

HOKKAIDO UNIVERSITY

Title	Differences in canopy and understorey diversities after the eruptions of Mount Usu, northern Japan-Impacts of early forest management
Author(s)	Végh, Lea; Tsuyuzaki, Shiro
Citation	Forest Ecology and Management, 510, 120106 https://doi.org/10.1016/j.foreco.2022.120106
Issue Date	2022-04-15
Doc URL	http://hdl.handle.net/2115/91651
Rights	© 2022. This manuscript version is made available under the CC-BY-NC-ND 4.0 license http://creativecommons.org/licenses/by-nc-nd/4.0/
Rights(URL)	http://creativecommons.org/licenses/by-nc-nd/4.0/
Туре	article (author version)
Additional Information	There are other files related to this item in HUSCAP. Check the above URL.
File Information	Library_Species diversity after the eruptions of Mount Usu.pdf



© 2022. This manuscript version is made available under the CC-BY-NC-ND 4.0 license <u>https://creativecommons.org/licenses/by-nc-nd/4.0/</u>

For the published version, please visit: <u>https://doi.org/10.1016/j.foreco.2022.120106</u>

Differences in canopy and understorey diversities after the eruptions of Mount Usu, northern Japan — impacts of early forest management

Lea Végh¹ ORCID iD: https://orcid.org/0000-0001-7948-480X Shiro Tsuyuzaki¹ ORCID iD: https://orcid.org/0000-0003-3010-8699 ¹Graduate School of Environmental Science, Hokkaido University, Japan

Correspondence

Lea Végh, Graduate School of Global Food Resources, Hokkaido University, Sapporo, Japan, 060-8589

Email: vegh@cen.agr.hokudai.ac.jp

1 Abstract

2 Evaluating the effects of management on successional trajectories, plant composition, and 3 diversity has been difficult due to the scarcity of long-term studies. This study examined the 4 composition and diversity of species in natural and artificially regenerated forests at two 5 eruption sites of Mount Usu, northern Japan, during 2015–2019, to compare the effects of 6 active and passive management. The two sites are Yosomi, damaged by the 1910 eruptions, 7 and the summit, damaged by the 1977–78 eruptions. Various natural and artificial forests 8 developed at both sites, whose species composition was analyzed by non-metric 9 multidimensional scaling to measure similarity between the forest types, and whose diversity 10 was compared by the true diversity index, showing the effective number of species, from 11 order 0 (presence-absence) to order 2 (weighted species) for two layers: the canopy (woody 12 species with DBH larger than 3 cm) and understorey (less than 2 m high plants). Canopy 13 diversity was measured by stem density in five $10 \text{ m} \times 10 \text{ m}$ plots in each forest type, and 14 understory diversity was measured by shoot density in four $1 \text{ m} \times 1 \text{ m}$ guadrats in each plot. 15 The canopy and understorey species compositions were distinct between the forest types, but 16 the canopy was more affected by management than the understorey, indicating that early 17 forest management had long-term effects on species composition. Species composition of the 18 plantations resembled those of the natural forests when the plantations had patchy spatial 19 structure. The naturally regenerated forests showed the highest diversities at both eruption 20 sites, while the plantations displayed low diversities, except in one case, when the plantation 21 showed heterogeneous forest structure. The plantations changed their species composition 22 slowly and did not transform into natural forests. In conclusion, we suggest using a patchy 23 plantation design with some space between patches instead of dense planting, to create 24 resilient, diverse, and native forests after disturbances.

Keywords: succession, plant diversity, management, species composition, volcano, true diversity

27 **1. Introduction**

28 When disturbances destroy vegetation, management agencies need to decide between passive 29 and active restoration. Early studies of plant succession promoted direct development from 30 pioneer communities toward the climax community (Clements, 1916), suggesting that no 31 intervention is needed. Although pioneer species often colonize in a deterministic manner 32 (Efford et al., 2014; Marler and del Moral, 2013; Tsuyuzaki, 2019), successional trajectories 33 are modified by subsequent disturbances (del Moral et al., 1995; Karadimou et al., 2018), 34 biotic legacy (Talbot et al., 2010), and stochastic events (del Moral, 2009; Lichter, 2000), 35 which change community composition and structure. Therefore, following the outcomes of 36 active and passive restoration is important to understand the mechanism of succession.

Passive restoration is slow and often leads to undesirable communities; to restore high quality habitats, active management (e.g., seeding, planting, and mowing) is often required to accelerate revegetation and to influence the outcome (Perrow and Davy, 2002). However, the resultant communities may differ from the former vegetation (Mansourian et al., 2005), and natural forests often show higher species richness and diversity than managed forests (Prach and Walker, 2011).

43 Patterns of succession are frequently studied by substituting space for time, called 44 successional chronosequence, where a successional sere is constructed by observing plant 45 communities at various locations arranged by recovery time since the disturbance (Cutler et 46 al., 2008; Irl et al., 2019; Sutomo et al., 2011). These locations should be matched 47 geographically and by their management histories to minimize differences in conditions other 48 than recovery time (White and Walker, 1997), so volcanic eruptions, affecting different parts 49 of the volcano, create ideal conditions for chronosequence studies. Volcanic eruptions can 50 completely destroy the vegetation and thus provide suitable sites for monitoring primary

51 succession after the eruptions. However, only a few studies have observed successional 52 processes on a timescale over 20 years after eruptions (e.g., Fridriksson 1982; Karadimou et 53 al. 2018). Mount Usu, an active volcano in northern Japan (42°32'N, 140°50'E, 733 m 54 elevation), erupted at distinct locations in 1910 and 1977–1978: at a foothill called Yosomi 55 and at the summit, respectively. These two sites were covered with forests prior to the 56 eruptions that denuded them, and by now they regained their forest cover.

57 Due to active (plantations) and passive (natural regeneration) management practices at 58 both sites, a mosaic of different forest types developed on the mountain. This mosaic of 59 forests provided an opportunity to compare the canopy and understorey species richness and 60 diversity, and also species composition between Yosomi and the summit, close to 40 and 110 61 years after the eruptions.

We expected that the effect of active management (plantations) will lessen with time, and species composition will become closer to those of naturally recovered forests. Therefore, the first hypothesis was that at Yosomi, the older eruption site, active management displayed less impact than at the summit. The second hypothesis was that passive management (naturally regenerated forests) resulted in more diverse vegetation than active management. Following these two hypotheses, we expected that the plantations at the summit had the lowest diversity indices and similarity to naturally regenerated forests.

69

70 **2. Methods**

71 2.1 Location

Mount Usu is a basalt-andesite stratovolcano in Hokkaido, which erupts every 30 to 50 years
at different locations on the mountain (Katsui et al. 1981). The mountain belongs to the
temperate zone, with an average annual precipitation of 891 mm and annual mean

temperature of 8°C during 1976–2018 (Date Meteorological Station at 5 km from Mount Usu;
JMA 2019). The climax vegetation is deciduous oak or mixed broad-leaved forests in the
lowlands of this region, including Mount Usu (Okitsu, 2003).

78 The 1910 eruption site was covered with well-developed forest prior to the eruptions 79 (developed after the eruptions of 1822 and 1853; Kadomura, Okada, and Araya 1988) which 80 was completely destroyed due to the tephra fall (~ 2 meters thick) and topographical changes 81 which caused part of the area to slid into a nearby lake and the other part to raise and form the 82 foothill called Yosomi. The site was not damaged by later eruptions, and the area is covered 83 with broad-leaved forests (Populus suaveolens, Acer pictum, and Kalopanax septemlobus), a 84 young (~50 yrs) plantation of Abies sachalinensis and an old (~70 yrs) plantation of A. 85 sachalinensis in which broadleaved trees are mixed in. The area of the plantations had not 86 shown positive recovery prior to the intervention, as their surface had no vegetation or was 87 covered by dwarf bamboo (Forestry Agency, pers. comm.). The 1910 eruptions site is referred

to as Yosomi hereafter.

