

1 **Title:** More lianas on larger host trees on steep slopes in a secondary temperate forest, Japan

2

3 **Authors:** Ikumi Nakada¹, Iwao Uehara¹, Hideki Mori^{2*}

4 ¹ Tokyo University of Agriculture, 1-1-1 Sakuragaoka, Setagaya-ku, Tokyo, 156-8502, Japan

5 ² Forestry and Forest Products Research Institute, Matsunosato 1, Tsukuba, Ibaraki, 305-8687, Japan

6

7 ***Corresponding author:** Hideki Mori

8 Address: Matsunosato 1, Tsukuba, Ibaraki, 305-8687 Japan

9 Email: morih@ffpri.affrc.go.jp

10

11 ORCID: Hideki Mori (0000-0001-7496-5217)

12

13 Word count: 4344 words

14 **Acknowledgments**

15 We wish to express our gratitude to Dr. Megumi Tanaka and Mr. Yu Hirano for their invaluable advice

16 throughout this study. We also extend our appreciation to the students from the Laboratory of Silviculture,

17 along with the other members of the Department of Forest Science at the Tokyo University of Agriculture,

18 and Mr. and Mrs. Murao, who were the staff of the Okutama research forest, for their indispensable

19 assistance during the field survey. We would like to thank Dr. Takashi Masaki (FFPRI) for his valuable
20 ~~advise~~advice on this study. In this study, we utilized the supercomputer of AFFRIT, MAFF, Japan. This
21 study was partly supported by the JSPS KAKENHI Grant-in-Aid for Early-Career Scientists (21K14882).
22

23 **Abstract**

24 Lianas (woody vines) are important components of forest ecosystems and are often found to proliferate in
25 young forests that have experienced large-scale disturbances. However, little is known regarding the
26 mechanisms of the spatial assembly patterns of co-occurring lianas and trees in the temperate secondary
27 forest stands. In this study, we examined the woody plants (lianas and trees) with a stem diameter >1 cm
28 within a one-hectare plot on a steep mountain slope (32° average slope angle) in a temperate secondary
29 forest in central Japan. We investigated the impact of the host trees, topography, and canopy gaps on the
30 distribution of liana. We aimed to determine the factors that influence the spatial distribution differences
31 between the co-occurring lianas and trees. The results were validated using the $10\text{ m} \times 10\text{ m}$ quadrats
32 ($N=40$) distributed across 23 ha within the study site. We recorded 123 liana stems on 1,536 trees belonging
33 to 57 woody species in the one-hectare plot. The findings revealed that lianas are more abundant on larger
34 host trees and less common in high tree density areas. Small and large lianas preferred steep and moderate
35 slopes, respectively, whereas larger trees were primarily found on steep slopes. These variations in liana
36 and tree distribution patterns on steep slopes, which we observed throughout their life history, may be
37 attributed to the combined effects of varied historical anthropogenic disturbances and grazing impacts. This
38 highlights the need to consider the diverse environmental responses of lianas and trees at the different life
39 history stages to accurately understand liana colonization and proliferation in forests.

40 **Keywords:** Woody vines; life history; topography; spatial assembly pattern; liana–tree interaction

41 **Introduction**

42 Understanding the distribution of organisms within an environment is a central ecology question. Within
43 forest ecosystems, lianas (woody vines) provide novel insights into the mechanisms that drive plant
44 distribution and biodiversity maintenance, as discussed by Schnitzer (2018); while these mechanisms have
45 largely been investigated using trees in forests, focusing exclusively on a single growth form may limit the
46 scope of understanding, due to the convergent life-history characteristics within growth forms (e.g.,
47 dispersal mode). Hence, including a variety of growth forms could enhance our overall understanding of
48 the factors that influence plant distribution and the sustainability of biodiversity (Schnitzer 2018). A
49 comparative analysis of the distribution and abundance patterns between trees and lianas is essential to
50 develop a comprehensive understanding of the spatial assembly patterns of woody plants in forests
51 (Schnitzer et al. 2012). While a multitude of studies have focused on lianas in the tropical regions due to
52 their prevalence and diversity (Schnitzer 2005; Schnitzer & Bongers 2011; DeWalt et al. 2015),
53 fundamental knowledge regarding lianas in higher latitudes, such as temperate forests, remains limited.

