5	-	n.s.	10.5	-	n.s.	8.8	-	n.s.	-	-	n.s.	12.7	-	-	-	n.s.
Arisaema peninsulae	Fo	-2.14	0.5	-	n.s.	21.4	0.75	***	2.0	-	n.s.	28.3	0.21	***	3.5	-	-	-	n.s.
Cardamine leucantha	Fo	-5.77	0.1	-	n.s.	11.6	-5.41	***	0.3	-	n.s.	45.9	1.04	***	12.1	-	-	-	n.s.
Chamaele decumbens	Fo	6.95	1.1	-	n.s.	3.4	-	n.s.	5.3	-	n.s.	-	-	n.s.	8.6	-	-	-	n.s.
Chloranthus serratus	Fo	2.59	0.1	-	n.s.	11.0	0.87	*	4.7	-	n.s.	-	-	n.s.	20.1	0.79	1.26	-20.19	**
Codonopsis lanceolata	Fo	8.72	7.8	-1.42	*	6.7	-	n.s.	2.9	-	n.s.	-	-	n.s.	35.3	-1.56	0.20	-16.93	*
Eupatorium chinense var. *simplicifolium*	Fo	10.90	20.0	-2.80	***	2.4	-	n.s.	12.9	-	n.s.	-	-	n.s.	23.4	-	-	-	n.s.
Galium japonicum	Fo	0.43	5.4	-	n.s.	1.0	-	n.s.	0.1	-	n.s.	-	-	n.s.	7.3	-	-	-	n.s.
Galium paradoxum	Fo	-3.13	0.0	-	n.s.	0.1	-	n.s.	0.1	-	n.s.	15.8	0.53	***	7.0	-	-	-	n.s.
Galium trifloriforme	Fo	12.30	1.0	-	n.s.	2.5	-1.90	**	3.7	-0.50	*	-	-	n.s.	23.8	-0.83	-2.22	-19.10	**
Hypericum erectum	Fo	-1.39	10.3	-	n.s.	4.6	-	n.s.	25.0	-0.65	**	-	-	n.s.	4.4	-	-	-	n.s.
Lilium cordatum var. *glehnii*	Fo	3.86	0.8	-	n.s.	0.2	-	n.s.	0.1	-	n.s.	-	-	n.s.	3.2	-	-	-	n.s.
Maianthemum dilatatum	Fo	3.45	0.4	-	n.s.	15.1	-0.73	*	0.1	-	n.s.	-	-	n.s.	29.4	-1.22	-1.69	15.25	*
Moehringia lateriflora	Fo	2.58	14.2	-0.99	**	1.7	-	n.s.	6.3	-	n.s.	36.7	0.27	***	14.8	-	-	-	n.s.
Oxalis acetosella	Fo	-22.46	7.3	-	n.s.	18.0	-1.76	*	2.2	-	n.s.	-	-	n.s.	13.4	-	-	-	n.s.
Patrinia villosa	Fo	5.41	4.3	-	n.s.	1.1	-	n.s.	16.4	-	n.s.	18.9	0.19	*	15.9	-	-	-	n.s.
Peracarpa carnosa var. *circaeoides*	Fo	2.74	0.5	-	n.s.	12.2	-0.91	**	0.1	-	n.s.	21.1	-0.24	**	15.0	-	-	-	n.s.
Phryma leptostachya var. *asiatica*	Fo	47.08	14.2	4.01	***	3.2	-	n.s.	1.4	-1.81	**	-	-	n.s.	5.2	-	-	-	n.s.
Potentilla freyniana	Fo	-24.82	7.9	-	n.s.	3.2	-	n.s.	2.7	-	n.s.	24.4	0.75	*	24.0	-	-	-	n.s.
