Title: Which native legume or non-legume nitrogen-fixing tree is more efficient in restoring post-landslide forests along an environmental gradient?

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Data availability

The data is available from the following data repository.

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Abstract

Under climate change, heavy precipitation is predicted to trigger frequent shallow landslides. To accelerate vegetation recovery after landslides, planting nitrogen (N)-fixing trees is a promising technique. However, a comparison of the performance of non-legume and legume N-fixing species planted across a wide range of environments after landslides has not been conducted, which is problematic for determining the most efficient tree species for restoration. We planted the seedlings of a native legume (*Lespedeza bicolor*) and a native non-legume (*Alnus hirsuta*) tree species and monitored their survival in 15 landslide forests artificially established across a variety of environments in northern Japan. The landslides were mimicked by removing standing trees and surface soil with heavy machinery from the sites. There was a significant difference in the survival rate of seedlings between the two species. The survival rate was significantly higher for *L. bicolor* than for *A. hirsuta*. Furthermore, the performance of the two species differed along the environmental gradient of post-landslide forests. Interestingly, *L. bicolor* seedlings survived better in the steeper post-landslide forests, probably due to less exposure to ungulate herbivory. On the other hand, the warmer air temperature and serpentine soil negatively influenced the survival of *A. hirsuta*, which indicates different environmental preferences of N-fixing plants in post-landslide forests.

Our results suggest that for efficient forest restoration after landslides, careful selection of N-fixing plants based on slope conditions is essential.

Keywords: disturbance, plant and soil interaction, functional traits, nature-based solution, geodiversity

Introduction

Extreme climate is predicted to occur more frequently worldwide until the end of the 21st century (IPCC, 2021). Climate change is one of the major drivers of changing disturbance regimes (Seidl et al., 2017). In northern Japan, heavy precipitation exceeding 30 mm per hour is expected to increase (Sapporo District Meteorological Observatory, 2017) and trigger frequent shallow landslides (Gariano and Guzzetti, 2016). In addition, Japanese forests have been suffering from intermittent earthquakes and consequent landslides (Kasai and Yamada, 2019). Landslides are a form of slope failure characterized by the rapid mass movement of soil and/or rock (Walker et al., 2009) and one of the most severe disturbance in temperate forests (Hotta et al., 2024). After landslide, because of the unstable surface soil as well as the limited soil nitrogen (N) availability for plants, the revegetation is often difficult (Walker et al., 1996). To efficiently rehabilitate the ecosystem functions damaged by landslides in the future, it is urgently necessary to develop a technique to accelerate the re-vegetation of damaged forests.

Planting N-fixing plants is a promising traditional technique for accelerating vegetation recovery after severe disturbance (Walker & Del Moral, 2009) but little is understood about which of the legume or non-legume N fixing plants is efficient for re-

77 vegetation. In terrestrial ecosystems, soil N availability often limits the performance of
78 plants, especially at early stages after severe disturbance (Wardle et al., 2004). N-fixing
79 plants can utilize fixed N for their growth and subsequent survival with less influence
80 from soil N limitation than in non-N-fixing plants (C.Martínez-Garza et al., 2013). In
81 fact, the seedlings of legumes, which are the most dominant N-fixing group, had higher
82 survival rates than those of non-N-fixing species after being planted in post-landslide
83 forests of the Himalayas (Chaudhry et al., 1996). As in this example, the performance of
84 N-fixing plants in the context of ecosystem restoration has been evaluated often by
85 comparison with non-N-fixing plants (e.g., Gao, Wang, Fu, & Zhao, 2017; Siddique et
86 al., 2008). In addition, among legume species, interspecific comparisons of plant
87 performance were conducted to identify the efficient species of N-fixing plants for
88 restoration (Jaquetti and Gonçalves, 2021). On the other hand, there are many non-
89 legume N-fixing plants (actinorhizal plants) across the world (Steidinger et al., 2019): at
90 least 220 species of non-legume N-fixing plants, which belong to 25 genera and eight
91 families (Sprent and Parsons, 2000). However, to the best of our knowledge, little is
92 known about the relative performance including growth and survival of non-legume and
93 legume N-fixing plants after their plantation in post-landslide forests (but see Chaudhry
94 et al., 1996), which is problematic for determining the most efficient tree species for

95 restoration with high survival and growth. Functional traits, which can determine the
96 species-specific environmental preference and affect plant survival after disturbance
97 (Pérez-Harguindeguy et al., 2013). In tropical rainforests, for instance, not leaf N
98 contents but specific leaf area (SLA), leaf water contents, and wood density differ
99 between legume and non-legume N-fixing plants (Powers and Tiffin, 2010). The large
100 interspecific difference in leaf functional traits even between legume and non-legume
101 N-fixing plants can result in differential survival and growth of the two. Therefore,
102 understanding differences in performance of legume and non-legume N-fixing plant
103 species after landslides based on their functional traits is critical toward better
104 restoration practices.

105 Furthermore, to understand the fundamental principle of restoration practice
106 adaptable across large area, it is important to clarify the context-dependent survival and
107 growth of N fixing plants across a variety of post-landslide forests. In addition to the
108 soil N availability, stability of surface soil and soil water availability influence the plant
109 survival and growth in post-landslide forests (Chaudhry et al., 1996; Walker et al., 1996).
110 However, because landslides often occur sporadically across space, little is understood
111 about the survival and growth of planted seedlings across a number of post-landslide
112 forests (but see the example testing eight landslides (Pang et al., 2018). This knowledge

gap could be overcome, for example, by conducting a large-scale, artificial landslide experiments with replications across a variety of environments.

