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

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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 m × 10 m plots in each forest type, and
14 understorey diversity was measured by shoot density in four 1 m × 1 m quadrats 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.

25 **Keywords: succession, plant diversity, management, species composition, volcano, true**
26 **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.

37 Passive restoration is slow and often leads to undesirable communities; to restore high
38 quality habitats, active management (e.g., seeding, planting, and mowing) is often required to
39 accelerate revegetation and to influence the outcome (Perrow and Davy, 2002). However, the
40 resultant communities may differ from the former vegetation (Mansourian et al., 2005), and
41 natural forests often show higher species richness and diversity than managed forests (Prach
42 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 understory species richness and
60 diversity, and also species composition between Yosomi and the summit, close to 40 and 110
61 years after the eruptions.

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

69

70 **2. Methods**

71 2.1 Location

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

75 temperature of 8°C during 1976–2018 (Date Meteorological Station at 5 km from Mount Usu;
76 JMA 2019). The climax vegetation is deciduous oak or mixed broad-leaved forests in the
77 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
88 to as Yosomi hereafter.

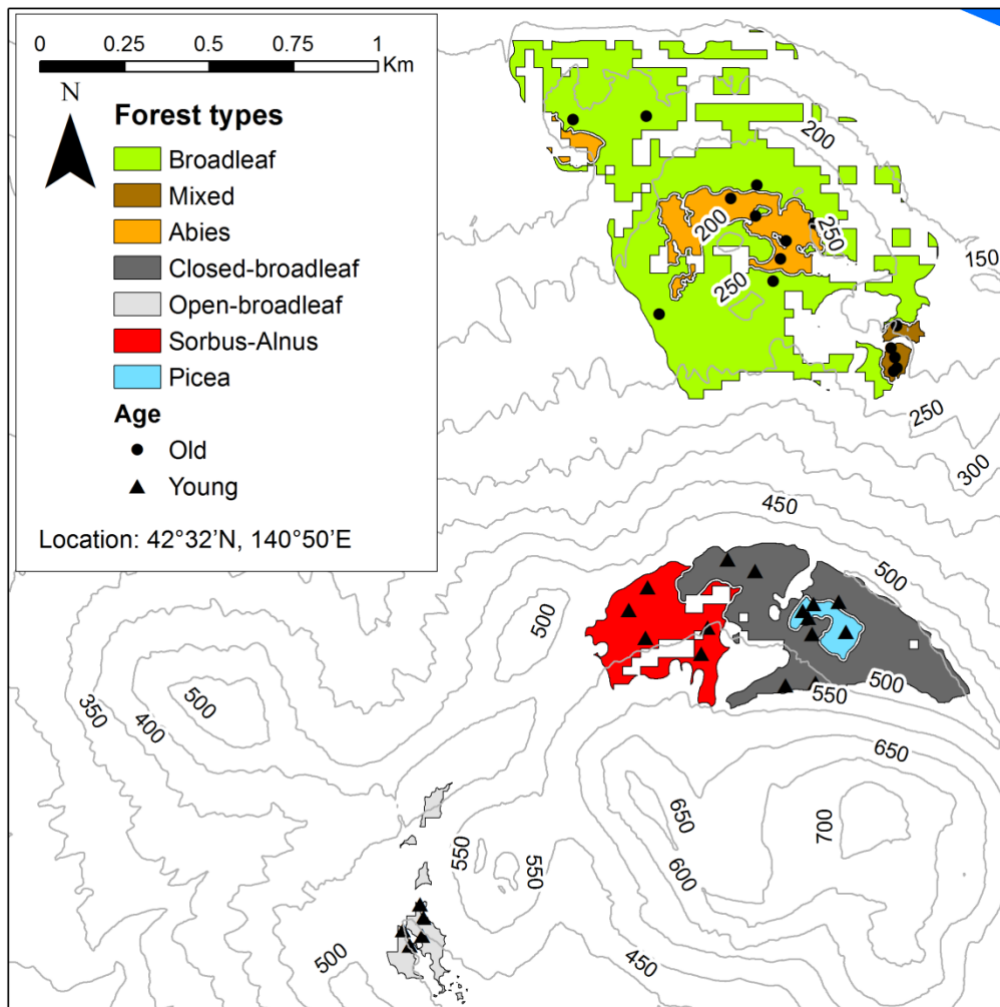
89 In contrast to Yosomi, the eruptions, damages, and subsequent revegetation processes
90 are well studied at the 1977–1978 eruptions site. The eruptions occurred at the summit, which
91 was covered with seeded pastures and broad-leaved forests of *P. suaveolens*, *Betula*
92 *platyphylla* var. *japonica*, *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).
97 Because the eruption destroyed an area of 291 ha, the centre still lacks vegetation cover (Végh
98 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,
107 while a smaller area is covered by an open *P. suaveolens* forest. The 1977–78 eruptions site is
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
128 Figure 1. The forest types and plots examined during the study. The first three forests in the
129 legend 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
131 each forest type measured 5 m × 5 m in 2015, and were enlarged to 10 m × 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 understory vegetation were damaged. Later, the area was

