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Author(s)	Takafumi, Hino; Hiura, Tsutom
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1 **Effects of disturbance history and environmental factors on the diversity and**
2 **productivity of understory vegetation in a cool-temperate forest in Japan**

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4 *Authors List:* Hino Takafumi and Tsutom Hiura

5

6 *Affiliation:* Tomakomai Research Station, Field Science Center for Northern Biosphere,
7 Hokkaido University, Japan

8

9 *Corresponding author:* Takafumi Hino

10 Tomakomai Research Station, Field Science Center for Northern Biosphere, Hokkaido
11 University, Tomakomai 053-0035, Japan

12 *E-mail:* Hino Takafumi takafumi@fsc.hokudai.ac.jp

13 Tsutom Hiura hiura@fsc.hokudai.ac.jp

14 *Tel:* +81-144-332171

15 *Fax:* +81-144-332173

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1 **Abstract**

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

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

3

4 **Introduction**

5 The determination of the mechanisms that control species diversity is a major issue in
6 forest ecology. According to current theory, disturbance regime and resource availability
7 are key factors in the structuring of plant communities (Denslow, 1980; McIntyre *et al.*,
8 1995). The availability of resources such as light and soil nutrients affects species
9 richness through competition for resources. For example, high levels of resources
10 decrease plant diversity because they enhance competitive exclusion (Tilman, 1984;
11 Goldberg and Miller, 1990; Wedin and Tilman, 1993). In contrast, natural disturbances
12 caused by strong winds, wildfires, and volcanic eruptions, and anthropogenic
13 disturbances caused by forest management (e.g., plantation, harvesting) affect species
14 richness by altering resource availability. For example, the removal of canopy trees
15 increases light availability on the forest floor (Malcolm, 1994) and soil nutrient and water
16 availability because of a decrease in uptake by disturbed canopy trees (e.g., Parsons *et al.*,
17 1994); these changes in resource availability can increase species richness via the
18 immigration of early successional species (Brunet *et al.*, 1996; Decocq *et al.*, 2004).

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

5 The diversity of plant species in most cool-temperate forest communities is
6 much higher for understory forbs, ferns, and shrubs than for canopy trees (Halpern and
7 Spies, 1995; Gilliam, 2007). Furthermore, the decomposition of understory plant litter is
8 more rapid than that of canopy tree litter; the former accounts for only 10-15% of the
9 annual total litter production in cool-temperate forests (Muller, 2003). Therefore,
10 understory plants play important roles not only in maintaining species diversity but also
11 in nutrient cycling in forest ecosystems (Siccama *et al.*, 1970; Fukuzawa *et al.*, 2006).
12 Once the understory species composition is altered by disturbance, the changes may
13 persist for many decades or centuries, and the understory species composition of
14 old-growth forests may not recover for centuries after disturbance (Whitney and Foster,
15 1988; Halpern and Spies, 1995; Singleton *et al.*, 2001; Dupouey *et al.*, 2002). Two
16 mechanisms explain the maintenance of species composition (Donohue *et al.*, 2000).
17 First, limitations in dispersal and establishment can restrict recolonization at a site where
18 species were previously removed by disturbance, even if the environmental conditions

1 have recovered. We defined this mechanism as the effects of disturbance history. Second,
2 current environmental conditions can restrict the establishment and growth of species that
3 were formerly present at a site. Numerous studies have demonstrated the importance of
4 the effects of disturbance history on diversity; however, few studies have quantitatively
5 examined the relative importance of disturbance history and current environmental
6 conditions.

7 The natural local flora corresponds to the local disturbance regime (Hiura, 1995).
8 Anthropogenic disturbances caused by forest management greatly affect biodiversity;
9 these effects differ from those caused by natural disturbance because anthropogenic
10 disturbances differ from natural disturbances in severity and frequency (Halpern and
11 Spies, 1995; Roberts and Gilliam, 1995b). The management of forests to sustain
12 biodiversity and ecosystem functioning has become a major challenge for modern
13 forestry (Bengtsson *et al.*, 2000; Lindenmayer *et al.*, 2000). Most cool-temperate forests
14 have been managed for timber production. In Hokkaido, the northern island of Japan,
15 plantation stands cover > 25% of the total forested area, and most of the remaining natural
16 forests have experienced some kind of forest management (Hokkaido Government, 2005).
17 The combination of natural and anthropogenic disturbance affects the diversity and
18 functions of understory plants in these cool-temperate forests. Therefore, to understand

1 the mechanisms underlying the maintenance of biodiversity for application to forest
2 management, it is necessary to examine the effects of both natural and anthropogenic
3 disturbances within a region (Roberts, 2004). However, most studies have only examined
4 the effects of anthropogenic disturbance on understory plants by comparing
5 anthropogenically disturbed forests and undisturbed old-growth forests (Duffy and Meier,
6 1992; Halpern and Spies, 1995; Singleton *et al.*, 2001), and the comparison of the effects
7 of natural and anthropogenic disturbance is rarely made within a region (but see Reich *et*
8 *al.*, 2001; Ramovs and Roberts, 2003).

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

17

18

1 **Methods**

2 Study site

3 This study was conducted in the Tomakomai Experimental Forest (TOEF), Hokkaido
4 University, Japan (42°41' N, 141°36' E). A large part of TOEF is located on flat land with
5 slope angle < 5°, and the forest covers 2715 ha. The mean monthly temperatures range
6 from −3.2 to 19.1°C, and the annual precipitation is 1450 mm. Snow cover reaches a
7 depth of 50 cm from December to March. Approximately 350 vascular plants have been
8 recorded in the TOEF (Kudo and Yoshimi, 1916). The dominant canopy tree species in
9 the natural stands are *Quercus crispula*, *Acer mono*, *Sorbus alnifolia*, and *Tilia japonica*,
10 and the understory species include *Dryopteris crassirhizoma*, *Maianthemum dilatatum*,
11 *Scisandra chinensis*, and *Sasa nipponica* (Hiura, 2001). The forest is formed on 2 m deep
12 volcanogenous regosols that accumulated from the eruptions of Mt. Tarumae in 1669 and
13 1739; the depth of the A horizon is 0–6 cm (Shibata *et al.*, 1998). In a study, investigating
14 the effects of anthropogenic disturbance due to forest management on diversity of
15 understory plants, both disturbance and site-specific effects (e.g., due to topography and
16 geology) were detected (Hannerz and Hanell, 1997). Thus, by using the sites where
17 topographic and geologic factors are homogenous, it allows us to separate the effects of
18 disturbance history from site-specific effects.