Sanicula chinensis	Fo	4.62	0.9	-	n.s.	1.0	-	n.s.	0.5	-	n.s.	-	-	n.s.	6.5	-	-	-	n.s.
Scutellaria indica	Fo	-2.52	0.5	-	n.s.	0.0	-	n.s.	1.7	-	n.s.	32.3	0.22	***	4.0	-	-	-	n.s.
Senecio cannabifolius	Fo	8.89	9.4	-2.85	***	1.1	-	n.s.	0.7	-	n.s.	-	-	n.s.	69.1	0.03	-0.96	22.54	***
Smilacina japonica	Fo	2.50	8.3	-	n.s.	7.2	-	n.s.	2.4	-	n.s.	-	-	n.s.	6.7	-	-	-	n.s.
Solidago virga-aurea var. *asiatica*	Fo	8.89	15.7	-1.35	*	2.9	-	n.s.	16.9	-0.25	*	-	-	n.s.	31.4	-	-	-	n.s.
Teucrium japonicum	Fo	6.69	6.4	-	n.s.	0.5	-	n.s.	5.4	-	n.s.	-	-	n.s.	31.9	0.54	1.83	0.69	***
Torilis japonica	Fo	2.68	10.3	-	n.s.	1.2	-	n.s.	0.1	-	n.s.	7.5	-0.24	**	15.7	-	-	-	n.s.
Tripterospermum japonicum	Fo	-1.10	8.2	-	n.s.	8.7	-	n.s.	2.8	-	n.s.	27.0	-0.24	***	20.0	-	-	-	n.s.
Turritis glabra	Fo	-1.46	2.7	-	n.s.	0.5	-	n.s.	1.2	-	n.s.	26.9	0.16	**	36.8	0.36	2.39	-16.39	***
Acer japonicum	T	-13.05	38.6	2.07	***	4.3	-	n.s.	1.2	-	n.s.	-	-	n.s.	21.0	-	-	-	n.s.
Acer palmatum var. *matsumurae*	T	9.74	4.0	-	n.s.	10.8	-	n.s.	3.9	-	n.s.	-	-	n.s.	5.0	-	-	-	n.s.
Aralia elata	T	41.03	23.7	-7.85	***	10.0	-5.90	*	5.1	-	n.s.	-	-	n.s.	2.6	-	-	-	n.s.
Euonymus alatus	T	4.79	13.4	-1.81	***	4.7	1.24	**	3.7	-	n.s.	7.9	0.22	**	1.1	-	-	-	n.s.
Euonymus oxyphyllus	T	1.05	0.7	-	n.s.	11.6	0.57	**	0.3	-	n.s.	-	-	n.s.	3.6	-	-	-	n.s.
Fraxinus lanuginosa	T	-1.06	11.1	-	n.s.	0.0	-	n.s.	5.0	-	n.s.	-	-	n.s.	18.1	-	-	-	n.s.
Magnolia kobus var. *borealis*	T	3.49	2.8	-	n.s.	0.9	-	n.s.	5.8	-	n.s.	-	-	n.s.	17.7	-	-	-	n.s.
Morus bombycis	T	0.96	2.7	-	n.s.	0.8	-	n.s.	3.5	-	n.s.	26.2	0.23	***	32.8	-0.48	1.21	1.70	*
Pinus koraiensis	T	-9.08	32.7	1.66	***	1.3	-	n.s.	0.4	-	n.s.	-	-	n.s.	2.9	-	-	-	n.s.
Prunus sargentii	T	4.79	0.5	-	n.s.	0.3	-	n.s.	0.9	-	n.s.	-	-	n.s.	24.6	-	-	-	n.s.