54 Lianas thrive in forests that have experienced large-scale disturbances like typhoons, logging,
55 and forest fragmentation (Allen et al. 2005; Londré & Schnitzer 2006; Ladwig & Meiners 2010a). Their
56 impact on the forest biomass can be considerable in secondary forests (Lai et al. 2017). Liana infestations
57 are increasing due to anthropogenic disturbances such as logging, and it is estimated that these infestations

58 are impacting selectively logged forests worldwide (Schnitzer et al. 2015; Putz et al. 2022, 2023), and liana
59 cutting can enhance both the carbon sequestration and timber yield, while minimally impacting the
60 biodiversity (Putz et al. 2023). On the other hand, as many lianas produce fleshy fruits, they are a vital food
61 source for forest-dwelling animals (Ladwig & Meiners 2014; Michel et al. 2014). Therefore, the evaluation
62 of the liana community structure and colonization patterns in secondary forests is essential for both
63 ecological knowledge and effective forest management (e.g., liana-cutting) and conservation.

64 At the forest stand, the liana spatial distribution is shaped by abiotic factors such as light, water,
65 and nutrient availability, and biotic factors such as host tree availability (Kusumoto et al. 2013; Wright et
66 al. 2015; Waite et al. 2023). Because lianas are mechanical parasites, appropriately sized host supports and
67 adequate tree density are crucial for their establishment, growth, and survival (Putz 1984; Ichihashi &
68 Tateno 2011; Roeder et al. 2015). Therefore, when assessing the impact of the host tree availability on the
69 liana distribution, tree size and density and liana size should be considered. Canopy gaps, which are the
70 light sources in closed-canopy forests, are crucial determinants of liana abundance and diversity in tropical
71 forests (Schnitzer et al. 2000; Ledo & Schnitzer 2014); lianas are recognized for their rapid establishment
72 and colonization in environments following treefall, and canopy gaps have been identified as a primary
73 factor contributing to the long-term increase in liana abundance within tropical forests (Schnitzer et al.
74 2021). Landscape topography often determines the water and nutrient availability and soil surface

75 disturbances and thus shapes the liana distribution within forest stands (Putz & Chai 1987; Kusumoto et al.
76 2013; Mori et al. 2018; Liu et al. 2021). Topography can induce divergent liana and tree distribution patterns
77 within forest stands. For example, Kusumoto et al. (2008) observed a higher frequency of liana in concave
78 and steep-sloped sites, while the trees predominantly occupied the convex and moderately sloped sites.
79 They attributed these differences to variations in the soil disturbances, soil conditions, and wind stress.
80 Generally, plants on the steep slopes develop asymmetric root systems to overcome the strong mechanical
81 forces (Chiatante et al. 2002). However, the root systems of lianas and trees are markedly different, with
82 trees allocating more biomass to the roots since lianas rely on external support (Wyka et al. 2019). Therefore,
83 ~~by~~ studying the distribution patterns of lianas and trees on steep slopes could enhance our understanding of
84 the spatial assembly mechanisms of woody plant communities in forest ecosystems.

85 This study aimed to evaluate the liana community structure in a secondary temperate forest
86 and the relative influence of host trees, topography, and canopy gaps on the liana distribution patterns,
87 while taking liana size into account. We also evaluated the distribution patterns of the co-occurring trees
88 and identified environmental factors that influence and differentiate the spatial assembly patterns of lianas
89 and trees. To achieve this, we measured, mapped, and identified the woody plants to species level (with a
90 stem diameter >1 cm) in a one-hectare plot of a secondary forest in Japan, which experienced a large-scale
91 anthropogenic disturbance (logging) over 50 years ago. Specifically, we addressed two questions: 1) What

92 factors among the host trees, topography, and canopy gaps most influenced the spatial distribution patterns
93 of lianas in a young temperate forest? 2) What are the factors that influence and differentiate the spatial
94 assembly patterns of lianas and trees?