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

138 In 2015, two randomly selected 1 m × 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.

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

152 In four plots of the Mixed forests, the quadrats were not monitored from 2017 due to
153 typhoon damage.

154 2.3 Species diversity and composition measurements

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

159 species may dominate the communities. In contrast, species diversity incorporates evenness
160 and more information about vegetation recovery, especially when coupled with species
161 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 (N_0), order 1 (N_1), and order 2 (N_2)
171 (Jost, 2006) for each forest by annually monitoring their plots. N_0 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

186 The vegetation surveys in autumn and summer were compared using linear models (LM) and
187 Pearson's correlation coefficient (r). Species composition of the plots were compared by non-
188 metric multidimensional scaling (nMDS) using the vegan package in R (Oksanen et al. 2019).
189 ANOSIM was used to determine the uniqueness of forest groupings with ten thousand
190 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

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

206 (Kendall's $\tau = 0.80\text{--}0.85$ 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*
 218 and *A. pictum* saplings, while in the Abies plantation they were *Hylodesmum podocarpum* and
 219 *Phryma leptostachya*.

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

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

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

Yosomi	Broadleaf		Mixed		Abies	
	n	%	n	%	n	%
<i>Asperula odorata</i>	74.3	24.4	28.9	14.6	69.1	25.2
<i>Rhus ambigua</i>	17.3	31.6	12.0	19.6	19.2	42.8
<i>Sanicula chinensis</i>	16.3	20.8			15.7	18.0
<i>Onoclea orientalis</i>	11.9	28.4				
<i>Disporum sessile</i>	11.5	20.8				
<i>Acer pictum</i>	8.8	25.0				
<i>Abies sachalinensis</i>			21.7	25.8		
<i>Dryopteris crassirhizoma</i>			2.5	30.0		
<i>Hydrangea petiolaris</i>			14.4	23.1		
<i>Hylodesmum podocarpum</i>					9.4	17.4
<i>Phryma leptostachya</i>					13.8	18.6
<i>Schizophragma hydrangoides</i>			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* spp. 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.*
233 *suaveolens*, and *Alnus hirsuta*. The Broadleaf canopy composition resembled the natural
234 forests in the area around Mount Usu. The Mixed forest had a higher density of immigrating
235 species than the Abies forest, but also had unique species, such as *H. paniculata* and *Swida*
236 *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.

240 Table 2. Stem number of dominant trees by forest types. Species with the five highest stem
 241 numbers are shown. The total area sampled is 500 m² for each forest.