Prunus ssiori	T	2.67	2.9	-	n.s.	4.1	-0.97	*	1.9	-	n.s.	-	-	n.s.	13.6	-	-	-	n.s.
Quercus mongolica var. *grosseserrata*	T	9.56	2.7	-	n.s.	0.4	-	n.s.	35.0	-0.46	***	-	-	n.s.	10.8	-	-	-	n.s.
Rubus crataegifolius	T	-12.42	2.7	-	n.s.	3.2	-	n.s.	16.5	-0.77	*	-	-	n.s.	14.8	-	-	-	n.s.
Rubus idaeus var. *aculeatissimus*	T	7.52	32.4	-4.07	***	6.0	-	n.s.	3.8	-	n.s.	-	-	n.s.	5.9	-	-	-	n.s.
Sorbus alnifolia	T	4.54	6.9	-	n.s.	11.6	-0.65	*	6.7	-	n.s.	-	-	n.s.	18.9	-	-	-	n.s.
Sorbus commixta	T	-17.64	4.4	-	n.s.	9.3	-	n.s.	2.5	-	n.s.	-	-	n.s.	15.8	-	-	-	n.s.
Spiraea salicifolia	T	0.45	25.1	-1.08	***	0.2	-	n.s.	0.5	-	n.s.	18.8	0.17	**	26.1	-	-	-	n.s.
Syringa reticulata	T	-5.62	4.5	-	n.s.	7.6	-	n.s.	1.8	-	n.s.	24.0	0.20	***	15.2	-	-	-	n.s.
Taxus cuspidata	T	12.78	3.4	-	n.s.	0.5	-	n.s.	12.0	-	n.s.	-	-	n.s.	7.5	-	-	-	n.s.
Athyrium conilii	Fe	-1.36	0.1	-	n.s.	7.5	-	n.s.	0.0	-	n.s.	-	-	n.s.	35.1	0.58	-1.04	-17.15	**
Dryopteris austriaca	Fe	-3.87	10.2	-	n.s.	0.4	-	n.s.	7.1	-	n.s.	44.6	-0.34	***	13.7	-	-	-	n.s.
Dryopteris monticola	Fe	7.07	0.9	-	n.s.	2.9	-	n.s.	0.0	-	n.s.	-	-	n.s.	35.5	-3.14	-2.06	-17.73	**
Osmundastrum cinnamomum var. *fokiense*	Fe	13.27	23.4	-1.09	*	28.1	-1.35	***	3.8	-	n.s.	-	-	n.s.	17.1	-	-	-	n.s.
Agropyron yezoense	M	4.81	2.3	-	n.s.	0.0	-	n.s.	0.7	-	n.s.	11.4	-0.28	**	4.9	-	-	-	n.s.
Diarrhena japonica	M	13.87	1.3	-	n.s.	7.7	-	n.s.	14.6	-0.57	***	-	-	n.s.	3.4	-	-	-	n.s.
Festuca parvigluma	M	-6.90	3.5	-	n.s.	0.2	-	n.s.	1.2	-	n.s.	-	-	n.s.	19.9	-	-	-	n.s.
Muhlenbergia japonica	M	-1.00	4.6	-	n.s.	0.8	-	n.s.	1.5	-	n.s.	17.8	0.25	**	12.5	-	-	-	n.s.
Hydrangera petiolaris	V	-1.79	4.7	-	n.s.	5.1	-	n.s.	5.7	-	n.s.	-	-	n.s.	22.9	-	-	-	n.s.
Schizophragma hydrangeoides	V	-6.61	23.9	0.95	***	10.3	-	n.s.	0.0	-	n.s.	-	-	n.s.	17.5	-	-	-	n.s.