95

96 **Materials and Methods**

97 *Study site*

98 This study was conducted in a secondary temperate deciduous forest within the Okutama Practice Forest
99 of the Tokyo University of Agriculture, that is located on the northern slope of Mt. Karikura, Tokyo, Japan
100 (Fig. 1). Spanning approximately 120 hectares, the Okutama Practice Forest has a mean annual temperature
101 and precipitation of 11.9°C and 1623.5 mm, respectively (Automated Meteorological Data Acquisition
102 System of the Japan Meteorological Agency;
103 <https://www.jma.go.jp/jma/en/Activities/amedas/amedas.html>). We established a one-hectare plot (100 m
104 × 100 m) centrally located within the Okutama Practice Forest (35° 48' 52.4664"N, 139° 3' 53.9994"E;
105 1,106 m a.s.l) in 2021 to conduct inventory of the trees and lianas. The results of the data analysis in a one-
106 hectare plot were validated with 40 quadrats (10 m × 10 m) established randomly across approximately 23
107 ha in the Okutama Practice Forest (Fig. 1). These quadrats were positioned at least 50 m from each other.
108 The study site, which has previously been exposed to large-scale anthropogenic disturbances (logging), has

109 remained free from intensive logging activities for over half a century. In the study site, we frequently
110 observed coppiced tree stems (Fig. S1). Coppiced forests, a common occurrence following anthropogenic
111 disturbances, are especially prevalent on steep terrains in Japan (Stanko 2013).

112

113 *Field methods*

114 Within the one-hectare plot and the 40 quadrats, we recorded the woody species names and locations and
115 measured the stem diameter of all the woody plants (trees and lianas) that were >1 cm (Fig. S2). We
116 measured the diameter of tree stems at breast height (DBH) and that of lianas at 130 cm from their
117 rooting point, following the method described by Gerwing et al. (2006). Climbing types (i.e., stem twiner,
118 tendril climber, root climber; Putz & Holbrook 1991) were also recorded for lianas. The nomenclature used
119 was as described by Yonekura & Kajita (2003). Seed dispersal mode was classified into abiotic and biotic
120 dispersal based on Yohsuke et al. (2003). The one-hectare plot was segmented into a 5 m × 5 m grids (total
121 of 400 grids) for the environmental variables in the subsequent analysis (Table 1). We measured the canopy
122 height classes (<2, 2–5, 5–10, 10–15, and >15 m) at the center of each grid, based on the procedure
123 described by Nakashizuka et al. (1995), using a height-measuring pole. In a previous study in a closed
124 canopy forest located in a similar region of Japan, the average canopy height was found to be over 15 meters
125 (Tanaka and Nakashizuka 1997), in contrast to the predominantly over 10-meter canopy height observed at
126 our study site. This difference is likely due to the smaller stature of trees on steep slopes (Saremi et al.

127 2014). In our study, canopy gaps were defined as areas where the canopy height was less than 10 meters;
128 notably, our study site's gap area proportion of 12.5% aligns with the 9-25% range reported by Tanaka and
129 Nakashizuka (1997). The topographical data for the plots were obtained from the 5-m digital elevation
130 model retrieved from the Geospatial Information Authority of Japan website
131 (<https://fgd.gsi.go.jp/download/menu.php>). We calculated the slope angle and curvature for each 5 m × 5 m
132 grid using the “r.slope.aspect” function in QGIS version 3.30.1 (QGIS Development Team, 2023). The
133 curvature of each grid (cell) is calculated based on the elevation of the surrounding grids and expressed as
134 1/metre. Positive curvature values indicate a convex form, while negative values signify a concave form.

135

136 *Data analysis*

137 **Distribution patterns of lianas**

138 Probability (p_{ij}) of the occurrence (presence, absence) of an individual of the j -th liana species on the i -th
139 tree stem was analyzed using a Bayesian hierarchical modeling with Markov chain Monte Carlo (MCMC)
140 simulation, assuming the Bernoulli distribution, as follows:

$$141 \quad \text{logit}(p_{ij}) = \alpha_j + \sum_{k=1}^5 X_{ijk}\beta_{jk} + \varphi + \epsilon$$

142 where X_{ijk} is the explanatory variable ($k = 1, 2, \dots, 5$); X_{ij1} is the host tree size; and X_{ij2} , X_{ij3} ,
143 X_{ij4} , X_{ij5} is the tree density, canopy gap, slope angle, and curvature of the 5 m × 5 m grid of the liana
144 rooting point, respectively. α_j is the intercept, β_{jk} represents the parameter of X_{ijk} , φ is a sparse