By considering the interspecific difference of plant functional traits and large environmental gradients across post-landslide forests, we hypothesize that 1) there are significant interspecific differences in the survival and growth of legume and non-legume tree species after plantation in post-landslide forests. Furthermore, we also hypothesize that 2) the influential environmental factors on the survival and growth are different between the two N fixing species in post-landslide forests.

To test these hypotheses, we conducted large-scale, artificial landslide experiments with replications across a variety of environments in northern Japan. This experimental design allowed us to detect environmental preferences across the large range of environmental conditions established after landslides. The results are expected to be useful for understanding the general principles of the relationships between N-fixing plants' features and environmental preference across many landslides, in turn allowing the best plant species for a given landslide to be planted efficiently.

Material and Method

Experimental design

131 The tree plantation experiment was conducted at the “Artificial Landslide Experimental
132 Sites (ALES)” established across three experimental forests of Hokkaido University in
133 northern Hokkaido, Japan. We prepared 15 artificial landslide sites for our project
134 during summer 2020. The slope angle ranged from 1 to 26° (mostly from 11 to 26°) in
135 our study system (Table 1). We established our experimental sites on these slopes by
136 considering that, in the case of the recent catastrophic earthquake that occurred near the
137 region in 2018, the average slope angle of 6117 landslides was 26° with a range from 5
138 to 45° (Kasai and Yamada, 2019), and rehabilitation by plantation is planned on gentler
139 slopes (less than 29°) to decrease the injury risk during plantation in the damaged area
140 (Liaison Meeting for Forest Restoration and Forestry Recovery in the Eastern Iburi
141 Region, 2021). At each site, all trees in a 40 m by 40 m area were harvested between
142 December 2019 to March 2020, and the root system, understory vegetation and surface
143 soil were removed in an area of 30 m by 30 m by using bulldozers and power shovels in
144 summer 2020. The removed roots and soil were accumulated on the lower side of each
145 site to mimic the accumulation zone after a landslide, although this experimental
146 treatment primarily mimicked the erosional zone of a landslide (Furusawa et al., 2023).
147 The whole A horizon (on average approximately 20 cm) and the upper 30 cm of the B
148 horizon (approximately 50 cm in depth from the ground surface), which together reflect

149 the depth at which the soil starts to fail on the slope to cause shallow landslides
150 (Dietrich et al., 2007), were removed from the soil profile. Removal of deeper soil
151 would have preferable, but 50 cm was the maximum and most realistic depth to which
152 we could remove soil to create artificial landslides. The aerial photography of a
153 experimental site can be seen in Furusawa et al. (2023).
154
155 *Environmental variables*
156 At each site, the average slope angle was measured by surveying in the field. The soil
157 properties included soil type, inorganic N content (which is the sum of ammonium N
158 and nitrate N), the clay fraction, soil moisture content, and the erosion rate of surface
159 soil. Specifically, the bedrock (either sedimentary rocks or ultramafic rocks
160 (serpentine)) was determined by using the geological map and by digging to examine
161 the soil profile in the field. Following the World Reference Base for Soil Resources, the
162 soil type developed on sedimentary rock was identified as Dystric Cambisol while that
163 on serpentine was done as Eutric Cambisol. To differentiate the two types of Cambisol
164 on two types of bedrock conveniently, we call the soil developed on sedimentary rock as
165 “brown forest soil” and that on serpentine as “serpentine soil” in this study by following
166 the identification in Kayama et al. (2005). For inorganic N, the soil samples were

obtained from the upper 10 cm at nine locations at each site, and the composite of the nine samples was used as the representative soil for that site. The composite soil was sieved through a 2 mm mesh, and 8 g of soil was shaken with 40 ml of 2 M KCl solution for one hour and filtered (Advantec 5B, Advantec Co. Ltd., Tokyo). The concentrations of NH_4^+ and NO_3^- in the extract solutions were determined using a continuous flow injection analyser (AACS-4, BL-Tech Co. Ltd., Osaka) (see the details in Makoto, Minamiya, & Kaneko, 2016). Additionally, for the determination of clay (particles with diameters under 0.005 mm) content, we used the composite sample for sedimentation particle size analysis. The soil moisture at each site was measured at the centre of the site by conducting continuous monitoring every 10 minutes over the growing season of the plants with a soil moisture sensor (10HS, ONSET, US) and averaging the values over the season at each site. The erosion rate of the surface soil was measured by using sediment traps (Miura et al., 2003). The traps were set from the middle of summer 2020 to the beginning of winter (November) because this is the rainiest season during the year. The width of the traps was 25 cm, and three traps were set at each site (a total of 45 traps). Measurements were expressed as transport rates, which corresponded to the amount of transported mass per millimetre of rainfall ($gm^{-1}mm^{-1}$) (the precipitation was measured for each site as explained below).