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

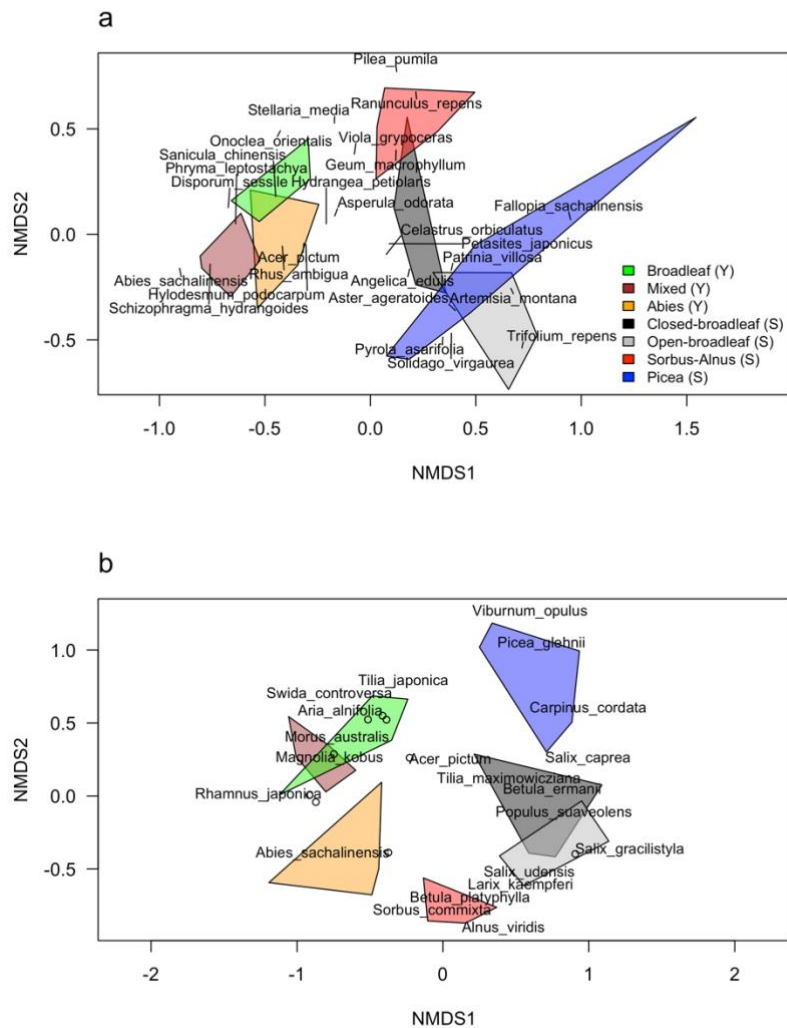
Yosomi	Broadleaf	Mixed	Abies
<i>Acer pictum</i> subsp. <i>Mayrii</i>	18		
<i>Kalopanax septemlobus</i>	8		
<i>Morus australis</i>	8	4	
<i>Populus suaveolens</i>	8		2
<i>Acer pictum</i> subsp. <i>Mono</i>	7		
<i>Abies sachalinensis</i>		28	62
<i>Alnus hirsuta</i>		3	3
<i>Betula platyphylla</i>			2
<i>Hydrangea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

242

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

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

268

The canopy composition changed little during the five years, not considering the

269

damages from the 2017 typhoon, which mainly affected plantations (Supplementary table S1).

270

However, the nMDS showed that the understory composition of the forests was altered: the

271

scores of the summit forests displayed leftward movement, and those of the Yosomi forests

272

displayed downward movements in the nMDS space apart from the Broadleaf forest (Figure