145 conditional auto-regression term which is a spatial random effect to reduce the bias of the spatial auto-
 146 correlation (Joseph 2016), and ϵ is the error. The above model effectively estimates the effects of variables
 147 on liana distribution, particularly where these variables do not switch from negative to positive effects (or
 148 vice versa) throughout liana life history (Figs. S3, S4). While size dependency can be accounted for by
 149 dividing the dataset into different size classes (as suggested by Mori et al. 2016), setting an accurate size
 150 threshold is critical and requires prior knowledge of the study species. This classification could also increase
 151 estimation uncertainty due to the reduced amount of liana occurrence data (Fig. S4). In our study, the
 152 magnitude of the parameter β_{jk} was defined to vary with liana size (stem diameter; D_l) as follows:

$$153 \quad \beta_{jk} = a_{jk} \times D_l + b_{jk}$$

$$154 \quad a_{jk} \sim N(a_{j_0k}, \sigma_{a_k})$$

$$155 \quad b_{jk} \sim N(b_{j_0k}, \sigma_{b_k}),$$

156 here, a_{jk} and b_{jk} are parameters indicating species-specific effects for lianas. These are derived from
 157 normal distributions with means a_{j_0k} and b_{j_0k} , representing the overall species-wide effects, and standard
 158 deviations σ_a and σ_b , respectively. Thus, β_{jk} represents the variable parameter of X_{ijk} , which changes
 159 with the size of the liana. Similarly, the magnitude of the intercept α_j was defined to have overall species-
 160 wide effects and species-specific effects as defined for the β_{jk} .

161 The explanatory variable values previously mentioned were verified using the liana inventory
 162 dataset from 40 randomly placed quadrats (10 m x 10m each), spanning 23 hectares at the study site (Fig.

163 1). These quadrats covered a broader elevation range (907–1234 m; Table S1) which is about five times
 164 greater than that of the one-hectare plot. Therefore, an elevation variable was incorporated into the model
 165 to assess its impact on liana distribution. Due to the absence of canopy gaps (defined as areas where canopy
 166 height is less than 10 m) in these 40 quadrats, the canopy gap variable was omitted from the model for this
 167 dataset.

168

169 **Distribution patterns of trees**

170 Distribution patterns of the trees were analyzed based on the model as described above. Probability (p_{ij}) of
 171 occurrence (presence, absence) of an individual of the j -th tree species in the i -th $5 \text{ m} \times 5 \text{ m}$ grid was
 172 analyzed using a hierarchical linear model assuming the Bernoulli distribution as follows:

$$173 \quad \text{logit}(p_{ij}) = \alpha_j + \sum_{k=1}^3 X_{ijk} \beta_{jk} + \varphi + \epsilon$$

$$174 \quad \beta_{jk} = a_{jk} \times D_t + b_{jk}$$

$$175 \quad a_{jk} \sim N(a_{j_0k}, \sigma_{a_k})$$

$$176 \quad b_{jk} \sim N(b_{j_0k}, \sigma_{b_k}),$$

177 where X_{ij1} , X_{ij2} , X_{ij3} is the canopy gap, slope angle, and curvature, respectively, and D_t is the tree DBH.

178 The tree DBH was log-transformed prior to analysis for normality. Other parameters are the same as the
 179 above model of the liana occurrence probability.

180 Prior to analysis using the above two models, all variables were standardized to have a mean of
181 0 and standard deviation (SD) of 1. The noninformative improper flat priors over the reals were used for
182 the prior distribution of the parameters. Four chains were used for the initialization with 5,000 iterations,
183 of which the first 2,000 were used as the burn-in. Convergence of the chains was assessed using Gelman
184 and Rubin’s convergence diagnostics ($\hat{R} < 1.1$; Gelman et al. 2014). The above detailed analyses were
185 performed in R version 4.1.3 (R Core Team, 2021) using the “rstan” package (Stan Development Team
186 2022) for the estimation of the posteriors, and the Stan code from the “brms” package (Bürkner 2017) to
187 construct the models.