Explained (%): Proportions of variance explained by the parameter. Given as the percentage of the total explained variance (Total = independent + joint).

Each categories' coefficients were estimated based on following categories. Aspect: north, Harvested:unharvested, Plantation: unplanted, Typhoon: undisturbed.

P : Significance of independent contribution of a certain parameter. Values of *P* shown are the results of the randomization test. ***: $P < 0.001$, **: $P < 0.01$, *: $P < 0.05$, n.s.: not significant.

χ-value*:* χ-statistics (d.f. = 103). Life form abbreviation Fo: forbs, T: trees, Fe: ferns, M:monocots, V:vines.

Full model *P* -value: The likelihood-ratio test was used for the difference in deviance between the full model and the null model, from GLM (binomial distribution) with dependent variable.

Appendix A. (*continued*).

Disturbance factor												χ-value	Full model *P* -value
Plantation				Harvesting			Typhoon						
Explained (%)	Coefficient		*P*	Explained (%)	Coefficient	*P*	Explained (%)	Coefficient			*P*		
	One time	Two times						Low	Middle	High			
31.4	31.61	26.92	*	16.9	-	n.s.	12.5	-	-	-	n.s.	28.18	0.009
3.6	-	-	n.s.	7.7	-	n.s.	12.3	-	-	-	n.s.	25.64	0.019
38.4	-1.24	-17.42	***	15.2	-	n.s.	6.6	-	-	-	n.s.	25.62	0.019
14.1	-	-	n.s.	14.9	-	n.s.	15.3	-	-	-	n.s.	25.88	0.018
18.5	-	-	n.s.	8.0	-	n.s.	3.6	-	-	-	n.s.	32.38	0.002
65.5	-2.94	-4.00	***	12.2	-0.52	*	3.7	-	-	-	n.s.	41.25	<0.001
53.1	-1.65	-36.77	***	1.0	-	n.s.	9.3	-	-	-	n.s.	48.03	<0.001
17.8	-1.27	-2.86	*	0.2	-	n.s.	19.4	-	-	-	n.s.	29.32	0.006
16.3	-0.18	-21.23	*	11.4	-	n.s.	11.1	-	-	-	n.s.	29.15	0.006
50.8	-1.47	-16.69	***	21.6	-1.33	***	13.4	-	-	-	n.s.	39.99	<0.001
36.0	-18.14	-16.49	***	28.8	-2.82	***	12.1	-	-	-	n.s.	45.73	<0.001
20.5	0.24	-17.34	*	24.7	-3.07	***	22.6	0.13	5.43	1.51	**	47.43	<0.001
1.6	-	-	n.s.	41.3	19.87	***	12.6	-	-	-	n.s.	22.81	0.044
50.5	-1.11	-16.84	***	41.4	-1.94	***	3.8	-	-	-	n.s.	36.20	<0.001
30.4	1.22	16.18	*	11.7	-	n.s.	12.3	-	-	-	n.s.	23.86	0.032
2.9	-	-	n.s.	6.6	-	n.s.	16.8	-	-	-	n.s.	30.82	0.004
35.1	3.84	-19.05	***	11.8	-	n.s.	7.1	-	-	-	n.s.	30.92	0.003
27.1	-0.92	-20.39	***	4.5	-	n.s.	11.8	-	-	-	n.s.	28.53	0.008
6.1	-	-	n.s.	1.9	-	n.s.	43.0	1.91	0.82	1.50	**	30.83	0.004
49.0	-7.36	-31.32	***	21.9	-25.96	***	5.1	-9.51	12.30	-5.97	*	80.90	<0.001