In contrast to Yosomi, the eruptions, damages, and subsequent revegetation processes are well studied at the 1977–1978 eruptions site. The eruptions occurred at the summit, which was covered with seeded pastures and broad-leaved forests of *P. suaveolens, Betula*

92 platyphylla var. japonica, Ulmus davidiana, and A. pictum ssp. mono prior to the eruptions

93 (Tsuyuzaki, 1987). The tephra explosions destroyed the summit, and due to the thick volcanic

94 deposits, for several years the vegetation recovered mostly by vegetative reproduction which

95 spread from the edges of the site. The dominant species were *Fallopia sachalinensis*,

96 Petasites japonicus, and Populus suaveolens (Kadomura et al., 1988; Tsuyuzaki, 1989).

Because the eruption destroyed an area of 291 ha, the centre still lacks vegetation cover (Végh
and Tsuyuzaki, 2021).

99 Revegetation occurred faster on the caldera rim than in the crater basin, because rain 100 and snow washed away the volcanic deposits from the caldera rim and plant propagules 101 buried in the former topsoil became exposed (Tsuyuzaki and Haruki, 1996). Parts of the 102 summit area were subject to aerial seeding and planting for erosion control (Kadomura et al., 103 1988). Currently, the caldera rim is covered by a mixture of natural broadleaved forest (P. 104 suaveolens, A. pictum), broadleaved forest plantations (B. platyphylla, Sorbus commixta, Salix 105 spp., Alnus hirsuta) and conifer plantations (Picea glehnii, ~ 25 yrs). Large areas of the crater 106 basin are still in the early stages of succession and are covered by bare ground or grassland, while a smaller area is covered by an open P. suaveolens forest. The 1977-78 eruptions site is 107 108 called the summit henceforward.

109

2.2 Field survey

110 The damage from the 1910 and 1977–1978 eruptions was identified based on satellite and 111 aerial images taken during 1972–2015 and supplemented by previous studies (Kadomura et 112 al., 1988). In each eruption site, image analyses and field observations found several forest 113 types. We called these forest types at Yosomi as Broadleaf, Abies, and Mixed forests (Abies 114 was the young and Mixed was the old plantation), and at the summit as Closed-broadleaf, 115 Open-broadleaf, Sorbus-Alnus, and Picea forests (Sorbus-Alnus was the broad-leaved and 116 Picea was the conifer plantation, Figure 1). The broadleaved forests, apart from the Sorbus-117 Alnus plantation, regenerated after the eruptions naturally. The Closed- and Open-118 broadleaved forests were classified as separate forests because the Open-broadleaved forest 119 was separated by a ridge from the other three forest types with an aerial distance of ~ 800 m, 120 and also because its light intensity was higher than that of the Closed-broadleaf forest (yearly 121 average 11.26 klux and 7.29 klux, respectively). For the survey, multiple random locations 122 were generated in each forest type using stratified random two-stage sampling after excluding

123 inaccessible steep areas. Randomization was done using the ArcGIS random point generator 124 function observing a minimum distance of 5 m between the points and from the given forest 125 type edge. For every forest type, five plots were established from these randomly selected

126 points and monitored from 2015 to 2019.



127

Figure 1. The forest types and plots examined during the study. The first three forests in thelegend box are at Yosomi (old plots), and the last four are at the summit (young plots).

130 To monitor canopy, defined as woody species with a DBH > 3 cm, the five plots in

- each forest type measured 5 m \times 5 m in 2015, and were enlarged to 10 m \times 10 m for five
- 132 forest types in 2016 and for the remaining two forest types, Open-broadleaf and Picea forests,
- 133 in 2019. A typhoon destroyed four Mixed forest plots in 2016 by breaking and uprooting
- 134 trees, so both the canopy and understorey vegetation were damaged. Later, the area was

cleared, causing the destruction of any surviving vegetation. We excluded the effects of the
typhoon in the canopy survey by using pre-typhoon census data from 2016 in all forest types
(reconstructed in the Open-broadleaf and Picea forest).

138 In 2015, two randomly selected 1 m \times 1 m quadrats were used for the understorey 139 survey (vegetation less than 2 m in height) in every plot, and in the subsequent years the 140 number of quadrats was increased to four. Cover percentage and shoot density were recorded 141 for every plant rooted inside the quadrat; the latter was either counted or estimated in an 142 interval scale if counting was not possible (categories based on shoot density: 0-5, 5-10, 10-143 25, 25–50, 50–100, 100 <). The shoot density and the midpoint of the interval categories 144 correlated well (Pearson's r = 0.93, p < 0.001), so the missing density values were 145 supplemented by the midpoints of the intervals. Cover was recorded at 5% intervals. 146 Unidentified species were treated at genus or family level and included in the diversity 147 analysis.

Plots and quadrats were surveyed once a year in August or September, except in 2016 and 2017, when understorey vegetation was surveyed an additional time in June or July. This repeated-sampling ensured that the early autumn survey was representative of species richness, diversity, and composition year-round.

In four plots of the Mixed forests, the quadrats were not monitored from 2017 due totyphoon damage.

154 2.3 Species diversity and composition measurements

Vegetation recovery is measured via biodiversity by considering only the number of species
present (species richness) and/or by considering the abundance of species (species diversity)
(Magurran and McGill, 2011). Species richness usually becomes high soon after disturbances
(Do et al., 2019; Rozendaal et al., 2019), yet it does not necessarily signal recovery, as few

species may dominate the communities. In contrast, species diversity incorporates evenness
and more information about vegetation recovery, especially when coupled with species
composition analysis. We combined all three approaches.

162 The richness and diversity of plant species were measured at two layers: canopy and 163 understorey. Canopy measurements were based on the stem number of woody species with a 164 DBH > 3 cm and understorey measurements were calculated from the number of shoots of 165 plants shorter than 2 m.

166 Species richness and diversity were evaluated by the true diversity index (Jurasinski 167 and Koch, 2011; Moreno and Rodríguez, 2011; Tuomisto, 2011), also known as Hill numbers 168 (Hill, 1973). We selected true diversity because it measures the effective species number, 169 which makes direct comparison possible between sites (Jost, 2006). The α -, β - (multiplicative) 170 and γ - true diversity indices were calculated for order 0 (N₀), order 1 (N₁), and order 2 (N₂) 171 (Jost, 2006) for each forest by annually monitoring their plots. No is based on presence-172 absence and corresponds to species richness, while $N_{1,2}$ take abundance into account: N_1 173 incorporates the relative abundance of all species equally, whereas N_2 emphasizes common 174 species, giving more weight to their relative abundance (less influence of rare species).

175 To describe dominant species, the understorey species were ranked by shoot density 176 and cover percentage: the scores of each species were added from the four quadrats to 177 calculate plot cover and density. Because a species theoretically could be observed in any of 178 the five plots in a forest type and in any of the five observation years, the average species 179 score was calculated by summing annual scores and dividing the sum by 25 (five plots \times five 180 years) — except for the Mixed forest, where the sum was divided by 13 (5 plots in 2015-181 2016, and 1 plot in 2017–2019). The dominant canopy species were identified by the sum of 182 stems from the five plots in 2016.

183 The differences in species composition of the forests were measured by the Bray-184 Curtis dissimilarity index (Bray and Curtis, 1957).

185

2.4 Statistical analysis

The vegetation surveys in autumn and summer were compared using linear models (LM) and Pearson's correlation coefficient (*r*). Species composition of the plots were compared by nonmetric multidimensional scaling (nMDS) using the vegan package in R (Oksanen et al. 2019). ANOSIM was used to determine the uniqueness of forest groupings with ten thousand permutations.