1

2 Disturbance history

3 There was no record of anthropogenic disturbance in TOEF until the early 20th century.

4 Plantations in TOEF are created following clear-cutting and mechanical site preparation.

5 Weeding and shrub clearing occur twice per plantation stand, and some stands are in their

6 second rotation. The plantation stands are between 11 and 80 years old. The main planted

7 tree species are *Larix kaempferi*, *Abies sachalinensis*, and *Picea glehnii*. Harvesting

8 operations in TOEF are performed as selective cutting in plantation stands and natural

9 forests. Although 3–56 years have passed since the last harvest, depending on the stand
10 age, most harvesting occurred 10–25 years ago. The only major natural disturbance in11 TOEF since it was established in 1904 was a severe typhoon in 1954, although there have
12 been some small disturbances caused by other typhoons. A secondary forest has13 developed in one-third of TOEF since the severe typhoon (Mishima *et al.*, 1958). TOEF

14 has approximately 300 permanent forest plots (Hiura, 2005). The permanent plots have

15 detailed disturbance history records and homogeneous forest structure within plots. These

16 features are useful for the study of the effects of disturbance history on understory

17 vegetation. We selected 116 square plots of 37 × 23 m to 50 × 60 m (mainly 40 × 50 m)

18 from the permanent plots. To determine when plantation and harvesting (including

1 salvage logging) occurred in the plots, we examined TOEF forest management records
2 beginning in 1924. Damage from the severe typhoon in 1954 was estimated at four levels:
3 undisturbed, low-severity disturbance with single canopy gaps, intermediate severity
4 with patchy disturbed areas, and high severity with overall disturbance. Typhoon damage
5 was determined using aerial photographs and maps created from field surveys of the
6 damage (Mishima *et al.*, 1958). In the study plots, the relation between damage from the
7 severe typhoon and harvesting or plantation frequency was not significant (likelihood
8 ratio test, $df = 112$, harvesting: $\chi = 64.54$, $P = 0.38$, plantation: $\chi = 95.04$, $P = 0.35$). The
9 study plots were divided into nine forest types based on disturbance history (Table 1).

10

11 Sampling design and data collection

12 Vegetation and environment surveys were conducted between 25 June and 23 July 2004.
13 These data and data collected in July 2000 (Hiura, 2001) were combined (78 plots in 2004,
14 38 plots in 2000) and analyzed, with the assumption that the environmental conditions did
15 not change between summer 2000 and summer 2004. The differences in current
16 environmental factors were not significant between the two data sets in stands that had the
17 same disturbance history (all $P > 0.09$). The 2000 data set had five quadrats within plots,
18 and we randomly selected two quadrats from each plot for analysis with the 2004 data. To

1 measure the diversity and productivity of understory plants, two 1×1 m quadrats were
2 established randomly at least 5 m from the plot edges in each plot (232 quadrats in total).
3 The plant species that appeared in each quadrat were recorded. To estimate aboveground
4 productivity, we clipped the current-year product parts of understory plants, i.e.
5 aboveground parts of forbs, ferns, monocots < 1 m tall, and current-year leaves and
6 shoots for woody species < 1 m tall. In which the non-woody plants in this study area
7 consisted mostly of current-year products. All samples were sorted by species, dried, and
8 weighed. Data from the two quadrats in each plot were summed for analysis. Diversity
9 was expressed using Simpson's index ($1/\sum p_i^2$), where p_i is the relative mass of species i .
10 The relative mass was calculated as the mass of a single species divided by the total mass
11 of vegetation from the plot for the two quadrats combined.

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

15 We collected environmental data on light availability, soil nutrients, and
16 topography as factors that might explain species diversity and productivity in the plots.
17 To estimate light availability, the leaf area index (LAI) at a height of 1 m was measured in
18 each plot using an optical analyzer (LAI-2000; Li-Cor, Lincoln, NE, USA). Some

1 previous study reported that the LAI-2000 analyzer may underestimate the actual LAI
2 (Kussner and Mosandl, 2000; Law *et al.*, 2001). However, previous studies in this region
3 found that the LAI-2000 produced reliable estimates that were not much smaller than
4 direct measurements made in a secondary stand (LAI of around 4.0; Takahashi *et al.*,
5 1999) and a mature stand (LAI of 7.59; Fukushima *et al.*, 1998).

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

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

16

17

18

1 Data analysis

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

13 Hierarchical partitioning alleviates problems of multicollinearity among
14 variables (MacNally, 2000, 2002) and has been used in numerous studies (e.g., Heikkinen
15 *et al.*, 2004; Banks *et al.*, 2005). Disturbance history and environmental factors are
16 closely related. For example, LAI (Kashian *et al.*, 2005) and soil N (Zimmerman *et al.*,
17 1995) both change with the number of years since the last disturbance. Thus, we used
18 hierarchical partitioning to examine the contribution of each explanatory variable to

1 species richness, Simpson index, productivity, and species presence/absence by
2 examining each explanatory variable separately. The significance of the independent
3 contribution of each explanatory variable was tested using randomizations (MacNally,
4 2002). Hierarchical partitioning examines all model combinations jointly to identify the
5 average influence of parameters, rather than just the single best model, and then estimates
6 the percentage independent contribution of each parameter to the total explained variation
7 in the dependent variable. This analysis was performed for life form richness and
8 productivity, as well as for all understory species. To assess the contributions of the
9 explanatory variables to the presence of each species, we analyzed the presence/absence
10 of individual understory species in the plots using the belt transect survey data. We show
11 the results for species presence/absence for species that occurred in more than five plots
12 and for which the full model was significant ($P < 0.05$). Because the productivity of all
13 understory plants can be affected by the dominant species, we estimated the contributions
14 of the explanatory variables to the productivity of each species using hierarchical
15 partitioning. We show the results for species productivity for species that occurred in
16 more than five plots and for which the full model was significant ($P < 0.05$). All statistical
17 analyses were conducted using R version 2.6.0 (R Development Core Team 2006).