188 The variables D_l and D_t do not exist for the trees that do not have lianas attached to them and
189 for the tree species that do not exist in a given 5 m × 5 m grid, respectively; however, it is necessary to
190 impute and standardize the D_l and D_t for the estimation of the models. The values of D_l and D_t for the
191 missing data were generated from the standard normal distribution to have an overall mean of 0 and variance
192 of 1 in the standardized D_l and D_t . To account for the stochastic uncertainty in the estimation of the
193 posteriors derived from the above imputation, the imputation was independently repeated 100 times for the
194 models of the lianas and trees, and the above models were also estimated using the imputed data for the
195 same number of repeats. The 95% and 80% credible intervals (CI) of the posteriors from each model were
196 calculated. To account for the stochastic uncertainty in the calculation of the CIs, the upper and lower

197 bounds of the CIs were defined as the median +1 SD for the upper bound and the median -1 SD for the
198 lower bound of the CIs, respectively. The proportion of the average variability (1 SD) of the CIs was 6.6%
199 and 8.2% in the lianas and trees models, respectively. This indicates that the effect of the uncertainty
200 resulting from the standardization of D_l and D_t on the results (i.e., 95% and 80% CIs) was minimal (Fig.
201 S5; S6). Additionally, to validate the impact of the previously mentioned imputation, D_l was set as missing
202 for all individuals, imputed, and analyzed using the same methodology previously described. This approach
203 effectively assumes the absence of any size-dependent patterns in the parameters. The analysis revealed
204 that a_{jk} was close to zero across all explanatory variables (Fig. S7), suggesting no size-dependency. It is
205 also crucial to note that this method of imputation is conservative for the estimation of the CIs for extreme
206 sizes (Fig. S7). Thus, the trends identified in the model are expected to be a reliable representation of the
207 size-dependency in the variables.

208

209 **Results**

210 *Community structure of the lianas and trees*

211 We mapped and measured the stem diameters of 1,659 stems (1,536 tree and 123 liana stems) belonging to
212 57 woody species (48 tree and nine liana species) in the one-hectare plot (Table 2 and 3). The basal area
213 and mean stem diameter \pm 1 SD of the trees and lianas were $38.2 \text{ m}^2\text{ha}^{-1}$ and $14.3 \pm 10.5 \text{ cm}$, and 0.198

214 m²ha⁻¹ and 4.2 ± 2.0 cm, respectively (Fig. S2). The lianas comprised of 15.8% of the number of species,
215 7.4% of the number of stems, and 0.5% of the basal area of all the woody plants in the study forest. It was
216 found that 123 liana stems attached to 82 tree stems, accounting for 5.3% of the total (averaging 1.4 liana
217 stems per tree stem). Additionally, lianas were present in 78 of the 5 m x 5 m grids, covering 24.2% of the
218 total 400 grids. The climbing types of the lianas observed in this study were stem twiners (five species),
219 tendril climbers (three species), and root climbers (one species) (Table 2). The dominant tree species were
220 *Castanea crenata* (Fagaceae), *Carpinus japonica* (Betulaceae), and *Quercus crispula* var. *crispula*
221 (Fagaceae), and the dominant liana species were *Actinidia arguta* var. *arguta* (Actinidiaceae), *Vitis*
222 *coignetiae* (Vitaceae), and *Berchemia racemosea* (Rhamnaceae), in order of the basal area. The most
223 dominant tree and liana species were, *Castanea crenata*, and *Actinidia arguta* var. *arguta*, respectively,
224 which accounted for 26.2% and 71.2% of the total basal area of the trees and lianas, respectively. Eight out
225 of nine liana species and 18 out of 48 tree species were animal-dispersed species. Lianas represented 31%
226 (8 out of 26 species) and 39.2% (129 out of 329 stems) of the species count and density, respectively, of all
227 animal-dispersed woody plants in this forest.

228

229 *Effects of the trees, canopy gaps, and topography on the liana distribution*

230 The effect of the host tree size on the liana occurrence probability was significantly positive at the 95% and
231 80% confidence levels in eight and one of the liana species in the one-hectare plot, respectively (Fig. 2),

232 and the effects of the host tree size became larger with the increasing liana size, indicating that larger lianas
233 had a higher occurrence probability on larger trees (Fig. S8). There was a significantly negative effect of
234 the tree density on the liana occurrence probability at the 95% and 80% confidence levels in three and five
235 liana species, respectively, which indicated that lianas had a lower occurrence probability in areas with
236 higher tree density. There was no significant effect of the canopy gaps on the liana occurrence probability.
237 There was a significantly positive effect of the slope angle on the liana occurrence probability at the 95%
238 and 80% confidence levels for each of the two liana species, and the positive effect of the slope angle were
239 found in the small lianas (Fig. 2). This indicated that small lianas had a higher occurrence probability on
240 steep slopes. A significantly negative effect at the 95% CI of slope angle was found in large individuals of
241 a liana species (*A. arguta* var. *arguta*) which also showed a positive effect with the slope angle. Thus, the
242 effects of slope angle on the occurrence probability of this species changed from significantly positive to
243 negative between the small and large liana individuals, respectively. The negative relationship of the effect
244 of the slope angle and liana size were also found in other liana species (Figs. 2 and 3; Fig. S8). Data analysis
245 from the 40 quadrats additionally indicated significant positive effects of host trees, significant negative
246 effects of tree density and size-dependent effects of slope angle on liana occurrence (Figs. 4, 5). However,
247 it is noteworthy that the trends identified in the 40-quadrat dataset (723 tree and 119 liana stems) were
248 somewhat less pronounced compared to those in the one-hectare plot. This suggests the possibility of a bias
249 linked to the dataset size used in this study. Nevertheless, these results lend further support to the robustness