185 The meteorological parameters were measured or estimated for mean annual air
186 temperature, annual precipitation, and solar radiation. The mean annual temperature at
187 each site was estimated based on monitoring data from the nearest meteorological
188 station and the rate of decrease with increasing altitude (0.6 °C/100 m) at each site.
189 Because the 15 sites are distributed across a wide region of northern Hokkaido, we
190 employed data from four meteorological stations in four experimental forests (Toyotomi
191 meteorological station, Otoineppu meteorological station, Shumarinai meteorological
192 station and Horokanai meteorological station). On average, the distance between the site
193 and each of the four stations was 10 km. The sum of precipitation during the growing
194 season (from June to October) at each site was measured by a tipping bucket rain gauge
195 (RG3-M, ONSET, USA). Solar radiation was measured by using light sensors for
196 relative photosynthetically active photon flux density (rPPFD) (S-LIB-M003, ONSET,
197 USA) set at each site. In addition, we also determined the difference in land use (natural
198 forests or artificial forests) to cover the wide range of vegetation types in our region.
199
200 *Functional traits*
201 The trait measurement was conducted by following (Pérez-Harguindeguy et al., 2013).
202 For *Lespedeza bicolor* Turcz. (Fabaceae) and *Alnus hirsuta* Turcz. (Betulaceae), we

measured specific leaf area (SLA), leaf C:N, stem tissue density (STD), fine root diameter (RD), root tissue density (RTD), specific root length (SRL) and maximum root depth (hereafter max. root depth) as functional traits which can potentially related with the performance of seedlings in post-landslide forests (also see our previous study Zeng and Makoto, 2023). Both species are native species and are often used for restoration purposes in the Hokkaido region. To know the representative value of the functional traits in each species, the above-mentioned traits were measured for 5 one-year old seedlings respectively for each species planted in a common garden in Nayoro Forest Research Office which distribute the middle of three experimental forests where plantation experiment was conducted.

First, max. root depth was determined by excavating and measuring the deepest soil depth reached by the roots of each seedling. After the excavation, we carefully washed the seedlings and three fine roots (< 2mm in diameter) were collected randomly from the root system of each seedling and scanned with a double-lamp bed scanner (GT-X970, Epson, Suwa City, Japan). By using the scanned image, the fine root diameter, fine root length and fine root volume were determined using WinRHIZO Reg (version 2009a, Regent Instrument, Sainte Foy, QC, Canada). Then, the scanned fine roots were dried at 70ºC for 48 h and weighed dry mass to calculate the RTD

221 (g/cm^3) from the ratio of dry mass to volume of the fine root samples and SRL (m/g)
222 from the ratio of length to dry mass. For the aboveground traits, we also scanned the
223 stem and three leaves respectively for each seedling. Then, the scanned leaves were
224 dried at 70ºC for 48 h and weighed to calculate the SLA from the ratio of area to dry
225 mass (m^2/kg) and stem tissue density (STD) from the ratio of dry mass to stem volume
226 (g/cm^3). The dried leaves were grounded by using ball mill and measured carbon and N
227 contents with CHNO analyzer (PE-2400 series, Perkin-Elmer, Norwalk, CT). By using
228 C and N contents data, leaf C:N ratio was calculated.
229
230 *Survival and Growth*
231 One-year-old seedlings of *L. bicolor* and *A. hirsuta* were planted at 15 artificial
232 landslide sites. At each site, a total of 24 seedlings of each species were planted in
233 September 2020 when the trees had already shed their leaves. In August 2021, tree
234 survival was assessed after one year of plantation. In a previous study, 12 months was
235 found to be informative enough to predict tree survival under restoration practices in
236 degraded terrestrial ecosystems (Cristina Martínez-Garza et al., 2013). Survival was
237 evaluated based on the presence of leaves and the freshness of the leaves and branches.
238 Furthermore, when the seedlings were uplifted and/or disappeared from their position in

239 the planation, they were inferred to have died. For the surviving seedlings, the height
240 and basal area were also measured. The basal area was calculated based on the diameter
241 at the bottom of the stem together with the number of resprouting stems if the seedling
242 resprouted.
243 As supplementary data, the major cause of mortality was visibly speculated based
244 on the condition of the seedlings. The causes were categorized into drought, break,
245 herbivory (by mammals), uplift, and missing for each individual. When the trees
246 possessed dry leaves (often black in colour) and dry winter buds with non-fresh
247 branches, the cause of mortality was defined as drought. When the branches of the main
248 stem of the trees were broken physically, the leaves and primary branches were not
249 eaten, and the broken branches were not fresh, the cause of the mortality was defined as
250 break. When the leaves and/or primary branches were eaten and the branches were not
251 fresh, the cause of mortality was defined as herbivory. When the seedlings were uplifted
252 and the entire root system was exposed, the cause of mortality was defined as uplifted.
253 Last, when the seedlings disappeared from the position where they were planted, the
254 cause of mortality was defined as “missing”.
255
256 *Statistical analysis*

The difference of each functional traits between the two species was analysed with Student's t-test. When the p value was less than 0.05, the functional traits was identified to be significantly different between the two species.

The relationships between survival (response variable) and the environmental factors (explanatory variable) were analysed with generalized linear mixed models (GLMMs). In the mixed model, the site ID was set as the random intercept factor. The survival data were assumed to follow a binomial distribution (0 represented mortality, and 1 represented survival), and height and basal area were assumed to follow a Gaussian distribution. First, the multicollinearity of the explanatory variables was assessed for the model including all environmental factors by employing the vif function in the library “car”. If the variance inflation factor (VIF) was larger than 10, the variable was excluded from the model. This procedure was repeated until the VIF of all explanatory variables was less than 10. The model excluding the explanatory variables with multicollinearity was set as a full model, and then pairwise model selection was conducted by using the dredge function in the MuMIn library. Afterwards, for the explanatory variables included in the selected best model, we conducted the Wald test. When the p value was less than 0.05, the explanatory variable was identified

as having a significant influence on the survival of the seedlings. All statistical analyses were conducted in R software version 4.3.0. (R development core team 2023).