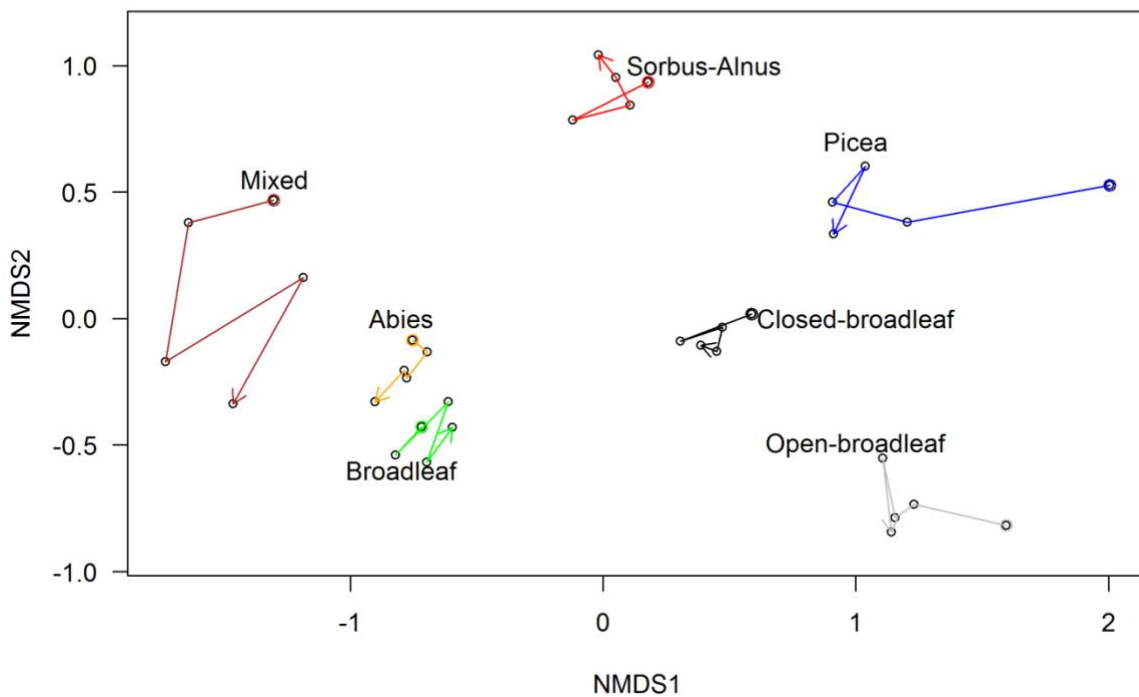
273

3). The relative position of the forest types did not change either within Yosomi or within the

274

summit, but as the summit forests were located on the right side in the nMDS space and the

275 Yosomi forests on the left, the young summit forests' scores moved towards the mature
 276 Yosomi forest communities. The movement was slow, except between 2015 and 2016 at the
 277 summit, when a large shift occurred in the understorey communities. This shift resulted from
 278 the doubling of the understorey sampling area between those years. At Yosomi, no large shift
 279 was observed between 2015 and 2016, suggesting that increasing the surveyed area had less
 280 effect there.

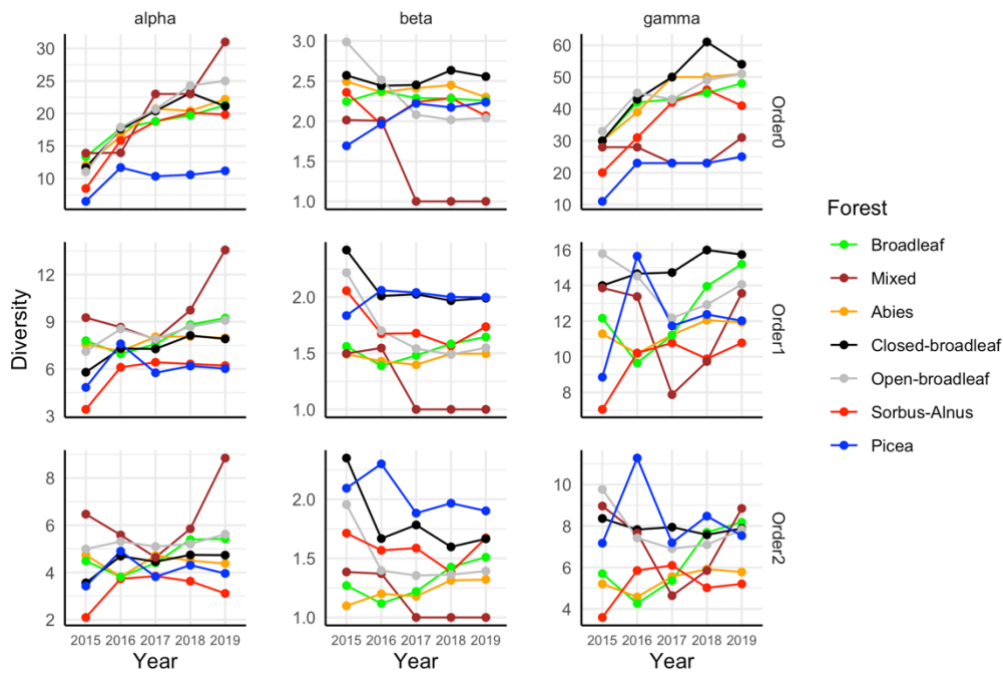


281
 282 Figure 3. Annual changes of forests' scores in the nMDS space by understorey density. The
 283 start of the arrow represents 2015 and the arrowhead shows 2019.