18

1 **Results**

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

7

8 Effects of disturbance history on understory plants

9 The type of disturbance history had a significant effect on species richness (in quadrats: χ^2
10 = 46.838, $df = 8$, $P < 0.001$, in belts: $\chi^2 = 72.794$, $df = 8$, $P < 0.001$). However, the number
11 of years since the last anthropogenic disturbance did not significantly affect species
12 richness or the Simpson index (all $P > 0.24$), except for plantation species richness in the
13 belt surveys ($P < 0.001$). The sum of the variance explained by disturbance history
14 variables (i.e., plantation frequency, harvesting, and typhoon severity) composed a large
15 portion of the variation in species richness (69% in quadrats; 77% in belts; Fig. 1A, B). In
16 particular, plantation frequency explained 34.6% of the variation in species richness, and
17 species richness decreased as plantation frequency increased (Fig. 2). In contrast, species
18 richness tended to be higher in harvested stands than in unharvested stands (Table 2).

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

5 For productivity, the sum of the variance explained by parameters representing
6 disturbance history (18.4%) was lower than that of environmental factors. The
7 disturbance history parameters were not statistically significant, although the type of
8 disturbance history had a significant effect on productivity ($F = 2.573$, $df = 8, 107$, $P =$
9 0.013). For the Simpson index, disturbance history and current environmental factors
10 explained similar amounts of variance (disturbance history: 46.8%, current
11 environmental factors: 46.2%).

12

13 Effects of current environmental factors on understory plants

14 The sum of the variance explained by current environmental factors constituted a large
15 part of the variation in productivity (81.6%): LAI explained 45.3% and NH_4^+ explained
16 15.0% (Fig. 1D, Table 2). However, these parameters explained only a small part of the
17 variation in species richness. LAI and NH_4^+ had significant negative effects on
18 productivity and species richness (Table 2). The topographic variables were not

1 significant in explaining the variation in species richness, the Simpson index, or
2 productivity.

3

4 Life form and species differences

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

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

15

16 **Discussion**

17 Our results clearly illustrate that disturbance history has a stronger influence on the
18 species richness of understory plants than do current environmental factors. In particular,

1 as the plantation frequency increased, species richness decreased. In contrast, current
2 environmental factors had a stronger influence on the productivity of understory plants
3 than did disturbance history. The responses of presence and productivity to disturbance
4 history and current environmental factors varied among the species, although there were
5 some common responses within life forms.

6

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

9 Disturbance history affects species richness by altering propagule availability and habitat
10 structure (Meier *et al.*, 1995; Buckley *et al.*, 1997; Halpern *et al.*, 1999; Astrom *et al.*,
11 2005). In contrast, environmental factors affect species richness through resource
12 competition (Tilman, 1984; Goldberg and Miller, 1990; Wedin and Tilman, 1993). We
13 found that disturbance history explained more of the variation in species richness (69% in
14 quadrats; 86% in belts) than did current environmental factors, even long after the
15 disturbance had occurred (50 years after the typhoon, an average of 58 years since
16 plantation, and an average of 16 years since harvesting). Therefore, for local flora in this
17 area, the effects of propagule availability and habitat structure on species richness were
18 most likely greater than the effects of resource competition. These results agree with

1 previous studies that indicated that species that are lost from the understory might not
2 reappear even by one century after severe disturbance (Whitney and Foster, 1988;
3 Singleton *et al.*, 2001; Dupouey *et al.*, 2002) because of dispersal and establishment
4 limitations (Donohue *et al.*, 2000). There are two possible explanations for these results.
5 First, the number of forb species, which are particularly sensitive to disturbance,
6 composed approximately half of the total species in our study. The dispersal ability of
7 forbs is generally low (Cain *et al.*, 1998); thus, forbs tend to retain disturbance effects
8 longer than other life forms. Second, species that are adapted to the predisturbance
9 canopy tree phenology might have difficulty persisting in highly disturbed stands. The
10 seasonality of light resource availability for understory plants is greatly affected by
11 canopy tree phenology (Uemura, 1994). If most canopy trees are removed from stands by
12 clear-cutting in preparation for plantation establishment or by a severe typhoon, the forest
13 floor receives abundant light throughout the year.

14

15 Effects of anthropogenic and natural disturbance on species richness

16 Species richness and the Simpson index decreased as the plantation frequency increased
17 (Fig. 2). There are two possible explanations for these results. First, the creation of a
18 plantation is a very severe form of disturbance that involves clear-cutting and mechanical

1 site preparation (Roberts and Zhu, 2002). Thus, species that prefer a stable habitat in the
2 forest may be extirpated. Second, the establishment of a plantation usually creates a
3 homogenous environment (microtopography, coarse woody debris, light distribution, and
4 litter content), in contrast to the environment of an old-growth forest. Machinery
5 preparation with plantation obliterates heterogeneity in microtopography (e.g. mound,
6 pit), which allows coexistence and higher richness in stands (Beatty, 1984). Several
7 studies reported that diversity of understory plants in clear cutting stands recover more
8 quickly than our plantation stands (Reiners, 1992; Ford *et al.*, 2000; Gilliam, 2002). One
9 of the reason why diversity of understory plants recover more slowly in plantation stands,
10 the heterogeneity in microtopography would not recover in long-term (Beatty, 2003).

11 Clear-cutting and site preparation eliminate coarse woody debris, which is related to
12 heterogeneity on the forest floor (Goodburn and Lorimer, 1998; Roberts and Zhu, 2002;
13 Ramovs and Roberts, 2003), and reduce plant species diversity (Thomas *et al.*, 1999;
14 Miller *et al.*, 2002). Furthermore, because plantations are usually even aged and have
15 only one or several canopy species, the understory light distribution and litter content are
16 homogeneous. The conversion of a stand from deciduous broadleaf tree species to one or
17 several coniferous tree species changes the seasonality of resource availability on the
18 forest floor via leaf phenology of canopy, thus decreasing species that are adapted to the

1 seasonality of resource availability (Sparks *et al.*, 1996; Amezaga and Onaindia, 1997).
2 This type of forest conversion also changes the litter quality on the forest floor because
3 coniferous leaf litter has lower pH (Binkley and Valentine, 1991; Brandtberg *et al.*, 2000)
4 and greater accumulation because of slower decomposition (Klemmedson, 1992;
5 Cornelissen, 1996) than does broadleaf leaf litter. This may also affect the understory
6 species composition. The replanting of stands through rotations may increase the
7 negative effects on species richness over those of a single plantation.