Results

Except RD and Max. root depth, the functional traits were significantly different between the two plant species. For the aboveground traits, SLA and STD were significantly higher for *L. bicolor* than for *A. hirsuta*, while leaf C:N was significantly lower for *L. bicolor* than for *A. hirsuta* ($p<0.05$, Table 2). For the belowground traits, while SRL was significantly higher for *L. bicolor* than for *A. hirsuta,* RTD was significantly lower for *L. bicolor* than for *A. hirsuta* ($p<0.05$, Table 2).

There was a significant difference in the survival rate of seedlings between the two species. The survival rate was significantly higher for *L. bicolor* than for *A. hirsuta* ($p<0.001$, Fig. 1). For *A. hirsuta*, air temperature and soil type significantly influenced the survival rate. Specifically, air temperature negatively influenced the survival of *A. hirsuta* ($p<0.05$, Table 3), and the survival rate of *A. hirsuta* was significantly lower in serpentine soil than in brown forest soil ($p<0.001$, Fig. 2). For *L. bicolor*, slope angle, soil clay content, soil water content and soil N content significantly influenced the survival rate. Specifically, in the post-landslide forests with steeper

292 angles ($p<0.01$), less clay ($p<0.05$), drier soil ($p<0.01$), and infertile soil ($p<0.05$), the *L.*
293 *bicolor* seedlings survived better (Table 3).

294 For *A. hirsuta*, there were no environmental factors that influenced the
295 height of the seedlings (Table 3). Meanwhile, for *L. bicolor*, air temperature, slope
296 angle, soil type, soil clay content, and soil water content significantly influenced the
297 height of the seedlings. Specifically, in the post-landslide forests with warmer
298 temperatures ($p<0.05$), steeper slopes ($p<0.05$), serpentine soil ($p<0.01$, Fig. 3), less
299 clay ($p<0.001$) and drier soil ($p<0.05$), the height of *L. bicolor* seedlings was
300 significantly higher (Table 3).

301 For *A. hirsuta*, air temperature, solar radiation, and slope angle significantly
302 influenced the basal area of the seedlings. Specifically, warmer temperatures, more solar
303 radiation and steeper slopes increased the basal area of *A. hirsuta* seedlings (Table 3).
304 For *L bicolor*, solar radiation, slope angle, and clay content significantly influenced the
305 basal area of the seedlings. Specifically, more solar radiation, steeper slopes and less
306 clayey soil increased the basal area of *L. bicolor* seedlings (Table 3).

307

308 **Discussion**

309 Consistent with the first hypothesis, even within the N-fixing trees, there was a

significant interspecific difference in survival. Furthermore, as predicted by the second hypothesis, the influential environmental factors on the survival and growth were different between the two N fixing species in post-landslide forests, which indicated the interspecific environmental preferences of N-fixing plants. To the best of our knowledge, this is the first study to compare the performance of legume and non-legume N-fixing species in terms of their restoration efficiency after disturbance.

The higher survival rate of *L. bicolor* than *A. hirsuta* can be due to the differential functional traits (as can be seen in Table 2). High stem tissue density of woody species is known to be advantageous to be resistant for the physical damage such as soil erosion after landslide (Kang et al., 2022; Pérez-Harguindeguy et al., 2013). Furthermore, high SRL can be beneficial to explore soil nutrients in disturbed forests (Cheng et al., 2012) such as N-limited post-landslide forests (Walker et al., 1996).

Based on the survival data, while *A. hirsuta* preferred brown forest soil under cooler temperatures, *L. bicolor* survived better after landslides with less clay and water in the soil and on steeper slopes. Compared to serpentine soil, brown forest soil has a higher content of phosphorous (P) (Toro et al., 2023). Soil P availability is often a limiting factor for the nutrient relations of N-fixing plants (Toro et al., 2023), which may explain why *A. hirsuta* prefers brown forest soil over serpentine soil, with higher

328 survival in the former. The smaller limitation of N in *L. bicolor*, which is highlighted
329 with lower leaf C:N, allow us to expect a greater P limitation *L. bicolor* and thus
330 negative effect of serpentine on the survival of *L. bicolor,* which is contradictory to our
331 results. The absence of negative effect of serpentine soil on *L. bicolor* could be due to
332 that legume plants with rhizobial symbiosis can activate root phosphomonoesterase
333 (PME) to acquire soil P under P limited soil condition while actinorhizal plants
334 generally show low PME activity in such condition (Ardley and Sprent, 2021; Png et al.,
335 2017) It should be noted that the survival rate of *A. hirsuta* was higher at cooler sites. It
336 is known that *Alnus* species show higher N fixation performance as well as
337 photosynthesis at cooler temperatures compared to legume species (Bytnerowicz et al.,
338 2022), which can partly contribute to the higher survival of *A. hirsuta* in cooler
339 environments. The preference of cooler climate by *A. hirsuta* can be consistent with the
340 latitudinal pattern that northern hemisphere is dominated with *Alnus* north of 35°
341 whereas N-fixing legume is done equatorward of 35° .(Menge et al., 2014). Meanwhile,
342 *L. bicolor* is known to prefer well-drained soil (Mitchell, 1986), which explains its
343 negative response to higher soil clay and moisture contents (Table 3). The higher SRL
344 in *L. bicolor* (Table 2) can also contribute to the efficient water absorption from soil in
345 relatively drier soil. It is unclear why soil inorganic N availability had a negative impact