191 We used generalized linear models (GLM, log-normal distribution) and general linear 192 hypotheses comparison (GLH, Hothorn, Bretz, and Westfall 2008) to compare the canopy 193 diversity indices, where the explanatory variable was the forest type, and the dependent 194 variables were the α -, β -, and γ -diversity indices at the forest level. The understorey α -, β -, 195 and γ -diversities were compared by generalized linear mixed-effects models (GLMM, log-196 normal distribution), where the fixed effects were forest type and order of diversity, and the 197 random factor was the year of survey. Data from 2015 were excluded from the analysis of the 198 understorey diversity due to the smaller sample area in that year. Spatial autocorrelation was 199 examined by Moran's I (Moran, 1950), and the effect of elevation on the different order of 200 diversities was tested with LM. All analyses were conducted in R programming environment 201 (Hlavac, 2018; Pedersen, 2020; R Core Team, 2018; Wickham et al., 2019).

202 **3. Results**

203 3.1 Species composition

The dominant species differed within the forest types depending on whether species wereranked by density or cover (Table 1), but the rankings of all species correlated with each other

206 (Kendall's $\tau = 0.80-0.85$ for all forest types). Therefore, density ranking was used to describe 207 the dominant species.

208 At the summit, the understorey species *Pyrola asarifolia*, *F. sachalinensis*, and

209 Petasites japonicus were observed in three or more forest types. At Yosomi, Rhus ambigua

210 and Sanicula chinensis established in two or more of the forest types. Species common at both

- 211 sites were Asperula odorata and Hydrangea petiolaris. Some species ranked only in certain
- 212 forests: at the summit, S. chinensis and Ranunculus repens were recorded in the Closed-

213 broadleaf forest, Artemisia montana and Trifolium repens in the Open-broadleaf forest,

214 Celastrus orbiculatus and Stellaria media in the Sorbus-Alnus forest, and R. ambigua in the

215 Picea forest. At Yosomi, the dominant understorey species of the Mixed forest were different

216 from those of other forests, with A. sachalinensis and three other species being unique to that

- 217 forest type. In the Broadleaf forest, the uniquely dominant species were Onoclea orientalis
- and A. pictum saplings, while in the Abies plantation they were Hylodesmum podocarpum and
- 219 Phryma leptostachya.

Table 1. Mean scores of dominant understorey species by forest types from 2015–2019. The species are sorted by the decreasing scores of the Closed-broadleaf (summit) and Broadleaf (Yosomi) forests. Density based scores are marked by n and cover based scores are marked by %. Species with the five highest scores are shown.

	Closed-broadleaf		Open-broadleaf		Sorbus-Alnus		Picea	
Summit	n	%	n	%	n	%	n	%
Asperula odorata	71.5	23.2	63.8	23.8	56.2	27.4		
Pyrola asarifolia	25.7	22.4	22.8	16.8			3.3	3.0
Ranunculus repens	21.3	16.8						
Fallopia sachalinensis	15.0	31.6	4.4	16.8			8.5	15.8
Sanicula chinensis	12.8	11.6						
Petasites japonicus	4.2	20.8	4.0	20.0	4.4	20.8	1.7	6.2
Artemisia montana			41.7	49.8				
Celastrus orbiculatus					4.1	10.4		
Geum macrophyllum var. sachalinense					9.4	18.0		
Hydrangea petiolaris					21.6	27.4	2.9	4.0
Onoclea orientalis					6.6	22.6		
Pilea pumila					62.0	23.2		

Rhus ambigua					1.1	3.4
Solidago virgaurea var. asiatica	10.4	23.8			2.7	5.0
Stellaria media			29.8	13.8		
Trifolium repens	18.0	8.8				

	Broadleaf		Mixed		Abies	
Yosomi	n	%	n	%	n	%
Asperula odorata	74.3	24.4	28.9	14.6	69.1	25.2
Rhus ambigua	17.3	31.6	12.0	19.6	19.2	42.8
Sanicula chinensis	16.3	20.8			15.7	18.0
Onoclea orientalis	11.9	28.4				
Disporum sessile	11.5	20.8				
Acer pictum	8.8	25.0				
Abies sachalinensis			21.7	25.8		
Dryopteris crassirhizoma			2.5	30.0		
Hydrangea petiolaris			14.4	23.1		
Hylodesmum podocarpum					9.4	17.4
Phryma leptostachya					13.8	18.6
Schizophragma hydrangoides			11.1	16.5		

224

225 The canopy composition of the forests varied between the naturally regenerated forests 226 and plantations (Table 2). At the summit, Salix ssp. and Betula spp. were common in all 227 forests, and P. suaveolens appeared everywhere except in the Sorbus-Alnus forest. The 228 dominant species of the conifer plantation was Picea glehnii, but Populus suaveolens and 229 Salix spp. immigrated from outside the plantation. The Sorbus-Alnus plantation had many 230 unique species, such as S. commixta and Alnus spp, whereas the natural broadleaved forests 231 were rich in *P. suaveolens* and *A. pictum*. 232 At Yosomi, the common canopy species were Abies sachalinensis, Morus australis, P.

suaveolens, and *Alnus hirsuta*. The Broadleaf canopy composition resembled the natural forests in the area around Mount Usu. The Mixed forest had a higher density of immigrating species than the Abies forest, but also had unique species, such as *H. paniculata* and *Swida controversa*. The dominant species of the broadleaved forests, *Acer* spp. and *K. septemlobus*, 237 did not occur at high density in other forests. In the Abies forest, the planted A. sachalinensis

238 was dominant and compared to it the other species, such as *Magnolia kobus* and *B*.

239 *platyphylla*, had low density.

Table 2. Stem number of dominant trees by forest types. Species with the five highest stem numbers are shown. The total area sampled is 500 m^2 for each forest.

Summit	Closed-broadleaf	Open-broadleaf	Sorbus-Alnus	Picea
Populus suaveolens	51	41		26
Acer pictum subsp. Mono	32	4		
Salix udensis	6	13	20	
Betula maximowicziana	5			
Ulmus davidiana	4			
Alnus hirsuta			19	
Alnus viridis subsp. Maximowiczii			4	
Betula ermanii		3		5
Betula platyphylla		8	16	
Larix kaempferi		2		
Picea glehnii				133
Salix caprea		2		9
Salix gracilistyla		2		
Sorbus commixta			22	
Viburnum opulus var. clavescens				3

Yosomi	Broadleaf	Mixed	Abies
Acer pictum subsp. Mayrii	18		
Kalopanax septemlobus	8		
Morus australis	8	4	
Populus suaveolens	8		2
Acer pictum subsp. Mono	7		
Abies sachalinensis		28	62
Alnus hirsuta		3	3
Betula platyphylla			2
Hydrangea paniculata		11	
Magnolia kobus			2
Swida controversa		4	

243

3.2 Forest and species ordination

244 The nMDS by density distinguished the forest types and showed distinct groups on both 245 understorey (ANOSIM, r = 0.57, p < 0.001) and canopy compositions (r = 0.88, p < 0.001). 246 The summit forests occupied the right half of the multidimensional space along the first axis, 247 while the Yosomi forests occupied the left half (Figure 2a). The understorey composition 248 overlapped within the Yosomi plots, although the Mixed plots remained separated from the 249 other forest plots (characteristic species: e.g., Schizophragma hydrangoides, A. 250 sachalinensis). At the summit, the Picea plots displayed large variations, as plots falling 251 below Picea spp. had low light and little vegetation and plots falling between rows of Picea 252 spp. had high light and moderate vegetation (pers. obs.). The Sorbus-Alnus forest plots also 253 displayed distinct understorey species composition, locating in the upper part of the nMDS 254 space (e.g., Pilea pumila, S. media).

255 The canopy species composition of the forests differed more than the understorey 256 composition and had distinct positions in the nMDS space (Figure 2b). Most canopy plots 257 were closest to their own forest centroid, whereas many understorey plots were closer to other 258 forest centroids. At Yosomi, the canopy composition of the Abies forest separated from those 259 of the others, and the species compositions of the Broadleaf and Mixed forests were close to 260 each other. At the summit, the canopy composition of the Closed- and Open-broadleaf forests 261 overlapped with each other, and the other forest plots formed unique groups on either side of 262 the broadleaved cluster.