8 Harvesting had a positive effect on species richness (Table 2). Previous studies in
9 broadleaf forest suggest that understory species richness increases after selective tree
10 harvesting because these species are tolerant to intermediate canopy disturbance and
11 some early successional species favor such disturbance (Brunet *et al.*, 1996; Gotmark *et*
12 *al.*, 2005). The presence of *Potentilla freyniana*, *Hypericum erectum*, *Rubus*
13 *crataegifolius*, *Rubus idaeus* var. *aculeatissimus*, and *Aralia elata* was positively related
14 to harvesting (Appendix A). These species prefer relatively open stands (Satake *et al.*,
15 1981, 1989) and their immigration would increase the total species richness.

16 In terms of natural disturbance, the species richness of quadrats indicated a
17 single peak model related to the 1954 typhoon: species richness was high in stands in
18 which only single trees were disturbed. Typhoons create canopy gaps that increase light

1 and soil nutrient availability in the understory (Liechty *et al.*, 1997; Carlton and Bazzaz,
2 1998), promoting the immigration of early successional species (Peterson and Pickett,
3 1995). Furthermore, typhoons can create microenvironmental heterogeneity (e.g., pit and
4 mound topography), allowing species with various ecological characteristics to coexist in
5 a stand. Nevertheless, stands that received severe typhoon disturbance had lower species
6 richness than undisturbed stands. Severe typhoon disturbance might result in excess
7 irradiance and dry soils, negatively affecting species that prefer dark and humid
8 environments. Moreover, if a poor disturbance-tolerant species becomes extirpated from
9 a stand because of high-severity disturbance, it may be difficult for the species to
10 reestablish if the available seed sources are located far from the center of the disturbed
11 area.

12

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

15 Current environmental factors, particularly LAI and NH_4^+ , explained much of the
16 variation in productivity (Fig. 1D). These results agree with the theory that light and soil
17 nutrients explain most of the variation in productivity when water availability is high
18 (Tilman, 1988). Furthermore, the predominance of LAI in explaining productivity was

1 consistent with previous findings that understory plant productivity is closely related to
2 the size of the canopy opening (Malcolm, 1994; Stone and Wolfe, 1996).

3

4 Management implications

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

17

18

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7

8

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

Disturbance history	Planted 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.

Table 2. 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	Explained (%)	Coefficient	Explained (%)	Coefficient	Explained (%)	Coefficient	Explained (%)	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	-	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.	
Species richness in belts	Vines (5%)	0.95	3.9	-	n.s.	9.8	-	n.s.	10.5	-	31.5	-	n.s.	0.5	-0.01	-0.02	-0.05 *
	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	-	3.3	-	n.s.	0.1	-	-	n.s.
	Trees (31%)	3.55	5.4	-0.12 *	0.3	-	n.s.	17.6	-	4.9	-	n.s.	0.1	-	-	n.s.	
	Ferns (10%)	2.11	0.5	-	n.s.	0.1	-	n.s.	0.5	-	21.6	-0.19 ***	39.8	-0.02	-0.07	-0.24 *	
Simpson index	Monocotyledons (9%)	2.35	10.3	-	n.s.	8.0	-	n.s.	11.3	-	6.5	-	n.s.	1.0	-	-	n.s.
	Vines (6%)	1.60	7.8	-	n.s.	12.5	-	n.s.	36.6	-	29.0	-	n.s.	10.0	-	-	n.s.
	All species	13.29	0.0	-	n.s.	14.4	0.51 *	n.s.	33.5	-0.51 ***	0.0	-	n.s.	11.8	-	-	n.s.
	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	-	30.7	-	n.s.	3.8	-	-	n.s.
Productivity	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	-	2.1	-	n.s.	22.9	-	-	n.s.	
	Monocotyledons (15%)	7.12	26.1	-0.95 ***	2.1	-	n.s.	8.4	-	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 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. 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.

1 **Figure captions**

2 Figure 1. The effects of the explanatory variables on species richness, the Simpson index,
3 and productivity. Solid and open bars indicate independent and joint explained variance,
4 respectively. Asterisks indicate the significance of independently explained variance: ***
5 $P < 0.001$, ** $P < 0.01$, * $P < 0.05$.