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

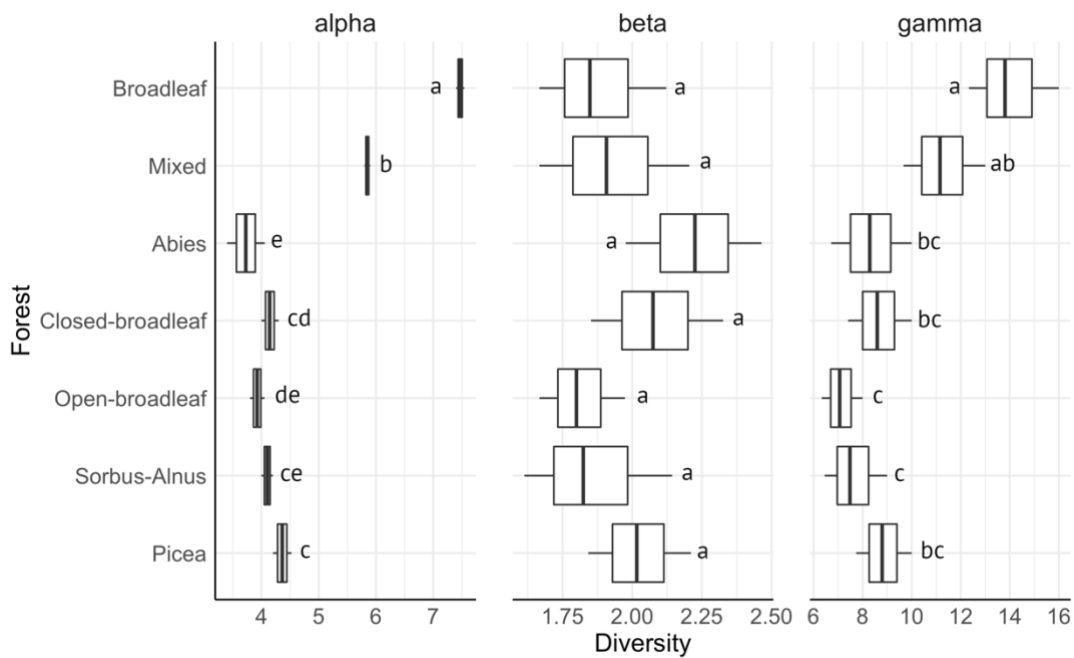
299 Table 3. Statistical summary of forest level understorey diversity. Mean is shown with
 300 standard deviation in parentheses. Statistical significance was calculated by GLMM models
 301 (log-normal distribution) using survey year as random effect and forest type as fixed effect.
 302 The first three forests are at Yosomi and letters mark significant difference at $p < 0.05$. *: $p <$
 303 0.05, **: $p < 0.01$, and ***: $p < 0.001$.

Order 0	Alpha			Beta			Gamma		
Broadleaf	19.4	(1.5)***	d	2.3	(0.1)***	a	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)	a	47.5	(5.7)	ab
Closed-broadleaf	20.6	(2.3)***	bc	2.5	(0.1)	a	52.0	(7.5)*	a
Open-broadleaf	22.0	(3.3)***	ab	2.2	(0.2)	a	47.0	(3.7)	ab
Sorbus-Alnus	18.6	(2.0)*	d	2.1	(0.2)	a	40.0	(6.4)	b
Picea	11.0	(0.6)***	e	2.1	(0.1)	a	23.5	(1.0)***	c

Order 1									
Broadleaf	8.1	(1.1)***	b	1.5	(0.1)***	b	12.5	(2.5)***	ab
Mixed	10.0	(2.5)***	a	1.1	(0.3)***	c	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)***	a	15.3	(0.7)**	a
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)***	a	12.9	(1.8)	ab
Order 2									
Broadleaf	4.8	(0.8)***	bc	1.3	(0.2)***	ce	6.4	(1.9)***	ab
Mixed	6.2	(1.8)***	a	1.1	(0.2)**	e	6.7	(1.9)	ab
Abies	4.4	(0.4)	bc	1.3	(0.1)	de	5.5	(0.6)	b
Closed-broadleaf	4.7	(0.1)	bc	1.7	(0.1)***	b	7.8	(0.2)	ab
Open-broadleaf	5.3	(0.2)	ab	1.4	(0.0)	cd	7.3	(0.4)	ab
Sorbus-Alnus	3.6	(0.3)**	c	1.6	(0.1)**	bc	5.5	(0.5)	b
Picea	4.2	(0.5)	bc	2.0	(0.2)***	a	8.6	(1.9)**	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.