8.9	-	-	n.s.	16.6	26.60	**	12.4	-	-	-	n.s.	34.98	<0.001
54.3	-1.49	-32.80	***	29.8	-1.57	***	6.9	-	-	-	n.s.	48.07	<0.001
48.3	-1.24	-2.34	***	12.5	-	n.s.	0.6	-	-	-	n.s.	25.17	0.022
10.2	-	-	n.s.	2.9	-	n.s.	0.6	-	-	-	n.s.	28.34	0.008
42.0	-0.77	-2.69	***	24.0	-1.40	***	8.7	-	-	-	n.s.	36.96	<0.001
6.1	-	-	n.s.	3.5	-	n.s.	21.7	-	-	-	n.s.	23.92	0.032
18.1	-	-	n.s.	19.0	-1.21	**	14.8	-	-	-	n.s.	34.78	<0.001
43.9	-1.28	-17.22	***	16.8	-1.26	***	4.4	-	-	-	n.s.	38.95	<0.001
21.3	-0.11	-29.51	**	1.4	-	n.s.	10.6	-	-	-	n.s.	39.28	<0.001
10.2	-	-	n.s.	7.5	-	n.s.	14.2	-	-	-	n.s.	30.60	0.004
10.1	-	-	n.s.	4.6	-	n.s.	15.6	-	-	-	n.s.	23.44	0.037
48.1	-2.42	-5.80	***	15.5	-	n.s.	10.4	-	-	-	n.s.	29.78	0.005
17.9	-	-	n.s.	24.3	24.74	***	16.1	9.99	-25.33	4.21	***	49.08	<0.001
14.8	0.73	-0.71	*	6.0	1.45	*	48.4	-18.75	-3.57	-1.02	***	55.49	<0.001
49.0	-0.98	-33.56	***	29.3	-1.02	***	4.5	-	-	-	n.s.	42.50	<0.001
18.3	-	-	n.s.	26.0	-1.31	***	11.5	-	-	-	n.s.	25.44	0.020
45.4	-0.55	-17.75	***	0.6	-	n.s.	25.3	-	-	-	n.s.	24.19	0.029
3.8	-	-	n.s.	0.0	-	n.s.	30.1	1.14	1.17	-17.09	*	29.48	0.006
22.4	-	-	n.s.	6.3	-	n.s.	33.7	-18.22	0.32	-0.02	*	23.03	0.041
34.6	-0.24	-2.61	*	0.4	-	n.s.	35.1	-0.89	-1.97	-1.77	*	24.77	0.025
31.0	-0.41	-16.69	**	25.8	-1.57	***	17.9	-	-	-	n.s.	34.98	<0.001
2.9	-	-	n.s.	3.0	-	n.s.	30.8	-	-	-	n.s.	24.28	0.029
9.6	-	-	n.s.	32.1	19.92	***	20.7	4.93	-15.24	2.61	**	32.31	0.002
24.8	2.46	1.72	*	20.8	19.31	**	6.0	-	-	-	n.s.	35.53	<0.001
9.1	-	-	n.s.	24.4	1.43	***	11.0	-	-	-	n.s.	26.32	0.015
18.3	-	-	n.s.	33.5	18.96	***	4.4	-	-	-	n.s.	27.30	0.011
19.9	-	-	n.s.	8.5	1.30	*	0.8	-	-	-	n.s.	28.25	0.008
22.6	-	-	n.s.	0.0	-	n.s.	24.3	-	-	-	n.s.	25.91	0.017
18.8	-	-	n.s.	20.0	-3.48	***	37.2	-	-	-	n.s.	23.65	0.035
9.3	-	-	n.s.	11.9	-	n.s.	29.6	2.28	-0.01	1.12	*	28.08	0.009
5.8	-	-	n.s.	2.5	-	n.s.	15.7	-	-	-	n.s.	37.99	<0.001
15.9	-	-	n.s.	30.8	-2.25	***	12.9	-	-	-	n.s.	24.65	0.026
1.0	-	-	n.s.	3.5	-	n.s.	18.6	-	-	-	n.s.	22.42	0.049
31.3	-	-	n.s.	38.6	-1.27	***	10.7	-	-	-	n.s.	23.62	0.035
39.2	-2.15	-5.77	***	8.6	-	n.s.	23.6	2.93	17.65	20.67	*	35.08	<0.001
20.9	-	-	n.s.	28.9	-1.86	***	20.4	-	-	-	n.s.	23.43	0.037
13.2	-	-	n.s.	1.4	-	n.s.	48.2	-0.52	1.66	-17.03	**	25.27	0.021
6.9	-	-	n.s.	7.0	-	n.s.	34.3	-	-	-	n.s.	27.72	0.010
1.4	-	-	n.s.	0.6	-	n.s.	39.8	1.86	1.99	1.37	**	24.04	0.031