263

Figure 2. Forest hulls by non-metric multidimensional scaling based on species composition and common species scores. (a) shows understorey scores by density, and (b) shows canopy scores by stem number. Yosomi forests are indicated by (Y) and summit forests by (S), and lines point to the position of species.

The canopy composition changed little during the five years, not considering the damages from the 2017 typhoon, which mainly affected plantations (Supplementary table S1). However, the nMDS showed that the understorey composition of the forests was altered: the scores of the summit forests displayed leftward movement, and those of the Yosomi forests displayed downward movements in the nMDS space apart from the Broadleaf forest (Figure 3). The relative position of the forest types did not change either within Yosomi or within the summit, but as the summit forests were located on the right side in the nMDS space and the Yosomi forests on the left, the young summit forests' scores moved towards the mature
Yosomi forest communities. The movement was slow, except between 2015 and 2016 at the
summit, when a large shift occurred in the understorey communities. This shift resulted from
the doubling of the understorey sampling area between those years. At Yosomi, no large shift
was observed between 2015 and 2016, suggesting that increasing the surveyed area had less
effect there.



281

Figure 3. Annual changes of forests' scores in the nMDS space by understorey density. The start of the arrow represents 2015 and the arrowhead shows 2019.

284 3.3 Forest diversities

285 The understorey diversities for each forest showed that the γ -diversities differed 286 depending on the order used, but that natural broadleaved forests had high diversity scores 287 (Figure 4). The β -diversities were higher at the summit than at Yosomi (GLMM, t = 5.3, p <288 0.001), with Closed-broadleaf forest having the highest scores for $N_{0,1}$ and Picea forest for N_2 289 (Table 3). N_0 of γ -diversities showed that the Mixed and Picea forests had the lowest scores (t 290 = -5.7 and t = -6.3, GLMM with log-normal distribution, p < 0.001) and the Closed-broadleaf 291 forest had the highest scores (t = 2.5, p < 0.05). As the order increased, the Picea forest 292 showed higher scores and was placed among the most diverse forests (t = 2.8, p < 0.01), while 293 the scores of the other plantations, such as the Sorbus-Alnus forest, remained low (t = -1.1, 294 NS).



295

Figure 4. Understorey diversity in forests evaluated by shoot density. β-diversity of the Mixed
forest after 2017 is 1 because of typhoon damages in four plots. The first three forests are at
Yosomi.

299Table 3. Statistical summary of forest level understorey diversity. Mean is shown with

300 standard deviation in parentheses. Statistical significance was calculated by GLMM models

301 (log-normal distribution) using survey year as random effect and forest type as fixed effect.

302 The first three forests are at Yosomi and letters mark significant difference at p < 0.05. *: p < 0.05.

303 0.05, **: p < 0.01, and ***: p < 0.001.

Order 0		Alpha			Beta		G	amma	
Broadleaf	19.4	(1.5)***	d	2.3	(0.1)***	а	44.5	(2.6)***	ab
Mixed	22.7	(7.0)***	a	1.3	(0.5)***	b	26.2	(3.9)***	c
Abies	20.0	(2.4)	cd	2.4	(0.1)	а	47.5	(5.7)	ab
Closed-broadleaf	20.6	(2.3)***	bc	2.5	(0.1)	а	52.0	(7.5)*	a
Open-broadleaf	22.0	(3.3)***	ab	2.2	(0.2)	а	47.0	(3.7)	ab
Sorbus-Alnus	18.6	(2.0)*	d	2.1	(0.2)	а	40.0	(6.4)	b
Picea	11.0	(0.6)***	e	2.1	(0.1)	а	23.5	(1.0)***	c

Order I									
Broadleaf	8.1	(1.1)***	b	1.5	(0.1)***	b	12.5	(2.5)***	ab
Mixed	10.0	(2.5)***	а	1.1	(0.3)***	с	11.1	(2.8)	b
Abies	7.8	(0.5)	bc	1.5	(0.1)	b	11.3	(0.9)	b
Closed-broadleaf	7.7	(0.4)	bc	2.0	(0.0)***	а	15.3	(0.7)**	а
Open-broadleaf	8.6	(0.5)	ab	1.6	(0.1)	b	13.4	(1.1)	ab
Sorbus-Alnus	6.3	(0.1)***	c	1.7	(0.1)	b	10.4	(0.4)*	b
Picea	6.4	(0.8)**	c	2.0	(0.0)***	а	12.9	(1.8)	ab
Order 2									
Order 2 Broadleaf	4.8	(0.8)***	bc	1.3	(0.2)***	се	6.4	(1.9)***	ab
Order 2 Broadleaf Mixed	4.8 6.2	(0.8)*** (1.8)***	bc a	1.3 1.1	(0.2)*** (0.2)**	ce e	6.4 6.7	(1.9)*** (1.9)	ab ab
Order 2 Broadleaf Mixed Abies	4.8 6.2 4.4	(0.8)*** (1.8)*** (0.4)	bc a bc	1.3 1.1 1.3	(0.2)*** (0.2)** (0.1)	ce e de	6.4 6.7 5.5	(1.9)*** (1.9) (0.6)	ab ab b
Order 2 Broadleaf Mixed Abies Closed-broadleaf	4.8 6.2 4.4 4.7	(0.8)*** (1.8)*** (0.4) (0.1)	bc a bc bc	1.3 1.1 1.3 1.7	(0.2)*** (0.2)** (0.1) (0.1)***	ce e de b	6.4 6.7 5.5 7.8	(1.9)*** (1.9) (0.6) (0.2)	ab ab b ab
Order 2 Broadleaf Mixed Abies Closed-broadleaf Open-broadleaf	4.8 6.2 4.4 4.7 5.3	(0.8)*** (1.8)*** (0.4) (0.1) (0.2)	bc a bc bc ab	1.3 1.1 1.3 1.7 1.4	(0.2)*** (0.2)** (0.1) (0.1)*** (0.0)	ce e de b cd	6.4 6.7 5.5 7.8 7.3	(1.9)*** (1.9) (0.6) (0.2) (0.4)	ab ab b ab ab
Order 2 Broadleaf Mixed Abies Closed-broadleaf Open-broadleaf Sorbus-Alnus	4.8 6.2 4.4 4.7 5.3 3.6	(0.8)*** (1.8)*** (0.4) (0.1) (0.2) (0.3)**	bc a bc bc ab c	1.3 1.1 1.3 1.7 1.4 1.6	(0.2)*** (0.2)** (0.1) (0.1)*** (0.0) (0.1)**	ce e de b cd bc	6.4 6.7 5.5 7.8 7.3 5.5	(1.9)*** (1.9) (0.6) (0.2) (0.4) (0.5)	ab ab b ab ab b
Order 2 Broadleaf Mixed Abies Closed-broadleaf Open-broadleaf Sorbus-Alnus Picea	4.8 6.2 4.4 4.7 5.3 3.6 4.2	(0.8)*** (1.8)*** (0.4) (0.1) (0.2) (0.3)** (0.5)	bc a bc bc ab c bc	1.3 1.1 1.3 1.7 1.4 1.6 2.0	(0.2)*** (0.2)** (0.1) (0.1)*** (0.0) (0.1)** (0.2)***	ce e de b cd bc a	6.4 6.7 5.5 7.8 7.3 5.5 8.6	(1.9)*** (1.9) (0.6) (0.2) (0.4) (0.5) (1.9)**	ab ab b ab ab b a

304

305 Forest level canopy diversities showed that the Broadleaf forest had low β -, but high 306 α - and γ -diversities, whereas the Abies forest had the highest β -diversity, but lowest α - and γ -307 indices (Figure 5). At the summit, both the Closed-broadleaf and the Picea forests had high α -, 308 β -, and γ -diversities, and the Open-broadleaf together with the Sorbus-Alnus forest had low 309 diversities.