346 on the survival of *L.bicolor*. Atmospheric N deposition can negatively influence the
347 survival of legume plants (Tognetti et al., 2021). However, considering that atmospheric
348 N deposition can decrease the survival of legume plants via the selective increase in
349 non-N fixing plants but that there were few plants surrounding the planted *L. bicolor* at
350 our sites, we should be careful in inferring the underlying mechanisms. The small
351 positive effect of N availability on N-fixing plants (especially on *L. bicolor* which is
352 little limited by soil N availability because of leaf C:N) can partly explain the non-
353 positive relationship between soil N availability and the survival of *L. bicolor*.
354 It was surprising that *L. bicolor* survived better on steeper slopes than on
355 gentler slopes (Table 3), as steeper slopes were expected to have a negative influence on
356 the trees via surface soil movement. The main cause of mortality in *L. bicolor* was the
357 disappearance of the planted seedlings (Fig. 4). Disappearance of seedlings can occur
358 either via washout during soil erosion or via mammal herbivory. The sika deer (*Cervus*
359 *nippon*) population has greatly expanded in the last few decades, and their density has
360 remained high in the Hokkaido region, seriously influencing forest vegetation
361 (Takatsuki, 2009). It is also known that the browsing of planted tree seedlings by sika
362 deer is dominant on gentler slopes compared to steeper slopes due to the difficulty of
363 accessing steeper slopes for sika deer (Nomiya et al., 2019). In fact, the automatic

364 shooting camera revealed a high frequency of deer visits to gentle slopes (Fig. S1).
365 Furthermore, the planted seedlings were sometimes found at higher positions on the
366 slope than those where they were originally planted (Makoto, personal observation).
367 These findings together suggest that the survival rate of *L. bicolor* was lower on gentler
368 slopes because of higher browsing and herbivory by deer on gentler slopes. It is also
369 interesting that the positive effect of steeper slopes on survival was evident not for *A.*
370 *hirsuta* but for *L. bicolor* (Table 3). This species difference is likely due to the
371 difference in palatability of the two species. While both are N-fixing plants, *Alnus*
372 species generally have higher leaf C:N ratios than other N-fixing species (Table 2) and
373 are thus less palatable (Suzuki et al., 2011), and Lespedeza species have lower leaf C:N
374 ratios (Table 2) and are known to be relatively palatable among the tree species in
375 temperate forests (Tashiro et al., 2013). For the use of N-fixing plants for restoration in
376 areas with dense herbivorous mammals, palatability should be considered for successful
377 plantation, especially at sites with gentler slopes.
378 While no environmental factors influenced the height growth in *A. hirsuta*,
379 warmer air temperatures, steeper slopes, serpentine soil, and less clayish N-limited soil
380 increased the height of *L. bicolor* (Table 3). The photosynthesis and N fixation of
381 legume N-fixing species are known to be more active at warmer temperatures

382 (Bytnerowicz et al., 2022), which can result in higher stature of the seedlings. Similarly,
383 in terms of survival, *L. bicolor* performs better in well-drained habitats, and thus, height
384 growth was higher in less clayish, drier soil in our study system (Mitchell, 1986),
385 although the negative effect of soil N on height growth was again not clear. Given the
386 significant negative effect of deer herbivory on *L. bicolor*, the higher soil N may have
387 resulted in a lower leaf C:N ratio of *L. bicolor*, which may have indirectly resulted in a
388 higher rate of deer herbivory and thus a decrease in the height of the planted seedlings.
389 In fact, higher soil N availability can increase deer browsing of trees in temperate
390 forests (Tripler et al., 2002).

391 While higher radiation and steeper slopes resulted in larger basal areas for
392 both species, a positive impact of warmer air temperature and a negative impact of
393 increasing soil clay content were observed for *A. hirsuta* and *L. bicolor* (Table 3). More
394 solar radiation generally increases basal area by accelerating the radial growth of plants.
395 Especially in habitats without canopies and competitors after disturbance, because of the
396 small limitation of light availability and the minimal need to compete for light in tree
397 seedlings, biomass is often allocated to developing the canopy and coincidentally basal
398 area for an efficient increase in leaves and photosynthesis there (Bebre et al., 2021).
399 Steeper slopes are known to increase the basal area (and diameter) of trees planted for

400 forest rehabilitation (Attarik et al., 2021), although the underlying ecophysiological
401 mechanisms are not well understood. One possibility is that on steeper slopes, to be
402 resistant to falling or soil erosion, the stem diameter must be larger. The positive effect
403 of temperature on *A. hirsuta* was contradictory to the result showing a negative
404 influence of air temperature on the survival rate. It is possible that the taller seedlings
405 were more sensitive to mortality-inducing stress on the slope. The most and second
406 most common causes of mortality were drought stress and uprooting of the seedlings of
407 *A. hirsuta,* respectively (Fig. 4). Warmer temperatures might increase seedling height,
408 but the higher stature of the seedlings (with greater slenderness) might increase their
409 susceptibility to uprooting on the slope (Hirata et al., 2014); thus, the survival rate was
410 low, and among the seedlings that survived, the height was greater. The negative impact
411 of the clay content in soil on the basal area of *L. bicolor* would be, similar to survival,
412 due to the preference of this species for well-drained soil with higher SRL.
413
414 **Conclusion**
415 The two native legume and non-legume N-fixing tree species showed differential
416 performance after landslides, and their performance differed along the environmental
417 gradients. Our results indicate that to improve the use N-fixing trees for restoration after

landslides, it is better not to simply choose any N-fixing species but to carefully choose the best N-fixing trees. From 2021 to 2020, the worldwide program “UN Decade on Ecosystem Restoration” promoted the development of practical techniques for efficient ecosystem restoration towards the attainment of sustainable developmental goals. Our results suggest that for efficient forest restoration after landslides, the careful selection of tree species within N fixation depending on slope conditions is useful.