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

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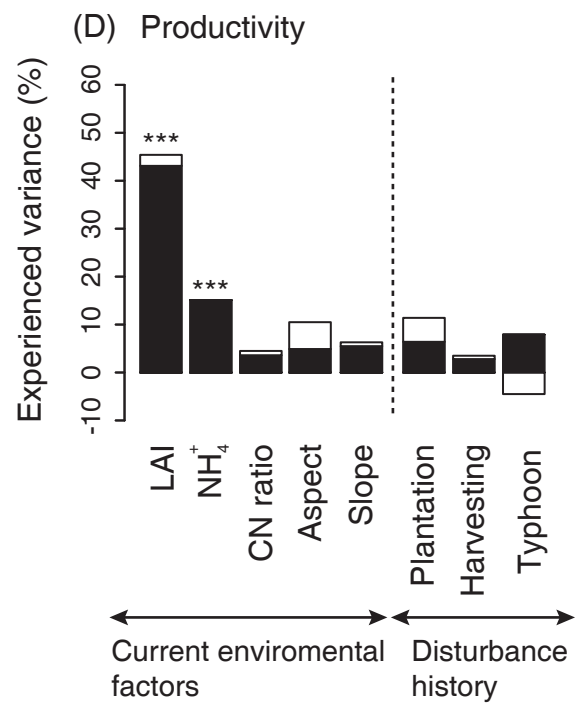
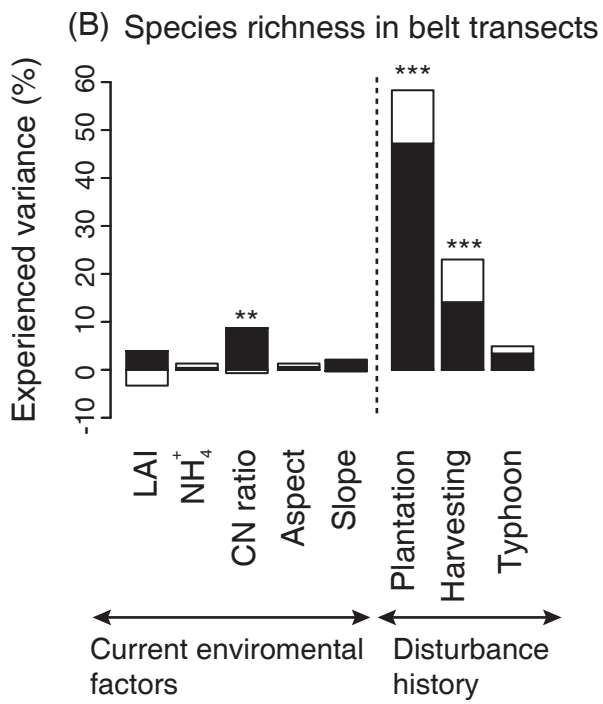
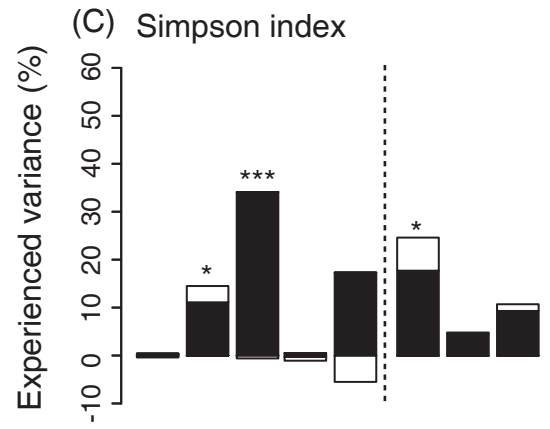
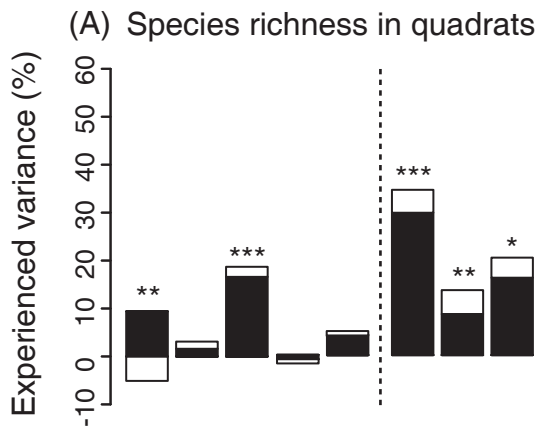
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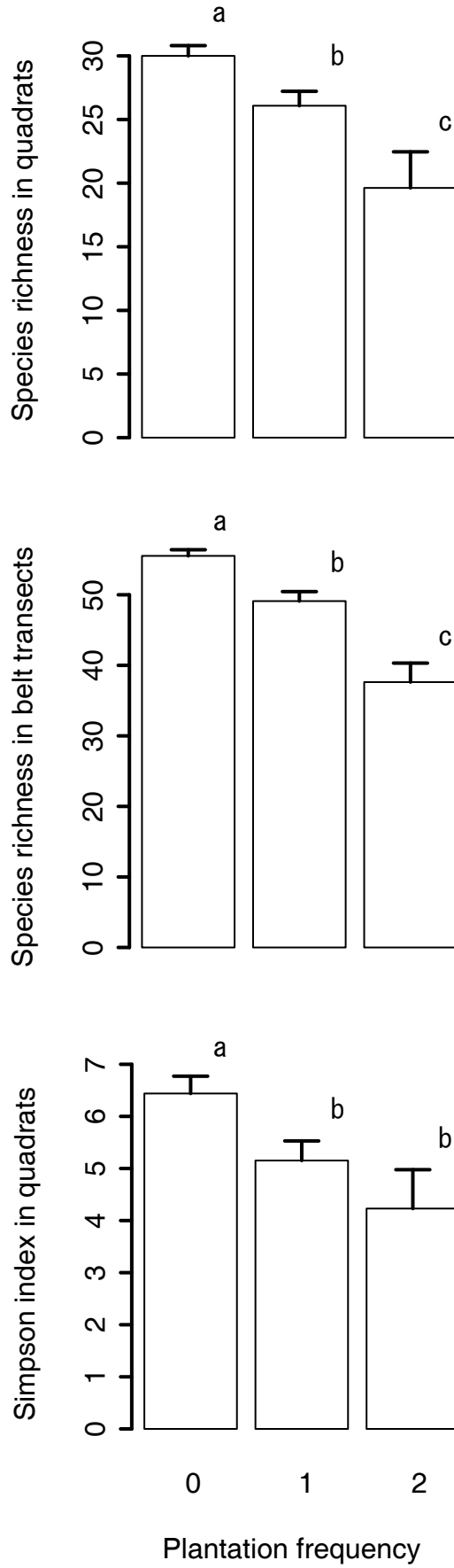
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Appendix A. Explained ratio and coefficients of variables of the presence/absence for species with significant full model ($p < 0.05$).