Figure 5. Forest level canopy diversities averaged from N_{0-2} . Significant differences are determined by GLM (log-normal distribution) at p < 0.05. The first three forests are at Yosomi.

High understorey diversity indices did not predict high canopy diversity indices and vice versa. For example, understorey N_0 and N_1 of the Picea forest were the lowest and medium-level respectively, whereas the same canopy indices were high. In general, the canopy showed higher β -diversity indices than the understorey at both sites, indicating that the canopy composition was more heterogeneous than the understorey composition.

319 3.4 Summer and autumn diversities

320 The summer and autumn plant diversity indices in 2016 and 2017 correlated significantly at p

- 321 < 0.001, with r ranging from 0.80 to 0.92 (Supplementary figure S1). Although the species
- 322 richness and density were higher during the summer surveys than during the autumn ones
- 323 (LM, p < 0.001), the diversity patterns were similar between autumn and summer. This
- 324 similarity indicated that the autumn diversity indices described patterns of the entire growing
- 325 season.

326

3.5 Spatial autocorrelation and elevation

327 Moran's I showed, that N_0 of the understorey spatially autocorrelated (I = 0.1, p = 0.03), but 328 for $N_{1,2}$, autocorrelation did not occur (p = 0.23 and 0.66 respectively). When the Yosomi and 329 summit plots were analyzed separately, spatial autocorrelation remained present for N_0 at the 330 summit, but not at Yosomi. Elevation did not influence any order of diversities, independent 331 of whether the Yosomi and summit plots were analyzed together or separately. 332 The canopy diversity indices did not show any autocorrelation (p > 0.05), but 333 elevation weakly influenced the indices (r = 0.25-0.27, p < 0.01) when the plots were not 334 separated into Yosomi and summit. 335 4. Discussion 336 4.1 Species composition of the canopy and understorey 337 The first hypothesis, that species composition was more similar among the forests of active 338 and passive management at Yosomi, was accepted for the Mixed forest canopy composition. 339 The Abies plantation maintained its own separate canopy cluster, although its understorey 340 composition overlapped with that of the Broadleaf forest. However, the largest overlap of 341 understorey species composition was observed in the Picea plantation at the summit. 342 Although forest age was the strongest predictor of species composition similarity in tropical 343 forests (Rozendaal et al., 2019), we found that the structure of the plantation was more 344 important in the temperate forests at Mount Usu. 345 The plantations retained their non-native canopy species and restricted the 346 establishment of native trees. Active management of post-disturbance areas often decreases 347 native species immigration. For example, the development of natural forests is impeded by 348 plantations of non-native Larix kaempferi on the volcano Mount Koma, northern Japan 349 (Kondo and Tsuyuzaki, 1999), and native trees appear less on seeded plots than on unseeded

ones on Mount St. Helens (Dale and Adams, 2003). Although native species started to
immigrate into the Picea forest by seed immigration from the surrounding natural forests, the
process was slow (Cain et al., 1998; Sorrells and Warren, 2011), shown also by the low ratio
of broadleaved trees in the older Mixed forest at Yosomi.

On Mount St. Helens, more than 30 years were required for the re-establishment of most native species after the eruption (del Moral and Wood, 2012). The present study examined areas 40 and 110 years after the eruptions, and because their geographic locations were close and they experienced similar abiotic conditions and management history, it can be assumed that the naturally regenerated forests followed the same successional trajectory. Yet, the species composition remained different between the two sites, indicating that reestablishment was still in progress at the summit, 40 years after the eruptions.

361 The canopy and understorey interactively influence each other during succession 362 (Gilliam, 2007), but tree establishment in the early successional stages can affect successional 363 trajectories strongly (Mudrák et al., 2016) or only weakly (Halpern and Lutz, 2013). On 364 Mount Usu, the Sorbus-Alnus forest displayed distinct canopy and understorey composition 365 compared to the other forest types, suggesting that in the broadleaf plantation the trees 366 strongly affected the development of the species composition in the understorey. In the other 367 plantations, even when the canopy composition was unique, the understorey composition 368 overlapped or was close to that of natural forests. Therefore, the understorey composition was 369 only weakly influenced by the canopy in the evergreen plantations.

Seed dispersal limitation influences the understorey species composition (Baeten et
al., 2015; Graae et al., 2004; Verheyen et al., 2003). Seed limitation can result from either
large distance to seed sources or from limited seed production. Both the Picea and SorbusAlnus forests were close to the natural forests surrounding the summit and to the Closedbroadleaf forest. The large overlap of the understorey species composition of the Picea forest

with those of the broadleaved forests indicated that distance dependent dispersal limitation
was not an issue. We suggest that the understorey composition in the Sorbus-Alnus forest was
determined not by seed dispersal limitation, but by competition for resources (Bourgeois et
al., 2016), and so it remained different.

379 Natural succession was slow on the summit where the tephra was thick because of the 380 lack of vegetative reproduction and dependence on seed dispersal (Tsuyuzaki and Haruki, 381 1996). The Open-broadleaf forest established on thick tephra, and was farther away from the 382 other forest types and far from the surviving forest patches, resulting in no connection to seed 383 sources soon after the eruptions. On Mount St. Helens, lack of seed sources causes slow seed 384 dispersal and establishment (Jones and del Moral, 2009). Therefore, we assume that seed 385 limitation delayed the development of a closed canopy in the Open-broadleaf forest. Areas 386 with slow revegetation immediately after the disturbance developed plant cover faster when 387 more time passed since the disturbance on Mount St. Helens and Surtsey (del Moral and 388 Magnússon, 2014), as well as on Usu (Tsuyuzaki, 2019). However, this trend was not 389 observed in the Open-broadleaf forest, suggesting that the positive effects of plant facilitation 390 (Cutler et al., 2008) were counterbalanced by harsh conditions, low seed immigration rate, 391 and lack of vegetative reproduction.

392

4.2 Active versus passive restoration

Our expectation that forests resulting from passive restoration will be more diverse was partially true. Active restoration resulted in low total understorey species richness, and apart from the Picea plantation, lower diversity than in the naturally recovered forests. The Picea plantation, when abundance of common species determined diversity, had the highest effective species number among all forests. Within their eruption sites, some plantations also reached canopy diversity indices comparable to those of the natural forests. At Yosomi the

Mixed forest and at the summit the Picea forest became the most diverse forests together withtheir respective natural neighbours, the Broadleaf and Closed-broadleaf forests.

401 Comparison of the Picea plantation with the other plantations showed that β -diversity 402 was highest in the Picea forest, because its structure was heterogeneous. The trees in the Picea 403 forest were planted in dense rows, but because there were a few meters distance between the 404 rows, light reached the forest floor. This mosaic structure resulted in quadrats falling between 405 the rows of trees including more species than quadrats falling below the trees. At Yosomi, the 406 Abies plantation had similar mosaic structure and had the highest β -diversity there. The 407 heterogeneous nature of the plantations resembles thinning, which is often used as a 408 management strategy to increase the diversity of understory species (Kitagawa et al., 2017). 409 While thinning can result in a decrease of diversity due to machines destroying the 410 understorey (Nagai and Yoshida, 2006), the high β -diversity of the plantations suggested that 411 spacious planting design had a long-lasting positive impact without additional management. 412 Spacious planting mimicks natural vegetation patches, and patches, when in proximity to each 413 other, are more likely to survive and merge, increasing vegetation cover after the eruptions of 414 Mount Usu (Végh and Tsuyuzaki, 2021). Patchy vegetation also promotes the development of 415 different communities thus high β -diversity, because early successional communities are 416 sensitive to small variations in their micro-environments (Endo et al., 2008). 417

417 Looking at the naturally recovered forests, the Broadleaf forest at Yosomi had lower 418 understorey $N_{1,2}$ than the broadleaved forests at the summit, due to its low β -diversity. 419 However, the canopy showed opposite trend: the Yosomi forests had higher richness and 420 diversity than the summit forests. As the Yosomi and summit sites are considered to be 421 different successional stages of the same trajectory, their diversity is expected to follow a 422 hump-shaped diversity pattern, explained by the intermediate disturbance hypothesis (IDH, 423 Grime 1973). The IDH curve is observed along the disturbance gradient on Mount St. Helens

424 (Chang et al., 2019), and also after windthrows in Germany, where the species richness of the 425 understorey and canopy displayed synchronised movement on it (Meyer et al., 2021). The 426 time-scale on which the IDH is observed depends on the type of community and the rate of 427 succession (Chang et al., 2019). This inverse pattern of the canopy and understorey diversities 428 between Yosomi and the summit suggested that if the canopy and understorey followed an 429 IDH curve over time, they moved at a different pace.