250 of the results found in the one-hectare plot.

251

252

253 *Effects of the canopy gaps and topography on the tree distribution*

254 The effects of the canopy gaps had a significantly positive effect at the 80% CI on the occurrence probability

255 of small individuals in four tree species, and a significantly negative effect at the 95% and 80% confidence

256 levels on the occurrence probability of large individuals in one and three tree species, respectively (Fig. 3,

257 Fig. S9). It was found that the effects of the slope angle were significantly positive at the 95% and 80%

258 confidence levels on the occurrence probability in eight and four tree species, respectively. The effects of

259 the slope angle were significantly negative at the 80% and 95% confidence levels in three tree species each.

260 The effect of the curvature was significantly positive at the 95% and 80% confidence levels on the

261 occurrence probability in five and nine tree species, respectively, and significantly negative at the 95% and

262 80% confidence levels in two and four tree species, respectively. None of the 48 tree species showed that

263 the effects of the variables changed from significantly positive to negative, or vice versa. The analysis of

264 the dataset from the 40 quadrats (Fig. 5, Fig. S10) also uncovered both significant positive and negative

265 topographical effects, and an absence of size-dependent slope angle effects on tree species distribution.

266

267 **Discussion**

268 *Liana community in a secondary temperate forest*

269 In this secondary temperate forest, lianas accounted for a minor proportion of the basal area (0.5%; 0.198
270 m²ha⁻¹) compared to that of the number of species and stem density of the woody plants. This proportion
271 is similar to that observed in other temperate forests (0.2%, Allen et al. 1997; 1.4%, Mori et al. 2016).
272 Additionally, within the animal-dispersed species, lianas accounted for a larger proportion of the density
273 and number of species compared to that of the trees, highlighting the importance of their fleshy fruit
274 production in the woody plant community. Indeed, the dominant liana species, *A. aruguta* var. *arguta*, is
275 known to be a preferred fruit of frugivorous mammals such as the Asian black bear (*Ursus thibetanus*) in
276 Japanese temperate forests (Koike & Masaki 2019; Naoe et al. 2019). However, it is crucial to acknowledge
277 that our study did not examine the production of fleshy fruits by lianas and trees. Additionally, the forest at
278 our study site was predominantly composed of species from Sapindaceae and Fagales, which are mainly
279 dispersed abiotically. This highlights the need for further research on the quantity, quality, and timing of
280 fleshy fruit production in co-occurring lianas and trees to precisely assess the role of lianas in temperate
281 secondary forests. The majority of lianas in this community were stem twiners and tendril climbers, while
282 root climbers were found only in four individuals of *Hydrangea petiolaris*. This is in line with the previous
283 findings that stem twiners and tendril climbers are prevalent in the young temperate forests, whereas root
284 climbers are often abundant in old-growth forests (Ladwig & Meiners 2010b; Mori et al. 2016). The
285 dominant canopy tree species in this study site, such as *Castanea crenata*, *Carpinus japonica*, and *Quercus*

286 *crispula* var. *crispula*, commonly occur in young temperate forests of Japan (Okitsu 2014; Shitara et al.
287 2021), confirming that this site was a typical young secondary temperate forest in Japan.