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			
<i>Aralia cordata</i>	Fo	-42.88	25.5	-	n.s.	3.0	-	n.s.	0.5	-	n.s.	-	-	n.s.	9.0	-	-	-	n.s.
<i>Agrimonia japonica</i>	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	*
<i>Angelica geniflexa</i>	Fo	-4.56	0.5	-	n.s.	10.5	-	n.s.	8.8	-	n.s.	-	-	n.s.	12.7	-	-	-	n.s.
<i>Arisaema pensinulae</i>	Fo	-2.14	0.5	-	n.s.	21.4	0.75	***	2.0	-	n.s.	28.3	0.21	***	3.5	-	-	-	n.s.
<i>Cardamine leucantha</i>	Fo	-5.77	0.1	-	n.s.	11.6	-5.41	***	0.3	-	n.s.	45.9	1.04	***	12.1	-	-	-	n.s.
<i>Chamaele decumbens</i>	Fo	6.95	1.1	-	n.s.	3.4	-	n.s.	5.3	-	n.s.	-	-	n.s.	8.6	-	-	-	n.s.
<i>Chloranthus serratus</i>	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	**
<i>Codonopsis lanceolata</i>	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	*
<i>Eupatorium chinense</i> var. <i>simplicifolium</i>	Fo	10.90	20.0	-2.80	***	2.4	-	n.s.	12.9	-	n.s.	-	-	n.s.	23.4	-	-	-	n.s.
<i>Galium japonicum</i>	Fo	0.43	5.4	-	n.s.	1.0	-	n.s.	0.1	-	n.s.	-	-	n.s.	7.3	-	-	-	n.s.
<i>Galium paradoxum</i>	Fo	-3.13	0.0	-	n.s.	0.1	-	n.s.	0.1	-	n.s.	15.8	0.53	***	7.0	-	-	-	n.s.
<i>Galium trifloriforme</i>	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	**
<i>Hypericum erectum</i>	Fo	-1.39	10.3	-	n.s.	4.6	-	n.s.	25.0	-0.65	**	-	-	n.s.	4.4	-	-	-	n.s.
<i>Lilium cordatum</i> var. <i>glehnii</i>	Fo	3.86	0.8	-	n.s.	0.2	-	n.s.	0.1	-	n.s.	-	-	n.s.	3.2	-	-	-	n.s.
<i>Maianthemum dilatatum</i>	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	*
<i>Moehringia lateriflora</i>	Fo	2.58	14.2	-0.99	**	1.7	-	n.s.	6.3	-	n.s.	36.7	0.27	***	14.8	-	-	-	n.s.
<i>Oxalis acetosella</i>	Fo	-22.46	7.3	-	n.s.	18.0	-1.76	*	2.2	-	n.s.	-	-	n.s.	13.4	-	-	-	n.s.
<i>Patrinia villosa</i>	Fo	5.41	4.3	-	n.s.	1.1	-	n.s.	16.4	-	n.s.	18.9	0.19	*	15.9	-	-	-	n.s.
<i>Peracarpa carnos</i> var. <i>circaeoides</i>	Fo	2.74	0.5	-	n.s.	12.2	-0.91	**	0.1	-	n.s.	21.1	-0.24	**	15.0	-	-	-	n.s.
<i>Phryma leptostachya</i> var. <i>asiatica</i>	Fo	47.08	14.2	4.01	***	3.2	-	n.s.	1.4	-1.81	**	-	-	n.s.	5.2	-	-	-	n.s.
<i>Potentilla freyniana</i>	Fo	-24.82	7.9	-	n.s.	3.2	-	n.s.	2.7	-	n.s.	24.4	0.75	*	24.0	-	-	-	n.s.
<i>Sanicula chinensis</i>	Fo	4.62	0.9	-	n.s.	1.0	-	n.s.	0.5	-	n.s.	-	-	n.s.	6.5	-	-	-	n.s.
<i>Scutellaria indica</i>	Fo	-2.52	0.5	-	n.s.	0.0	-	n.s.	1.7	-	n.s.	32.3	0.22	***	4.0	-	-	-	n.s.
<i>Senecio cannabifolius</i>	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	***
<i>Smilacina japonica</i>	Fo	2.50	8.3	-	n.s.	7.2	-	n.s.	2.4	-	n.s.	-	-	n.s.	6.7	-	-	-	n.s.
<i>Solidago virga-aurea</i> var. <i>asiatica</i>	Fo	8.89	15.7	-1.35	*	2.9	-	n.s.	16.9	-0.25	*	-	-	n.s.	31.4	-	-	-	n.s.
<i>Teucrium japonicum</i>	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	***
<i>Torilis japonica</i>	Fo	2.68	10.3	-	n.s.	1.2	-	n.s.	0.1	-	n.s.	7.5	-0.24	**	15.7	-	-	-	n.s.
<i>Tripterospermum japonicum</i>	Fo	-1.10	8.2	-	n.s.	8.7	-	n.s.	2.8	-	n.s.	27.0	-0.24	***	20.0	-	-	-	n.s.
<i>Turritis glabra</i>	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	***
<i>Acer japonicum</i>	T	-13.05	38.6	2.07	***	4.3	-	n.s.	1.2	-	n.s.	-	-	n.s.	21.0	-	-	-	n.s.
<i>Acer palmatum</i> var. <i>matsumurae</i>	T	9.74	4.0	-	n.s.	10.8	-	n.s.	3.9	-	n.s.	-	-	n.s.	5.0	-	-	-	n.s.
<i>Aralia elata</i>	T	41.03	23.7	-7.85	***	10.0	-5.90	*	5.1	-	n.s.	-	-	n.s.	2.6	-	-	-	n.s.
<i>Euonymus alatus</i>	T	4.79	13.4	-1.81	***	4.7	1.24	**	3.7	-	n.s.	7.9	0.22	**	1.1	-	-	-	n.s.
<i>Euonymus oxyphyllus</i>	T	1.05	0.7	-	n.s.	11.6	0.57	**	0.3	-	n.s.	-	-	n.s.	3.6	-	-	-	n.s.
<i>Fraxinus lamuginosa</i>	T	-1.06	11.1	-	n.s.	0.0	-	n.s.	5.0	-	n.s.	-	-	n.s.	18.1	-	-	-	n.s.