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639 **Captions to the tables and figures**

640 **Table 1**: The basic environmental information of 15 sites used in this experiment. Part
641 of the data is shown in Furusawa et al. (2023) because the study site was same with this
642 present study.

643

644 **Table 2**: Basic leaf and fine root functional traits of *A. hirsuta* (*Alnus*) and *L. bicolor*
645 (Lespedeza) seedlings. The value of each trait was shown as an average ± SD. The
646 different alphabets in each trait data indicates the existence of statistically significant
647 difference between the two species with Wald test ($p<0.05$), while n.s. indicates the
648 absence of statistically significant difference between the two species ($p \geqq 0.05$).

649

650 **Table 3**: The results of the generalized linear mixed model analysis for the standardized
651 explanatory variables. The explanatory variables included in the best model selected by
652 the model selection was shown as the numerical values. The values shown as bold
653 characters were those identified as statistically significant ($p<0.05$) with Wald test,
654 while those shown as non-bold characters were statistically non-significant with Wald
655 test.

656

Figure 1: The survival rates of *Alnus hirsuta* (*Alnus*) and *L. bicolor* (*Lespedeza*) seedlings.

Figure 2: The survival rates of *A. hirsuta* (*Alnus*) seedlings in brown forest soil and serpentine soil.

Figure 3: Tree height of the *L. bicolor* (*Lespedeza*) seedlings in brown forest soil and serpentine soil.

Figure 4: Estimated relative percentage of cause of mortality in *A. hirsuta* (*Alnus*) and *L. bicolor* (*Lespedeza*) seedlings.

669 Table 1

Locality	Latitude (°N)	Longitude (°E)	Land use	Soil type	Slope angle (°)
Teshio	44.986	141.994	Natural forest	Brown forest soil	24
Teshio	44.986	141.995	Natural forest	Brown forest soil	23
Teshio	44.987	141.996	Natural forest	Brown forest soil	21
Teshio	45.045	142.102	Natural forest	Serpentine soil	1
Teshio	44.931	141.977	Plantation	Brown forest soil	21
Nakagawa	44.786	142.252	Natural forest	Brown forest soil	19
Nakagawa	44.783	142.254	Natural forest	Brown forest soil	25
Nakagawa	44.796	142.249	Natural forest	Brown forest soil	12
Nakagawa	44.791	142.219	Natural forest	Serpentine soil	19
Nakagawa	44.785	142.255	Plantation	Brown forest soil	26
Uryu	44.382	142.194	Natural forest	Brown forest soil	11
Uryu	44.39	142.204	Natural forest	Brown forest soil	21
Uryu	44.392	142.204	Natural forest	Brown forest soil	21
Uryu	44.147	142.168	Natural forest	Serpentine soil	11
Uryu	44.367	142.246	Plantation	Brown forest soil	22

670

671

672 Table 2

Species	Specific leaf area (m^2 kg^{-1})	Leaf C:N	Stem tissue density (g cm^{-3})	Specific root length (m g^{-1})	Root diameter (mm)	Root tissue density (g cm^{-3})	Max. root depth (cm)
Alnus	206.7 ± 41.2 a	27.1 ± 5.1 b	0.35 ± 0.02 a	31.8 ± 9.9 a	0.34 ± 0.06 n.s.	0.38 ± 0.10 b	10.5 ± 2.3 n.s.
Lespedeza	310.3 ± 82.4 b	15.9 ± 3.9 a	0.48 ± 0.05 b	58.0 ± 21.0 b	0.31 ± 0.04 n.s.	0.25 ± 0.06 a	8.2 ± 2.3 n.s.