Appendix B. Explained ratio and coefficients of variables for the biomass of species that full model was significant ($P < 0.05$).

Species name	Life form	Intercepts	Environment factor																
			LAI (m^2/m^2)			NH_4^+ (mg/100g dry soil)			CN ratio			Slope (degree)			Aspect				
			Explained (%)	Coefficient	*P*	Explained (%)	Coefficient	*P*	Explained (%)	Coefficient	*P*	Explained (%)	Coefficient	*P*	Explained (%)	Coefficient			*P*
																W	S	E	
Actaea asiatica	Fo	-1.54	4.4	-	n.s.	0.7	-	n.s.	8.3	-0.14	**	0.2	-	n.s.	12.4	-	-	-	n.s.
Cacalia hastata var. *orientalis*	Fo	1.24	29.3	-0.87	***	0.3	-	n.s.	35.1	-0.20	***	3.2	-	n.s.	16.5	-	-	-	n.s.
Cardamine leucantha	Fo	-2.16	0.5	-	n.s.	1.5	-	n.s.	12.7	-0.15	***	24.6	0.06	***	4.8	-	-	-	n.s.
Chamaele decumbens	Fo	0.88	1.0	-	n.s.	4.9	-	n.s.	8.3	-0.13	*	0.4	-	n.s.	3.4	-	-	-	n.s.
Chloranthus serratus	Fo	-0.02	6.5	-	n.s.	16.3	0.60	*	6.9	-	n.s.	17.2	-	n.s.	13.0	-	-	-	n.s.
Cirsium kamtschatiam	Fo	-0.82	2.7	-	n.s.	0.4	-	n.s.	16.3	-0.15	**	20.4	-	n.s.	27.8	-	-	-	n.s.
Galium trifloriforme var. *nipponicum*	Fo	-3.86	0.0	-	n.s.	0.3	-	n.s.	10.5	-	n.s.	0.3	-	n.s.	9.3	-	-	-	n.s.
Lactuca raddeana var. *elata*	Fo	-2.68	0.5	-	n.s.	12.9	0.31	*	31.3	-0.09	**	4.2	-	n.s.	13.2	-	-	-	n.s.
Maianthemum bifolium	Fo	-3.40	0.2	-	n.s.	12.0	-	n.s.	0.8	-	n.s.	5.1	-	n.s.	2.2	-	-	-	n.s.
Moehringia lateriflora	Fo	-2.09	8.8	-0.31	*	0.1	-	n.s.	18.7	-0.09	***	21.5	0.04	**	26.1	-	-	-	n.s.
Patrinia villosa	Fo	-4.88	10.5	-0.35	*	9.5	0.32	**	0.0	-	n.s.	55.4	0.12	***	11.9	-	-	-	n.s.
Phryma leptostachya var. *asiatica*	Fo	2.11	1.1	-	n.s.	5.4	-	n.s.	1.0	-	n.s.	0.2	-	n.s.	1.5	-	-	-	n.s.
Sanicula chinensis	Fo	-1.00	0.8	-	n.s.	5.4	-	n.s.	0.1	-	n.s.	0.5	-	n.s.	3.4	-	-	-	n.s.
Scutellaria indica	Fo	-1.54	2.7	-	n.s.	0.0	-	n.s.	3.9	-	n.s.	16.6	0.07	*	4.1	-	-	-	n.s.
Smilacina japonica	Fo	-2.49	1.6	-	n.s.	9.3	-	n.s.	0.6	-	n.s.	2.2	-	n.s.	12.5	-	-	-	n.s.
Teucrium viscidum var. *miquelianum*	Fo	0.53	1.8	-	n.s.	2.4	-	n.s.	11.4	-0.19	**	11.5	-	n.s.	7.6	-	-	-	n.s.
Trillium smallii	Fo	3.08	0.2	-	n.s.	3.4	-	n.s.	7.7	-	n.s.	1.1	-	n.s.	2.4	-	-	-	n.s.
Tripterspermum japonicum	Fo	-3.61	0.3	-	n.s.	2.9	-	n.s.	0.1	-	n.s.	6.2	-	n.s.	25.9	-	-	-	n.s.