<i>Magnolia kobus</i> var. <i>borealis</i>	T	3.49	2.8	-	n.s.	0.9	-	n.s.	5.8	-	n.s.	-	-	n.s.	17.7	-	-	-	n.s.
<i>Morus bombycis</i>	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	*
<i>Pinus koraiensis</i>	T	-9.08	32.7	1.66	***	1.3	-	n.s.	0.4	-	n.s.	-	-	n.s.	2.9	-	-	-	n.s.
<i>Prunus sargentii</i>	T	4.79	0.5	-	n.s.	0.3	-	n.s.	0.9	-	n.s.	-	-	n.s.	24.6	-	-	-	n.s.
<i>Prunus ssiiori</i>	T	2.67	2.9	-	n.s.	4.1	-0.97	*	1.9	-	n.s.	-	-	n.s.	13.6	-	-	-	n.s.
<i>Quercus mongolica</i> var. <i>grosseserrata</i>	T	9.56	2.7	-	n.s.	0.4	-	n.s.	35.0	-0.46	***	-	-	n.s.	10.8	-	-	-	n.s.
<i>Rubus crataegifolius</i>	T	-12.42	2.7	-	n.s.	3.2	-	n.s.	16.5	-0.77	*	-	-	n.s.	14.8	-	-	-	n.s.
<i>Rubus idaeus</i> var. <i>aculeatissimus</i>	T	7.52	32.4	-4.07	***	6.0	-	n.s.	3.8	-	n.s.	-	-	n.s.	5.9	-	-	-	n.s.
<i>Sorbus alnifolia</i>	T	4.54	6.9	-	n.s.	11.6	-0.65	*	6.7	-	n.s.	-	-	n.s.	18.9	-	-	-	n.s.
<i>Sorbus commixta</i>	T	-17.64	4.4	-	n.s.	9.3	-	n.s.	2.5	-	n.s.	-	-	n.s.	15.8	-	-	-	n.s.
<i>Spiraea salicifolia</i>	T	0.45	25.1	-1.08	***	0.2	-	n.s.	0.5	-	n.s.	18.8	0.17	**	26.1	-	-	-	n.s.
<i>Syringa reticulata</i>	T	-5.62	4.5	-	n.s.	7.6	-	n.s.	1.8	-	n.s.	24.0	0.20	***	15.2	-	-	-	n.s.
<i>Taxus cuspidata</i>	T	12.78	3.4	-	n.s.	0.5	-	n.s.	12.0	-	n.s.	-	-	n.s.	7.5	-	-	-	n.s.
<i>Athyrium coniliti</i>	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	**
<i>Dryopteris austriaca</i>	Fe	-3.87	10.2	-	n.s.	0.4	-	n.s.	7.1	-	n.s.	44.6	-0.34	***	13.7	-	-	-	n.s.
<i>Dryopteris monticola</i>	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	**
<i>Osmundastrum cinnamomum</i> var. <i>fokiense</i>	Fe	13.27	23.4	-1.09	*	28.1	-1.35	***	3.8	-	n.s.	-	-	n.s.	17.1	-	-	-	n.s.
<i>Agropyron yezoense</i>	M	4.81	2.3	-	n.s.	0.0	-	n.s.	0.7	-	n.s.	11.4	-0.28	**	4.9	-	-	-	n.s.
<i>Diarrhena japonica</i>	M	13.87	1.3	-	n.s.	7.7	-	n.s.	14.6	-0.57	***	-	-	n.s.	3.4	-	-	-	n.s.
<i>Festuca parvigluma</i>	M	-6.90	3.5	-	n.s.	0.2	-	n.s.	1.2	-	n.s.	-	-	n.s.	19.9	-	-	-	n.s.
<i>Muhlenbergia japonica</i>	M	-1.00	4.6	-	n.s.	0.8	-	n.s.	1.5	-	n.s.	17.8	0.25	**	12.5	-	-	-	n.s.
<i>Hydrangera petiolaris</i>	V	-1.79	4.7	-	n.s.	5.1	-	n.s.	5.7	-	n.s.	-	-	n.s.	22.9	-	-	-	n.s.
<i>Schizophragma hydrangeoides</i>	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 Explained (%)	Harvesting			Typhoon						P	P		
	Coefficient		P	Explained (%)	Coefficient		P	Coefficient					
	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	<i>P</i>	Explained (%)	Coefficient	<i>P</i>	Explained (%)	Coefficient	<i>P</i>	Explained (%)	Coefficient	<i>P</i>	Explained (%)	Coefficient	<i>P</i>			
														W S E					
<i>Actaea asiatica</i>	Fo	-1.54	4.4	-	n.s.	0.7	-	n.s.	8.3	-0.14	**	0.2	-	n.s.	12.4	-	-	-	n.s.
<i>Cacalia hastata</i> var. <i>orientalis</i>	Fo	1.24	29.3	-0.87	***	0.3	-	n.s.	35.1	-0.20	***	3.2	-	n.s.	16.5	-	-	-	n.s.
<i>Cardamine leucantha</i>	Fo	-2.16	0.5	-	n.s.	1.5	-	n.s.	12.7	-0.15	***	24.6	0.06	***	4.8	-	-	-	n.s.
<i>Chamaele decumbens</i>	Fo	0.88	1.0	-	n.s.	4.9	-	n.s.	8.3	-0.13	*	0.4	-	n.s.	3.4	-	-	-	n.s.
<i>Chloranthus serratus</i>	Fo	-0.02	6.5	-	n.s.	16.3	0.60	*	6.9	-	n.s.	17.2	-	n.s.	13.0	-	-	-	n.s.
<i>Cirsium kamschatkianum</i>	Fo	-0.82	2.7	-	n.s.	0.4	-	n.s.	16.3	-0.15	**	20.4	-	n.s.	27.8	-	-	-	n.s.
<i>Galium trifloriforme</i> var. <i>nipponicum</i>	Fo	-3.86	0.0	-	n.s.	0.3	-	n.s.	10.5	-	n.s.	0.3	-	n.s.	9.3	-	-	-	n.s.
<i>Lactuca raddeana</i> var. <i>elata</i>	Fo	-2.68	0.5	-	n.s.	12.9	0.31	*	31.3	-0.09	**	4.2	-	n.s.	13.2	-	-	-	n.s.
<i>Maianthemum bifolium</i>	Fo	-3.40	0.2	-	n.s.	12.0	-	n.s.	0.8	-	n.s.	5.1	-	n.s.	2.2	-	-	-	n.s.