288 We observed a unimodal size distribution of lianas at the study site, where the mean stem
289 diameter was large (4.2 cm on average), which suggests a lack of smaller (younger) liana individuals in this
290 forest. This observation may be linked to the relatively sparse understory vegetation at our study site (Fig.
291 S1), and liana seedlings were merely found in this forest (Nakada personal observation). This lack of liana
292 recruitment may be due to the effects of grazing by large herbivores, particularly sika deer (*Cervus nippon*).
293 The negative impact of sika deer on the vegetation of Japanese forests have been criticized for decades
294 (Takatsuki 2009); the range of sika deer has expanded by about 70% from 1979 to 2002, with populations
295 in some regions increasing nearly twentyfold between 1988 and 2001 (Tsujino et al., 2004). Such intensive
296 browsing on seedlings and saplings disrupts forest regeneration and leads to the decline of forest
297 understories due to deer feeding (Takatsuki 2009); this is especially evident in *Fagus crenata* (Fagaceae)
298 and *Abies firma* (Pinaceae) forests, where excessive browsing severely hampers forest regeneration
299 (Takatsuki and Ito, 2009). The population density of sika deer in the Okutama region, where the study site
300 is located, has also increased dramatically since the 1990's, which has resulting in a reduction of the
301 understory vegetation, including shrubs and herbs (Ohashi et al. 2007; Yamada & Takatsuki 2015). This
302 suggests that the grazing pressure from large herbivores may inhibit the establishment of liana in this

303 temperate forest, and that the substantial proportion of liana individuals currently observed in this forest
304 were likely established following a previous large-scale disturbance.

305

306 *Distribution patterns of lianas and trees*

307 **Host tree size and density**

308 All liana species in this study had a high probability of occurrence on larger trees, and this probability
309 tended to increase with the increasing liana size. Interestingly, the host tree size was the only variable that
310 significantly affected the probability of the occurrence of all liana species at the study site. This is primarily
311 because lianas are structural parasites; i.e., larger lianas require larger host trees for mechanical support.
312 This highlights that the presence of suitably sized host trees is the key factor driving liana distribution
313 patterns in this forest. The importance of the host tree size for liana distribution are consistent with the
314 findings from both temperate (Leicht-Young et al. 2010; Mori et al. 2016) and tropical forests (Nabe-
315 Nielsen 2001; Nesheim & Økland 2007). Mori et al. (2016) found that the effect of tree size on the
316 distribution probability of stem-twining liana species varied depending on the size of the liana individuals;
317 where larger trees hosted more large liana individuals and smaller trees hosted more small liana individuals.
318 This is because lianas have a maximum host diameter size that they can climb (Putz & Holbrook 1991).
319 However, we did not find a high probability of the occurrence of small liana individuals on smaller trees.

320 This is probably because the majority of lianas were large (average diameter 4.2 cm) and few small lianas
321 were found at this site.

322 While tree density is often used as an indicator of host tree availability for lianas, as previous
323 studies have suggested that liana density increases with increasing tree density (Kusumoto et al. 2013;
324 Vivek & Parthasarathy 2015; Poulsen et al. 2017), contrasting results were found in the present study. We
325 observed a negative effect of tree density on the liana distribution, suggesting that lianas are less abundant
326 in regions with high tree density. This could be because lianas in this forest do not necessarily benefit from
327 a large number of smaller trees, as all liana species showed a preference for larger trees, which is a result
328 of the scarcity of smaller liana individuals as discussed above.

329

330 **Topography**

331 The results showed that the larger lianas were less abundant on the steeper slopes, which may in part be
332 due to increased tree-fall mortality of the host trees that are infested by these large lianas. Due to their
333 considerable crown size, larger lianas exhibit a top-heavy architecture, which increases the risk of falling
334 from the forest canopy (Ichihashi & Tateno 2011). In addition, tree-fall mortality is known to be increased
335 on slopes and bottomland compared to hilltops (Ferry et al. 2010). Given the steep slope of the study site
336 (22.1–43.1°; average 32.0°), it is plausible that infestation by larger lianas may have increased the treefall

337 mortality of the host trees, resulting in a lower probability of the occurrence of large lianas on the steep
338 slopes.

339 In contrast, the probability of the small lianas was generally higher on the steeper slopes, which
340 may partly be due to the grazing impact of large herbivores. As mentioned above, the scarcity of smaller
341 (young) lianas in the study area could be attributed to the increasing sika deer population in this region
342 since the 1990's (Ohashi et al. 2007). In general, deer tend to avoid steep slopes (Ganskopp & Vavra 1987),
343 suggesting that the steep slopes in the study site may have experienced less grazing impact, allowing lianas
344 to be establish in these environments. Indeed, a previous study in a temperate forest with similar climatic
345 conditions as our study site, but without large herbivores, examined the effect of slope angle on the liana
346 distribution patterns (Mori et al. 2016), and found that the effect of slope on liana distribution remained
347 constant regardless of the liana size. Another possible explanation for the colonization of small lianas on
348 the steep slopes could be the different soil conditions, including surface disturbance, moisture content, and
349 nutrient composition, which are influenced by topography and can shape the liana distribution patterns
350 (Putz & Chai 1987; Kusumoto et al. 2008).