673

674

675 Table 3

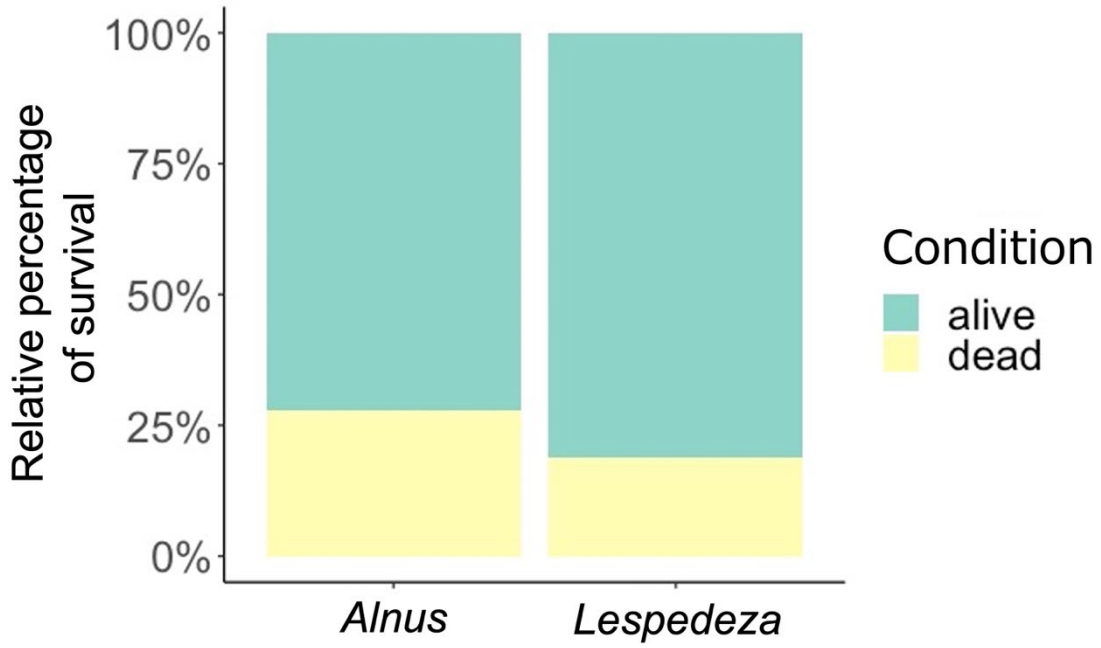
		Explanatory variables																	
		Air temperature		Solar radiation		Slope angle		Soil erosion		Soil type		Clay		Soil water		Soil nitrogen		Land use	
Species	Response variables	Estimate	*p*	Estimate	*p*	Estimate	*p*	Estimate	*p*	Estimate	*p*	Estimate	*p*	Estimate	*p*	Estimate	*p*	Estimate	*p*
Alnus	Survival rate	**-0.412**	**0.018**	n.s.		n.s.		0.436	0.134	**-1.918**	**0.000**	n.s.		n.s.		n.s.		n.s.	
	Height	n.s.		n.s.		n.s.		n.s.		4.759	0.085	-2.827	0.008	n.s.		n.s.		n.s.	
	Basal area	**3.875**	**0.002**	**2.061**	**0.030**	**2.478**	**0.014**	n.s.		n.s.		n.s.		n.s.		-1.345	0.156	n.s.	
Lespedeza	Survival rate	n.s.		n.s.		**0.628**	**0.002**	n.s.		n.s.		**-0.412**	**0.015**	**-0.624**	**0.006**	**-0.414**	**0.019**	n.s.	
	Height	**2.720**	**0.029**	n.s.		**2.569**	**0.016**	-0.889	0.172	**12.215**	**0.003**	**-4.350**	**0.000**	**-3.996**	**0.010**	1.444	0.157	n.s.	
	Basal area	n.s.		**1.444**	**0.048**	**2.353**	**0.005**	n.s.		n.s.		**-0.709**	**0.174**	n.s.		-1.116	0.084	n.s.	

676

677

678 Figure 1

679



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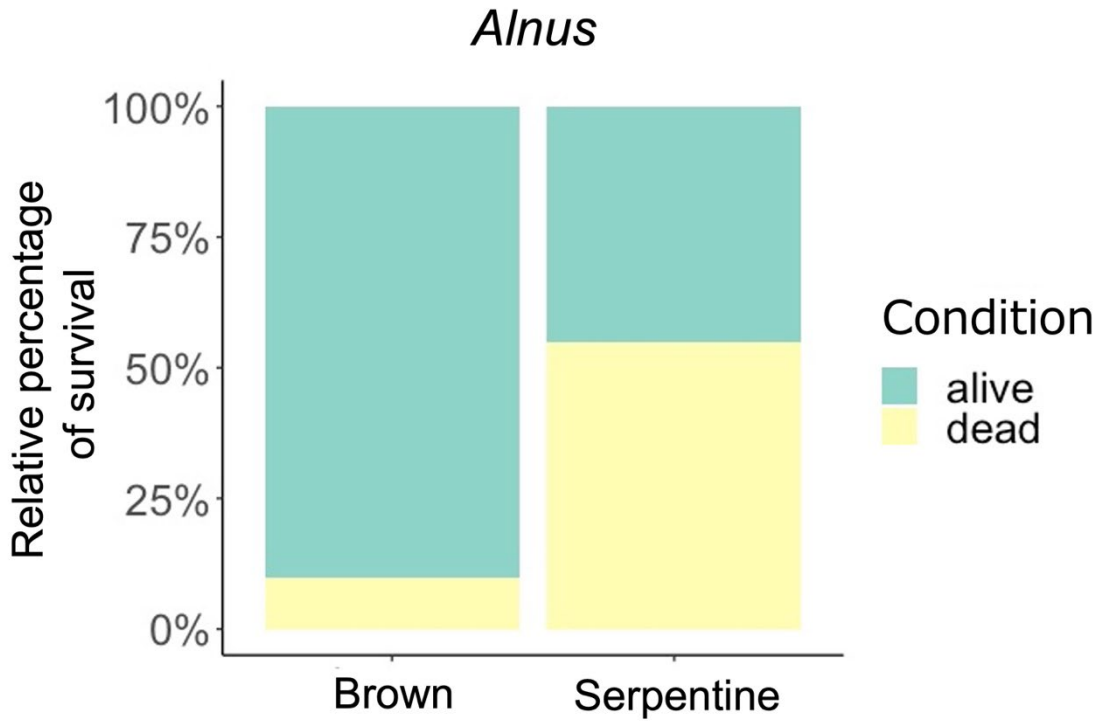
682 Figure 2