430 4.3 Management implications

431 Restoration costs are reduced if the management concentrates on establishment of plant 432 patches instead of dense plantations. However, monitoring is needed to ensure the 433 development of desired communities (Gilbert and Anderson, 1998). For example, the Sorbus-434 Alnus forest was successful in the context of developing vegetation cover quickly but was not 435 successful in the context of promoting high diversity and similar species composition to those 436 of naturally recovered forests, falling behind the coniferous plantations. Common species 437 from the neighbouring naturally recovered Closed-broadleaf forest, such as the P. suaveolens 438 did not establish in the Sorbus-Alnus plantation, likely because the conditions needed for its 439 establishment are different from the conditions needed for its survival as an adult (Young et 440 al., 2005).

441 The choice of planted species in the Sorbus-Alnus plantation could also have long-442 term impacts. *Alnus* spp. usually facilitate plant establishment by increasing soil nitrogen 443 (Kamijo et al., 2002; Titus, 2009). During early succession, nitrogen limits plant 444 development, and competition for underground resources might be more severe than for 445 aboveground resources (Haruki and Tsuyuzaki, 2001). Therefore, by planting *Alnus* spp., 446 species that otherwise might not have been able to establish because of being sensitive to lack 447 of nitrogen were able to thrive, and outcompete species established in the naturally recovered

forests. As the understorey composition of all summit forests moved closer to those of the
Yosomi forests during the five years of this study, the effect of early management is expected
to weaken further in the future.

451 The plantations were more sensitive to subsequent disturbances, as shown by the 452 intensive tree damage caused by the typhoon in 2016. Although wind speed is influenced by 453 the terrain (Nakajima et al., 2009), and may have contributed to differences in the resilience 454 of the forest types, the differences in species composition and root structure were 455 deterministic factors to withstand damage. The frequency of typhoons and other extreme 456 weather events is predicted to increase due to climate change (IPCC, 2021). Therefore, 457 restoration activities need to aim not only to create ecosystems which provide basic services, 458 but also to create ecosystems which are resilient against extreme weather events.

459 **5.** Conclusions

460 Species composition of the plantations resembled more the species composition of natural 461 forests not with increasing age, but with more diverse structure. The understorey diversity was 462 less affected by management activities than canopy diversity, but the understorey composition 463 was different between natural and planted forests. The seeds of native species dispersed to the plantations over time, but the immigration process was slow; additional actions are needed to 464 465 foster the transition of plantations into natural forests, and improve their resilience to 466 secondary disturbances. The plantations had lower species richness and diversity than the 467 naturally recovered forests, except for the Picea plantation, which reached comparable indices 468 due to its mosaicked structure. Patchy plantation design seemed to lead to higher species 469 similarity with natural forests and also increased species diversity, so we suggest active 470 management to focus planting in patches instead of dense plantations.

471 **6. Acknowledgements**

- 472 The study was partly funded by the Japan Society for the Promotion of Science and Japan Aerospace
- 473 Exploration Agency. We thank Gaku Kudo, Shin-ichiro Aiba, Ohara Masashi, and three anonymous
- 474 reviewers for providing comments. The authors declare that they have no conflict of interest.

475 **7. Author contributions**

- 476 Lea Végh: Conceptualization, Writing Original draft preparation, revision. Shiro Tsuyuzaki:
- 477 Supervision, Writing reviewing and editing.

8. References

479	Baeten, L., Davies, T.J., Verheyen, K., Van Calster, H., Vellend, M., 2015.
480	Disentangling dispersal from phylogeny in the colonization capacity of forest
481	understorey plants. Journal of Ecology 103, 175–183.
482	https://doi.org/10.1111/1365-2745.12333
483	Bourgeois, B., Vanasse, A., Poulin, M., 2016. Effects of competition, shade and soil
484	conditions on the recolonization of three forest herbs in tree-planted riparian
485	zones. Applied Vegetation Science 19, 679–688.
486	https://doi.org/10.1111/avsc.12246
487	Bray, J.R., Curtis, J., 1957. An ordination of the upland forest communities of southern
488	Wisconsin. Ecol. Monogr 27, 325–349.
489	Cain, M.L., Damman, H., Muir, A., 1998. Seed dispersal and the holocene migration of
490	woodland herbs. Ecological Monographs 68, 325–347.
491	https://doi.org/10.1890/0012-9615(1998)068[0325:SDATHM]2.0.CO;2
492	Chang, C.C., Halpern, C.B., Antos, J.A., Avolio, M.L., Biswas, A., Cook, J.E., del
493	Moral, R., Fischer, D.G., Holz, A., Pabst, R.J., Swanson, M.E., Zobel, D.B.,
494	2019. Testing conceptual models of early plant succession across a disturbance
495	gradient. Journal of Ecology 107, 517–530. https://doi.org/10.1111/1365-
496	2745.13120
497	Clements, F.E., 1916. Plant succession; an analysis of the development of vegetation.
498	Carnegie Institution of Washington, Washington.
499	Cutler, N.A., Belyea, L.R., Dugmore, A.J., 2008. The spatiotemporal dynamics of a
500	primary succession. Journal of Ecology 96, 231–246.
501	https://doi.org/10.1111/j.1365-2745.2007.01344.x
502	Dale, V.H., Adams, W.M., 2003. Plant reestablishment 15 years after the debris
503	avalanche at Mount St. Helens, Washington. Science of The Total Environment
504	313, 101–113. https://doi.org/10.1016/S0048-9697(03)00332-2
505	del Moral, R., 2009. Increasing deterministic control of primary succession on Mount
506	St. Helens, Washington. Journal of Vegetation Science 20, 1145–1154.
507	https://doi.org/10.1111/j.1654-1103.2009.01113.x
508	del Moral, R., Magnússon, B., 2014. Surtsey and Mount St. Helens: a comparison of
509	early succession rates. Biogeosciences 11, 2099–2111.
510	https://doi.org/10.5194/bg-11-2099-2014
511	del Moral, R., Titus, J.H., Cook, A.M., 1995. Early primary succession on Mount St.
512	Helens, Washington, USA. Journal of Vegetation Science 6, 107–120.
513	https://doi.org/10.2307/3236262
514	del Moral, R., Wood, D.M., 2012. Vegetation development on permanently established
515	grids, Mount St. Helens (1986–2010). Ecology 93, 2125–2125.
516	https://doi.org/10.1890/12-0344.1
517	Do, H.T.T., Grant, J.C., Trinh, N.B., Zimmer, H.C., Tran, L.D., Nichols, J.D., 2019.
518	Recovery of tropical moist deciduous dipterocarp forest in Southern Vietnam.
519	Forest Ecology and Management 433, 184–204.
520	https://doi.org/10.1016/j.foreco.2018.10.062
521	Efford, J., Clarkson, B., Bylsma, R., 2014. Persistent effects of a tephra eruption (AD
522	1655) on treeline composition and structure, Mt Taranaki, New Zealand. New