Tulotis ussuriensis	Fo	5.36	2.4	-	n.s.	0.2	-	n.s.	14.9	-0.31	***	2.8	-0.17	*	2.0	-	-	-	n.s.
Acer palmatum var. *matsumurae*	T	-0.22	0.2	-	n.s.	1.4	-	n.s.	2.4	-	n.s.	7.0	-	n.s.	1.3	-	-	-	n.s.
Euonymus oxyphyllus	T	-2.36	0.0	-	n.s.	4.7	-	n.s.	0.3	-	n.s.	3.3	-	n.s.	12.7	-	-	-	n.s.
Fraxinus lanuginosa	T	-0.94	7.6	-	n.s.	1.9	-	n.s.	0.5	-	n.s.	17.0	-0.19	***	18.0	-	-	-	n.s.
Fraxinus mandshurica var. *japonica*	T	-0.91	1.0	-	n.s.	1.0	-	n.s.	48.7	-0.20	***	3.6	-	n.s.	5.3	-	-	-	n.s.
Kalopanax pictus	T	-3.37	21.1	-	n.s.	4.7	-	n.s.	1.3	-	n.s.	17.3	0.04	*	5.0	-	-	-	n.s.
Morus australis	T	-2.27	35.8	-0.58	***	0.5	-	n.s.	0.3	-	n.s.	1.7	-	n.s.	9.2	-	-	-	n.s.
Quercus mongolica var. *grosseserrata*	T	0.11	2.1	-	n.s.	0.1	-	n.s.	0.9	-	n.s.	22.8	0.14	**	4.9	-	-	-	n.s.
Rubus idaeus var. *aculeatissimus*	T	-1.39	38.8	-0.80	***	1.5	-	n.s.	0.1	-	n.s.	0.0	-	n.s.	1.2	-	-	-	n.s.
Spiraea salicifolia	T	0.86	37.8	-0.90	***	1.5	-	n.s.	9.9	-0.14	*	13.6	0.11	*	18.7	-	-	-	n.s.
Dryopteris expansa	Fe	-3.61	19.0	0.72	*	3.2	-	n.s.	0.3	-	n.s.	43.9	-0.15	***	7.0	-	-	-	n.s.
Lastrea thelypteris	Fe	-3.45	2.2	-	n.s.	1.3	-	n.s.	5.4	-	n.s.	14.4	-0.21	*	39.5	-0.81	-0.09	-1.11	***
Onoclea sensibilis var. *interrupta*	Fe	-2.89	0.5	-	n.s.	6.4	-	n.s.	14.8	-	n.s.	3.2	-	n.s.	11.0	-	-	-	n.s.
Calamagrostis hakonensis	M	-4.12	10.8	-	n.s.	0.8	-	n.s.	1.9	-	n.s.	3.2	-	n.s.	58.4	0.35	0.09	-0.32	***
Carex leucochlora	M	0.11	6.3	-0.81	*	10.9	-	n.s.	21.1	-0.15	**	3.0	-	n.s.	24.6	-	-	-	n.s.
Diarrhena japonica	M	5.70	5.5	-	n.s.	8.1	-	n.s.	32.1	-0.41	***	4.8	-	n.s.	2.0	-	-	-	n.s.
Festuca parvigluma	M	-3.14	19.9	-0.49	**	2.1	-	n.s.	1.9	-	n.s.	12.9	-	n.s.	19.1	-	-	-	n.s.
Celastrus orbiculatus	V	-2.95	3.3	-	n.s.	7.3	-	n.s.	9.9	-	n.s.	26.7	0.12	***	17.0	-	-	-	n.s.
Hydrangera petiolaris	V	-0.64	2.2	-	n.s.	1.1	-	n.s.	3.4	-	n.s.	40.6	0.03	***	2.9	-	-	-	n.s.
Rhus ambigua	V	5.73	0.3	-	n.s.	0.3	-	n.s.	19.0	-0.30	***	16.2	0.01	*	7.9	-	-	-	n.s.
Schisandra chinensis	V	2.92	22.4	-1.13	***	7.0	0.82	**	7.2	-	n.s.	3.0	-	n.s.	15.8	-	-	-	n.s.
Schizophragma hydrangeoides	V	-7.26	6.3	-	n.s.	5.9	-	n.s.	0.1	-	n.s.	8.3	-	n.s.	14.0	-	-	-	n.s.
Vitis coignetiae	V	-5.44	4.4	-	n.s.	32.8	0.88	***	1.2	-	n.s.	4.7	-	n.s.	30.0	-0.82	-0.43	-0.93	*