310

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

314 High understorey diversity indices did not predict high canopy diversity indices and
 315 vice versa. For example, understorey N_0 and N_1 of the Picea forest were the lowest and
 316 medium-level respectively, whereas the same canopy indices were high. In general, the
 317 canopy showed higher β -diversity indices than the understorey at both sites, indicating that
 318 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 ($r = 0.25\text{--}0.27, p < 0.01$) 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

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

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

370 Seed dispersal limitation influences the understorey species composition (Baeten et
371 al., 2015; Graae et al., 2004; Verheyen et al., 2003). Seed limitation can result from either
372 large distance to seed sources or from limited seed production. Both the *Picea* and *Sorbus-*
373 *Alnus* forests were close to the natural forests surrounding the summit and to the Closed-
374 broadleaf forest. The large overlap of the understorey species composition of the *Picea* forest

375 with those of the broadleaved forests indicated that distance dependent dispersal limitation
376 was not an issue. We suggest that the understorey composition in the Sorbus-Alnus forest was
377 determined not by seed dispersal limitation, but by competition for resources (Bourgeois et
378 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

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

399 Mixed forest and at the summit the Picea forest became the most diverse forests together with
400 their 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 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

448 forests. As the understorey composition of all summit forests moved closer to those of the
449 Yosomi forests during the five years of this study, the effect of early management is expected
450 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
464 plantations over time, but the immigration process was slow; additional actions are needed to
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.

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475 **7. Author contributions**

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

478 **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](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-](https://doi.org/10.1111/1365-2745.13120)
496 [2745.13120](https://doi.org/10.1111/1365-2745.13120)
- 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](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](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](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&block_no=0132&year=&month=&day=&view= (accessed 9.27.19).
568

- 569 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 understory 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.1472-4642.1999.00056.x>
- 596
- 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.1365-2745.2000.00503.x>
- 600
- 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 Meyer, 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 Mudrak, O., Dolezal, 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. *Forest Ecology and Management* 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., Šrutek, 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., McGlenn, 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-Davila, E., Ascarrunz, N.,
643 Balvanera, P., Becknell, J.M., Bentos, T.V., Brancalion, P.H.S., Cabral, G.A.L.,
644 Calvo-Rodriguez, S., Chave, J., Cesar, 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., Duran, S.M., Dutrieux, L.P.,
647 Espiritu-Santo, M.M., Fandino, M.C., Fernandes, G.W., Finegan, B., Garcıa, H.,
648 Gonzalez, N., Moser, V.G., Hall, J.S., Hernandez-Stefanoni, J.L., Hubbell, S.,
649 Jakovac, C.C., Hernandez, A.J., Junqueira, A.B., Kennard, D., Larpin, D.,
650 Letcher, S.G., Licona, J.-C., Lebrija-Trejos, E., Marın-Spiotta, E., Martınez-
651 Ramos, M., Massoca, P.E.S., Meave, J.A., Mesquita, R.C.G., Mora, F., Muller,
652 S.C., Munoz, R., de Oliveira Neto, S.N., Norden, N., Nunes, Y.R.F., Ochoa-
653 Gaona, S., Ortiz-Malavassi, E., Ostertag, R., Pena-Claros, M., Perez-Garcıa,
654 E.A., Piotto, D., Powers, J.S., Aguilar-Cano, J., Rodriguez-Buritica, S.,
655 Rodriguez-Velazquez, J., Romero-Romero, M.A., Ruız, J., Sanchez-Azofeifa,
656 A., de Almeida, A.S., Silver, W.L., Schwartz, N.B., Thomas, W.W., Toledo, M.,
657 Uriarte, M., de Sa 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, 77–84.
664 <https://doi.org/10.3159/10-RA-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/s11258-008-9549-0>
- 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.1365-2745.2003.00807.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 Grolemond, 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