523	Zealand Journal of Botany 52, 245–261.
524	https://doi.org/10.1080/0028825X.2014.886599
525	Endo, M., Yamamura, Y., Tanaka, A., Nakano, T., Yasuda, T., 2008. Nurse-Plant
526	Effects of a Dwarf Shrub on the Establishment of Tree Seedlings in a Volcanic
527	Desert on Mt. Fuji, Central Japan. Arctic, Antarctic, and Alpine Research 40,
528	335–342. https://doi.org/10.1657/1523-0430(07-013)[ENDO]2.0.CO;2
529	Fridriksson, S., 1982. Life develops on Surtsey. Endeavour 6, 100–107.
530	https://doi.org/10.1016/0160-9327(82)90041-2
531	Gilbert, O.L., Anderson, P., 1998. Habitat creation and repair. Oxford University Press,
532	New York.
533	Gilliam, F.S., 2007. The Ecological Significance of the Herbaceous Layer in Temperate
534	Forest Ecosystems. BioScience 57, 845-858. https://doi.org/10.1641/B571007
535	Graae, B.J., Hansen, T., Sunde, P.B., 2004. The importance of recruitment limitation in
536	forest plant species colonization: a seed sowing experiment. Flora - Morphology,
537	Distribution, Functional Ecology of Plants 199, 263–270.
538	https://doi.org/10.1078/0367-2530-00154
539	Grime, J.P., 1973. Competitive Exclusion in Herbaceous Vegetation. Nature 242, 344–
540	347. https://doi.org/10.1038/242344a0
541	Halpern, C.B., Lutz, J.A., 2013. Canopy closure exerts weak controls on understory
542	dynamics: a 30-year study of overstory–understory interactions. Ecological
543	Monographs 83, 221–237. https://doi.org/10.1890/12-1696.1
544	Haruki, M., Tsuyuzaki, S., 2001. Woody plant establishment during the early stages of
545	volcanic succession on Mount Usu, northern Japan. Ecological Research 16,
546	451–457. https://doi.org/10.1046/j.1440-1703.2001.00407.x
547	Hill, M.O., 1973. Diversity and Evenness: A Unifying Notation and Its Consequences.
548	Ecology 54, 427. https://doi.org/10.2307/1934352
549	Hlavac, M., 2018. stargazer: Well-Formatted Regression and Summary Statistics
550	Tables, R package version 5.2.2. ed. Central European Labour Studies Institute
551	(CELSI), Bratislava, Slovakia.
552	Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous Inference in General Parametric
553	Models. Biometrical Journal 50, 346–363.
554	IPCC, 2021. Summary for Policymakers, in: Masson-Delmotte, V., Zhai, P., Pirani,
555	S.L., Connors, S.L., Péan, C., Berger, S., Caud, N., Chen, Y., Goldfarb, L.,
556	Gomis, M.I., Huang, M., Leitzell, K., Lonnoy, E., Matthews, J.B.R., Maycock,
557	T.K., Waterfield, T., Yelekçi, O., Yu, R., Zhou, B. (Eds.), Climate Change 2021:
558	The Physical Science Basis. Contribution of Working Group I to the Sixth
559	Assessment Report of the Intergovernmental Panel on Climate Change.
560	Cambridge University Press.
561	Irl, S.D.H., Schweiger, A.H., Hoffmann, S., Beierkuhnlein, C., Hartmann, H., Pickel,
562	T., Jentsch, A., 2019. Spatiotemporal dynamics of plant diversity and endemism
563	during primary succession on an oceanic-volcanic island. Journal of Vegetation
564	Science 30, 587–598. https://doi.org/10.1111/jvs.12765
565	JMA, 2019. Date Meteorological Station [WWW Document]. Japan Meteorological
566	Agency. URL
567	https://www.data.jma.go.jp/obd/stats/etrn/view/annually_a.php?prec_no=21&bl
568	ock_no=0132&year=&month=&day=&view= (accessed 9.27.19).

Jones, C.C., del Moral, R., 2009. Dispersal and establishment both limit colonization 570 during primary succession on a glacier foreland. Plant Ecology 204, 217–230. 571 https://doi.org/10.1007/s11258-009-9586-3 572 Jost, L., 2006. Entropy and diversity. Oikos 113, 363–375. 573 Jurasinski, G., Koch, M., 2011. Commentary: do we have a consistent terminology for 574 species diversity? We are on the way. Oecologia 167, 893–902. 575 https://doi.org/10.1007/s00442-011-2126-6 576 Kadomura, H., Okada, H., Araya, T., 1988. 1977-82 volcanism and environmental 577 hazards of Usu volcano. Hokkaido University Press, Japan. 578 Kamijo, T., Kitayama, K., Sugawara, A., Urushimichi, S., Sasai, K., 2002. Primary 579 succession of the warm-temperate broad-leaved forest on a volcanic island, 580 Miyake-jima, Japan. Folia Geobotanica 37, 71–91. 581 https://doi.org/10.1007/BF02803192 582 Karadimou, E., Kallimanis, A.S., Tsiripidis, I., Raus, T., Bergmeier, E., Dimopoulos, P., 583 2018. Functional diversity changes over 100 yr of primary succession on a 584 volcanic island: insights into assembly processes. Ecosphere 9, e02374. 585 https://doi.org/10.1002/ecs2.2374 586 Katsui, Y., Yokoyama, I., Murozumi, M., 1981. Usu volcano, in: Field Excursion Guide 587 to Usu and Tarumai Volcanoes and Noboribetsu Spa. Volcanological Society of 588 Japan, Japan. 589 Kitagawa, R., Ueno, M., Masaki, T., 2017. Thinning affects understorey tree 590 community assembly in monoculture plantations by facilitating stochastic 591 immigration from the landscape. Applied Vegetation Science 20, 673–682. 592 https://doi.org/10.1111/avsc.12327 593 Kondo, T., Tsuyuzaki, S., 1999. Natural regeneration patterns of the introduced larch, 594 Larix kaempferi (Pinaceae), on the volcano Mount Koma, northern Japan. 595 Diversity and Distributions 5, 223-233. https://doi.org/10.1046/j.1472-596 4642.1999.00056.x 597 Lichter, J., 2000. Colonization constraints during primary succession on coastal Lake 598 Michigan sand dunes: Colonization constraints during primary succession. 599 Journal of Ecology 88, 825-839. https://doi.org/10.1046/j.1365-600 2745.2000.00503.x 601 Magurran, A.E., McGill, B.J., 2011. Biological Diversity. Oxford University Press, 602 Oxford. 603 Mansourian, S., Vallauri, D., Dudley, N., 2005. Forest restoration in landscapes : 604 beyond planting trees. Springer, New York, N.Y. 605 Marler, T.E., del Moral, R., 2013. Primary succession in Mount Pinatubo: Habitat 606 availability and ordination analysis. Communicative & Integrative Biology 6, 607 e25924. https://doi.org/10.4161/cib.25924 608 Mever, P., Schmidt, M., Feldmann, E., Willig, J., Larkin, R., 2021. Long-term 609 development of species richness in a central European beech (Fagus sylvatica) 610 forest affected by windthrow-Support for the intermediate disturbance 611 hypothesis? Ecology and Evolution n/a. https://doi.org/10.1002/ece3.8028 612 Moran, P.A.P., 1950. Notes on Continuous Stochastic Phenomena. Biometrika 37, 17-613 23. https://doi.org/10.2307/2332142 614 Moreno, C.E., Rodríguez, P., 2011. Commentary: Do we have a consistent terminology 615 for species diversity? Back to basics and toward a unifying framework. 616 Oecologia 167, 889-892. https://doi.org/10.1007/s00442-011-2125-7