<i>Moehringia lateriflora</i>	Fo	-2.09	8.8	-0.31	*	0.1	-	n.s.	18.7	-0.09	***	21.5	0.04	**	26.1	-	-	-	n.s.
<i>Patrinia villosa</i>	Fo	-4.88	10.5	-0.35	*	9.5	0.32	**	0.0	-	n.s.	55.4	0.12	***	11.9	-	-	-	n.s.
<i>Phryma leptostachya</i> var. <i>asiatica</i>	Fo	2.11	1.1	-	n.s.	5.4	-	n.s.	1.0	-	n.s.	0.2	-	n.s.	1.5	-	-	-	n.s.
<i>Sanicula chinensis</i>	Fo	-1.00	0.8	-	n.s.	5.4	-	n.s.	0.1	-	n.s.	0.5	-	n.s.	3.4	-	-	-	n.s.
<i>Scutellaria indica</i>	Fo	-1.54	2.7	-	n.s.	0.0	-	n.s.	3.9	-	n.s.	16.6	0.07	*	4.1	-	-	-	n.s.
<i>Smilacina japonica</i>	Fo	-2.49	1.6	-	n.s.	9.3	-	n.s.	0.6	-	n.s.	2.2	-	n.s.	12.5	-	-	-	n.s.
<i>Teucrium viscidum</i> var. <i>miquelianum</i>	Fo	0.53	1.8	-	n.s.	2.4	-	n.s.	11.4	-0.19	**	11.5	-	n.s.	7.6	-	-	-	n.s.
<i>Trillium smallii</i>	Fo	3.08	0.2	-	n.s.	3.4	-	n.s.	7.7	-	n.s.	1.1	-	n.s.	2.4	-	-	-	n.s.
<i>Tripterspermum japonicum</i>	Fo	-3.61	0.3	-	n.s.	2.9	-	n.s.	0.1	-	n.s.	6.2	-	n.s.	25.9	-	-	-	n.s.
<i>Tulotia ussuriensis</i>	Fo	5.36	2.4	-	n.s.	0.2	-	n.s.	14.9	-0.31	***	2.8	-0.17	*	2.0	-	-	-	n.s.
<i>Acer palmatum</i> var. <i>matsumurae</i>	T	-0.22	0.2	-	n.s.	1.4	-	n.s.	2.4	-	n.s.	7.0	-	n.s.	1.3	-	-	-	n.s.
<i>Euonymus oxophyllus</i>	T	-2.36	0.0	-	n.s.	4.7	-	n.s.	0.3	-	n.s.	3.3	-	n.s.	12.7	-	-	-	n.s.
<i>Fraxinus lanuginosa</i>	T	-0.94	7.6	-	n.s.	1.9	-	n.s.	0.5	-	n.s.	17.0	-0.19	***	18.0	-	-	-	n.s.
<i>Fraxinus mandshurica</i> var. <i>japonica</i>	T	-0.91	1.0	-	n.s.	1.0	-	n.s.	48.7	-0.20	***	3.6	-	n.s.	5.3	-	-	-	n.s.
<i>Kalopanax pictum</i>	T	-3.37	21.1	-	n.s.	4.7	-	n.s.	1.3	-	n.s.	17.3	0.04	*	5.0	-	-	-	n.s.
<i>Morus australis</i>	T	-2.27	35.8	-0.58	***	0.5	-	n.s.	0.3	-	n.s.	1.7	-	n.s.	9.2	-	-	-	n.s.
<i>Quercus mongolica</i> var. <i>grosseserrata</i>	T	0.11	2.1	-	n.s.	0.1	-	n.s.	0.9	-	n.s.	22.8	0.14	**	4.9	-	-	-	n.s.
<i>Rubus idaeus</i> var. <i>aculeatissimus</i>	T	-1.39	38.8	-0.80	***	1.5	-	n.s.	0.1	-	n.s.	0.0	-	n.s.	1.2	-	-	-	n.s.
<i>Spiraea salicifolia</i>	T	0.86	37.8	-0.90	***	1.5	-	n.s.	9.9	-0.14	*	13.6	0.11	*	18.7	-	-	-	n.s.
<i>Dryopteris expansa</i>	Fe	-3.61	19.0	0.72	*	3.2	-	n.s.	0.3	-	n.s.	43.9	-0.15	***	7.0	-	-	-	n.s.
<i>Lastrea thelypteris</i>	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	***
<i>Onoclea sensibilis</i> var. <i>interrupta</i>	Fe	-2.89	0.5	-	n.s.	6.4	-	n.s.	14.8	-	n.s.	3.2	-	n.s.	11.0	-	-	-	n.s.
<i>Calamagrostis hakonensis</i>	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	***
<i>Carex leucochlora</i>	M	0.11	6.3	-0.81	*	10.9	-	n.s.	21.1	-0.15	**	3.0	-	n.s.	24.6	-	-	-	n.s.
<i>Diarrhena japonica</i>	M	5.70	5.5	-	n.s.	8.1	-	n.s.	32.1	-0.41	***	4.8	-	n.s.	2.0	-	-	-	n.s.
<i>Festuca parvigluma</i>	M	-3.14	19.9	-0.49	**	2.1	-	n.s.	1.9	-	n.s.	12.9	-	n.s.	19.1	-	-	-	n.s.
<i>Celastrus orbiculatus</i>	V	-2.95	3.3	-	n.s.	7.3	-	n.s.	9.9	-	n.s.	26.7	0.12	***	17.0	-	-	-	n.s.
<i>Hydrangera petiolaris</i>	V	-0.64	2.2	-	n.s.	1.1	-	n.s.	3.4	-	n.s.	40.6	0.03	***	2.9	-	-	-	n.s.
<i>Rhus ambigua</i>	V	5.73	0.3	-	n.s.	0.3	-	n.s.	19.0	-0.30	***	16.2	0.01	*	7.9	-	-	-	n.s.
<i>Schisandra chinensis</i>	V	2.92	22.4	-1.13	***	7.0	0.82	**	7.2	-	n.s.	3.0	-	n.s.	15.8	-	-	-	n.s.
<i>Schizophragma hydrangeoides</i>	V	-7.26	6.3	-	n.s.	5.9	-	n.s.	0.1	-	n.s.	8.3	-	n.s.	14.0	-	-	-	n.s.
<i>Vitis coignetiae</i>	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 category's 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					F-value	Full model P-value	
	Explained (%)	Coefficient		P	Explained (%)	Coefficient	P	Explained (%)	Coefficient				
		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