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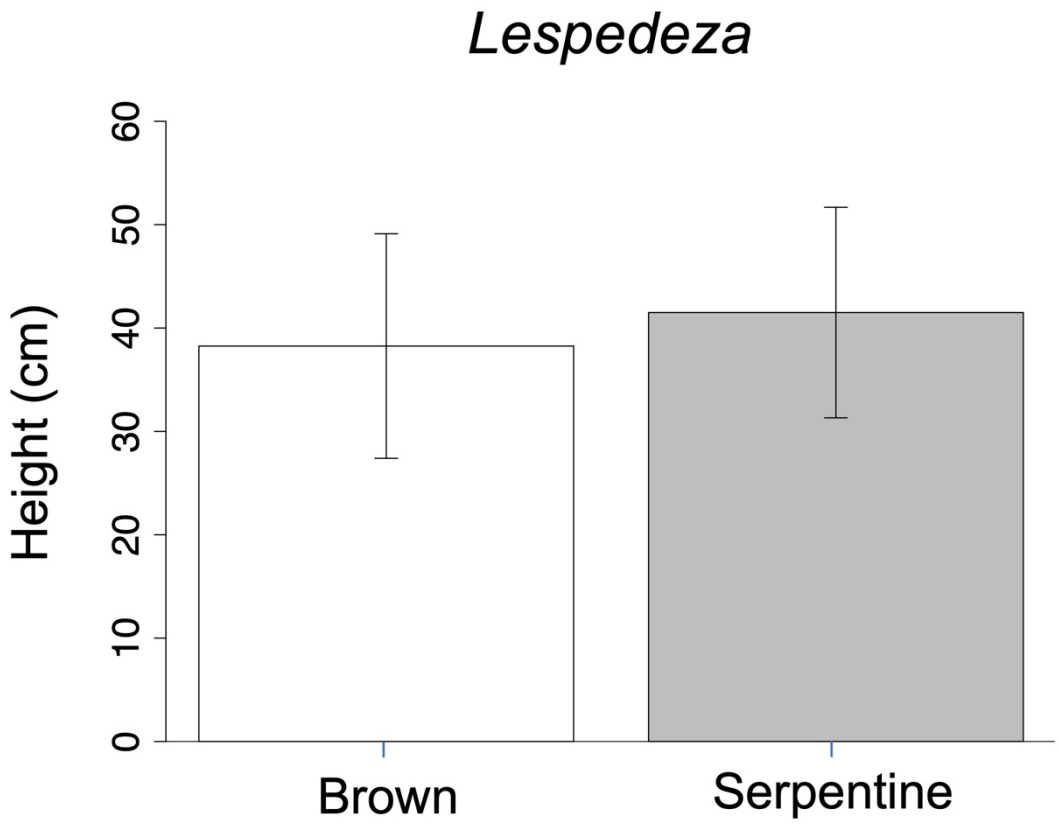
685 Figure 3



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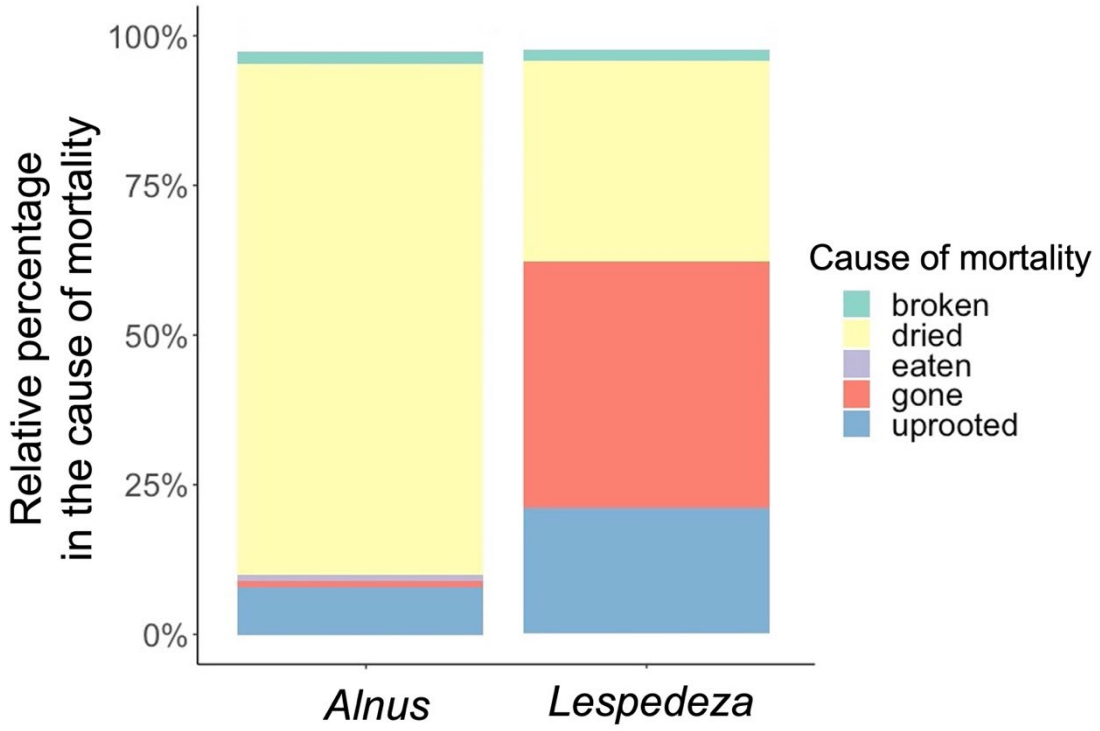
688 Figure 4



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