Explained (%): Proportions of variance explained by the parameter. Given as the percentage of the total explained variance (Total = independent + joint).

Each categories' coefficients were estimated based on following categories. Aspect: north, Harvested:unharvested, Plantation: unplanted, Typhoon: undisturbed.

P : Significance of independent contribution of a certain variable. Values of *P* shown are the results of the randomization test. ***: $P < 0.001$, **: $P < 0.01$, *: $P < 0.05$, n.s.: not significant.

Life form abbreviation Fo: forbs, T: trees, Fe: ferns, V: vines. *F* -value: F-statistics (d.f. = 12, 103).

Full model *P* -value: The likelihood-ratio test was used for the difference in deviance between the full model and the null model, from GLM (log-normal distribution) with dependent variable.

Appendix B. (*continued*).

Disturbance factor												*F* -value	Full model *P* -value
Plantation				Harvesting			Typhoon						
Explained (%)	Coefficient		*P*	Explained (%)	Coefficient	*P*	Explained (%)	Coefficient			*P*		
	One time	Two times						Low	Middle	High			
14.1	-	-	n.s.	26.1	-0.60	***	33.8	-0.22	0.83	0.64	**	2.75	0.002
5.4	-	-	n.s.	6.6	-	n.s.	3.5	-	-	-	n.s.	2.12	0.019
22.5	-	-	n.s.	27.7	-0.55	***	5.8	-	-	-	n.s.	2.41	0.007
51.2	-0.94	-1.85	***	17.8	-0.34	**	12.9	-	-	-	n.s.	3.11	<0.001
27.6	-0.67	-2.16	**	8.6	-	n.s.	4.0	-	-	-	n.s.	1.89	0.040
19.6	-	-	n.s.	1.9	-	n.s.	10.9	-	-	-	n.s.	1.94	0.033
22.4	-	-	n.s.	34.7	-0.55	***	22.7	0.80	-0.08	0.14	*	2.40	0.007
9.8	-	-	n.s.	9.2	0.46	*	18.9	-	-	-	n.s.	2.15	0.017
60.5	2.30	3.54	***	13.4	-	n.s.	5.9	-	-	-	n.s.	2.73	0.002
11.3	-0.49	-0.54	*	2.7	-	n.s.	10.9	-	-	-	n.s.	2.92	0.001
5.7	-	-	n.s.	0.1	-	n.s.	6.9	-	-	-	n.s.	3.32	<0.001
57.1	-1.29	-3.04	***	31.0	-1.42	***	2.7	-	-	-	n.s.	5.75	<0.001
42.4	-1.25	-1.98	***	27.0	-0.75	***	20.5	0.99	1.09	0.09	*	3.59	<0.001
61.4	-0.90	-1.53	***	4.7	-	n.s.	6.6	-	-	-	n.s.	2.27	0.012
32.7	-1.15	-2.07	***	20.8	-0.43	**	20.3	0.68	1.33	-0.61	*	2.91	0.001
32.5	-0.56	-1.16	*	22.0	-0.55	**	10.7	-	-	-	n.s.	2.08	0.022
42.7	-0.38	-1.79	***	3.1	-	n.s.	39.5	-0.94	-1.62	-0.89	**	1.98	0.030
17.8	-	-	n.s.	12.3	-	n.s.	34.6	0.52	1.24	0.67	*	1.97	0.031
59.3	-1.57	-3.14	***	11.1	-0.82	**	7.4	-	-	-	n.s.	4.73	<0.001
42.7	-0.78	-1.50	***	27.2	-0.94	***	17.8	1.00	1.41	0.51	*	3.00	<0.001
23.7	-	-	n.s.	32.4	-0.75	***	22.9	-	-	-	n.s.	1.91	0.037
27.5	-0.67	-2.03	**	9.3	-	n.s.	18.3	-	-	-	n.s.	2.63	0.003
10.2	-	-	n.s.	19.1	0.65	**	11.0	-	-	-	n.s.	1.98	0.030
8.3	-	-	n.s.	3.2	-	n.s.	39.2	-0.15	0.22	0.40	*	1.82	0.049
43.2	0.55	0.98	**	4.0	-	n.s.	5.3	-	-	-	n.s.	1.94	0.034
19.3	-	-	n.s.	31.2	-1.28	***	18.7	-	-	-	n.s.	2.12	0.019
48.0	0.12	1.89	***	3.3	-	n.s.	7.1	-	-	-	n.s.	5.50	<0.001
13.5	-	-	n.s.	3.0	-	n.s.	2.1	-	-	-	n.s.	2.20	0.014
18.9	-	-	n.s.	0.1	-	n.s.	7.6	-	-	-	n.s.	1.92	0.036
3.2	-	-	n.s.	30.9	-1.05	***	3.0	-	-	-	n.s.	2.57	0.004
1.5	-	-	n.s.	0.9	-	n.s.	61.8	1.25	0.03	0.19	***	1.99	0.029
10.3	-	-	n.s.	1.4	-	n.s.	13.2	-	-	-	n.s.	2.15	0.017
8.3	-	-	n.s.	4.6	1.26	**	21.3	-	-	-	n.s.	2.74	0.002
25.0	-0.88	-1.39	**	8.5	-	n.s.	13.9	-	-	-	n.s.	2.66	0.003
3.2	-	-	n.s.	0.5	-	n.s.	40.3	1.01	-0.20	0.11	*	1.91	0.038
8.3	-	-	n.s.	9.5	-	n.s.	18.0	-	-	-	n.s.	2.28	0.011
21.8	1.38	1.82	**	0.3	-	n.s.	27.7	2.04	1.12	0.54	*	2.06	0.023
17.6	-	-	n.s.	22.8	-1.58	***	15.8	-	-	-	n.s.	2.33	0.009
8.9	-	-	n.s.	23.0	1.58	***	12.7	-	-	-	n.s.	2.89	0.001
10.6	-	-	n.s.	8.3	0.93	*	46.4	2.35	1.39	0.51	***	2.51	0.005
3.1	-	-	n.s.	0.1	-	n.s.	23.7	-	-	-	n.s.	2.27	0.011