617	Mudrák, O., Doležal, J., Frouz, J., 2016. Initial species composition predicts the
618	progress in the spontaneous succession on post-mining sites. Ecological
619	Engineering 95, 665–670. https://doi.org/10.1016/j.ecoleng.2016.07.002
620	Nagai, M., Yoshida, T., 2006. Variation in understory structure and plant species
621	diversity influenced by silvicultural treatments among 21- to 26-year-old Picea
622	glehnii plantations. Journal of Forest Research 11, 1–10.
623	https://doi.org/10.1007/s10310-005-0176-5
624	Nakajima, T., Lee, J., Kawaguchi, T., Tatsuhara, S., Shiraishi, N., 2009. Risk
625	assessment of wind disturbance in Japanese mountain forests. null 16, 58–65.
626	https://doi.org/10.2980/16-1-3179
627	Okitsu, S., 2003. Forest Vegetation of Northern Japan and the Southern Kurils, in:
628	Kolbek, J., Šrůtek, M., Box, E.O. (Eds.), Forest Vegetation of Northeast Asia.
629	Springer Netherlands, Dordrecht, pp. 231–261.
630	Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D.,
631	Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H.,
632	Szoecs, E., Wagner, H., 2019. vegan: Community Ecology Package.
633	Pedersen, T.L., 2020. patchwork: The Composer of Plots.
634	Perrow, M.R., Davy, A.J., 2002. Principles of restoration, Handbook of ecological
635	restoration / edited by Martin R. Perrow and Anthony J. Davy; v. 1. Cambridge
636	University Press, Cambridge, UK.
637	Prach, K., Walker, L.R., 2011. Four opportunities for studies of ecological succession.
638	Trends in Ecology & Evolution 26, 119–123.
639	https://doi.org/10.1016/j.tree.2010.12.007
640	R Core Team, 2018. R: A language and environment for statistical computing. R
641	Foundation for Statistical Computing, Vienna, Austria.
642	Rozendaal, D.M.A., Bongers, F., Aide, T.M., Alvarez-Dávila, E., Ascarrunz, N.,
643	Balvanera, P., Becknell, J.M., Bentos, T.V., Brancalion, P.H.S., Cabral, G.A.L.,
644	Calvo-Rodriguez, S., Chave, J., César, R.G., Chazdon, R.L., Condit, R.,
645	Dallinga, J.S., de Almeida-Cortez, J.S., de Jong, B., de Oliveira, A., Denslow,
646	J.S., Dent, D.H., DeWalt, S.J., Dupuy, J.M., Durán, S.M., Dutrieux, L.P.,
647	Espírito-Santo, M.M., Fandino, M.C., Fernandes, G.W., Finegan, B., García, H.,
648	Gonzalez, N., Moser, V.G., Hall, J.S., Hernández-Stefanoni, J.L., Hubbell, S.,
649	Jakovac, C.C., Hernández, A.J., Junqueira, A.B., Kennard, D., Larpin, D.,
650	Letcher, S.G., Licona, JC., Lebrija-Trejos, E., Marín-Spiotta, E., Martínez-
651	Ramos, M., Massoca, P.E.S., Meave, J.A., Mesquita, R.C.G., Mora, F., Müller,
652	S.C., Muñoz, R., de Oliveira Neto, S.N., Norden, N., Nunes, Y.R.F., Ochoa-
653	Gaona, S., Ortiz-Malavassi, E., Ostertag, R., Peña-Claros, M., Pérez-García,
654	E.A., Piotto, D., Powers, J.S., Aguilar-Cano, J., Rodriguez-Buritica, S.,
655	Rodríguez-Velázquez, J., Romero-Romero, M.A., Ruíz, J., Sanchez-Azofeifa,
656	A., de Almeida, A.S., Silver, W.L., Schwartz, N.B., Thomas, W.W., Toledo, M.,
657	Uriarte, M., de Sá Sampaio, E.V., van Breugel, M., van der Wal, H., Martins,
658	S.V., Veloso, M.D.M., Vester, H.F.M., Vicentini, A., Vieira, I.C.G., Villa, P.,
659	Williamson, G.B., Zanini, K.J., Zimmerman, J., Poorter, L., 2019. Biodiversity
660	recovery of Neotropical secondary forests. Sci Adv 5, eaau3114.
661	https://doi.org/10.1126/sciadv.aau3114
662	Sorrells, J., Warren, R.J., 2011. Ant-dispersed herb colonization lags behind forest re-
663	establishment. The Journal of the Torrey Botanical Society 138, $7/-84$.
664	nttps://doi.org/10.3159/10-KA-037.1

665	Sutomo, S., Hobbs, R.J., Cramer, V., 2011. Plant community establishment on the
666	volcanic deposits following the 2006 nuées ardentes (pyroclastic flows) of
667	Mount Merapi: Diversity and floristic variation. Biodiversitas 12, 86–91.
668	Talbot, S.S., Talbot, S.L., Walker, L.R., 2010. Post-eruption Legacy Effects and Their
669	Implications for Long-Term Recovery of the Vegetation on Kasatochi Island,
670	Alaska. Arctic, Antarctic, and Alpine Research 42, 285–296.
671	https://doi.org/10.1657/1938-4246-42.3.285
672	Titus, J.H., 2009. Nitrogen-fixers Alnus and Lupinus influence soil characteristics but
673	not colonization by later successional species in primary succession on Mount
674	St. Helens. Plant Ecology 203, 289–301. https://doi.org/10.1007/s11258-008-
675	9549-0
676	Tsuyuzaki, S., 2019. Vegetation changes from 1984 to 2008 on Mount Usu, northern
677	Japan, after the 1977–1978 eruptions. Ecological Research.
678	https://doi.org/10.1111/1440-1703.12045
679	Tsuyuzaki, S., 1989. Analysis of revegetation dynamics on the volcano Usu, northern
680	Japan, deforested by 1977-78 eruptions. American Journal of Botany 76, 1468–
681	1477. https://doi.org/10.1002/j.1537-2197.1989.tb15128.x
682	Tsuyuzaki, S., 1987. Origin of plants recovering on the volcano Usu, northern Japan,
683	since the eruptions of 1977 and 1978. Vegetatio 73, 53–58.
684	Tsuyuzaki, S., Haruki, M., 1996. Tree regeneration patterns on Mount Usu, northern
685	Japan, since the 1977–78 eruptions. Vegetatio 126, 191–198.
686	Tuomisto, H., 2011. Commentary: do we have a consistent terminology for species
687	diversity? Yes, if we choose to use it. Oecologia 167, 903–911.
688	https://doi.org/10.1007/s00442-011-2128-4
689	Végh, L., Tsuyuzaki, S., 2021. Comparison of vegetation patch dynamics after the
690	eruptions of the volcano Mount Usu, northern Japan, in 1977–1978 and 2000,
691	detected by imagery chronosequence. Ecological Research 36, 329–339.
692	https://doi.org/10.1111/1440-1703.12199
693	Verheyen, K., Guntenspergen, G.R., Biesbrouck, B., Hermy, M., 2003. An integrated
694	analysis of the effects of past land use on forest herb colonization at the
695	landscape scale. Journal of Ecology 91, 731-742. https://doi.org/10.1046/j.1365-
696	2745.2003.00807.x
697	White, P.S., Walker, J.L., 1997. Approximating Nature's Variation: Selecting and Using
698	Reference Information in Restoration Ecology. Restoration Ecology 5, 338–349.
699	https://doi.org/10.1046/j.1526-100X.1997.00547.x
700	Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L.D., François, R.,
701	Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T.L.,
702	Miller, E., Bache, S.M., Müller, K., Ooms, J., Robinson, D., Seidel, D.P., Spinu,
703	V., Takahashi, K., Vaughan, D., Wilke, C., Woo, K., Yutani, H., 2019. Welcome
704	to the tidyverse. Journal of Open Source Software 4, 1686.
705	https://doi.org/10.21105/joss.01686
706	Young, T.P., Petersen, D.A., Clary, J.J., 2005. The ecology of restoration: historical
707	links, emerging issues and unexplored realms. Ecology Letters 8, 662–673.
708	https://doi.org/10.1111/j.1461-0248.2005.00764.x
709	