351 While liana distribution on the steep slopes followed the above pattern, the larger trees exhibited
352 a slightly higher average occurrence probability across all species on the steeper slopes, with substantial
353 interspecific variation among the trees. This tendency was also confirmed from the datasets in the 40

354 quadrats. This indicated that the steep slopes differentially influenced the distribution patterns of the lianas
355 and trees at different life history stages. The high presence of larger trees on the steep slopes might be due
356 to the mitigated impact of the previous anthropogenic disturbances on the steep slopes (Makimoto 2019),
357 and the large trees may have a higher probability of persisting on the steep slopes. Another possible
358 explanation could be the impact of bark stripping by large herbivores (sika deer), which are known to cause
359 severe damage to forests (Ando et al. 2004); ~~where a~~ approximately 60% of tree species have been reported
360 to suffer varying degrees of seasonal bark stripping by sika deer in the forests of Japan. Because deer tend
361 to avoid steep slopes (Ganskopp & Vavra 1987), it is possible that the impact of bark stripping by sika deer
362 was less on these slopes, which may have allowed the large trees to have a higher probability of survival in
363 this environment. Indeed, mature trees are known to be more abundant in suitable environments than trees
364 at earlier life history stages such as seedlings and juveniles in forests (Webb & Peart 2000; Masaki et al.
365 2015).

366 Distribution patterns of the lianas were not affected by curvature, while that of trees showed a
367 large interspecific variation. This indicates that the convex or concave landforms on the steep slopes shaped
368 the tree species' distribution, in line with previous findings that ~~as~~ the concave and convex topography can
369 drive the tree distribution, diversity and fitness as suggested by Heydari et al. (2023). It is important to note
370 that the interspecific variations of the effects of curvature were relatively small for trees in the 40 quadrats.

371 ~~is important to note that the interspecific variations of curvature were relatively small in trees using the 40~~
372 ~~quadrats.~~ _The lack of consistent effects of curvature could be derived from a sampling effect due to the
373 low number of species investigated in this study. In addition, the lack of substantial effects of curvature on
374 the liana distribution may be due to the limited area of the present study, and the impact of curvature on the
375 liana distribution could change when including the area at the hilltop and valley sites, as these landforms
376 are reported to impact the liana distribution and community structure in forests (Kusumoto et al. 2008).

377

378 **Canopy gap**

379 In this secondary temperate forest, none of the liana species showed a significantly high probability of
380 occurrence in the canopy gaps, suggesting that lianas do not colonize in the bright environments created by
381 these gaps. This observation is consistent with findings from other temperate forests (Carrasco-Urra &
382 Gianoli 2009; Leicht-Young et al. 2010; Mori et al. submitted), which indicates the minor role of canopy
383 gaps on the distribution and abundance of lianas on the trees could be common in temperate regions. One
384 possible explanation for this is that many temperate liana species exhibit shade tolerance (Valladares et al.
385 2011). Although canopy gaps potentially promote the establishment of lianas at the seed to seedling stages
386 (Leicht-Young et al. 2010; Mori et al. 2020), the understory of the study site was notably sparse, and lacked
387 young (small) liana individuals. This ~~indicates-suggests~~ that canopy gaps may have a minimal effect on the

388 distribution patterns of this liana community. Furthermore, the tree species distribution patterns were less
389 affected by canopy gaps, as evidenced by the comparatively lower number of tree species affected by the
390 canopy gaps compared to other environmental variables. This suggests that canopy gaps play a minor role
391 in shaping the spatial assembly patterns of this woody plant community.

392

393 **Conclusions**

394 In our study, we examined both the lianas and trees in a young temperate secondary forest and assessed the
395 relative influence of the host trees, topography, and canopy gaps on their distribution, using stem diameter
396 size as an indicator of the life history stage. Our results revealed a notable contrast in the distribution
397 patterns between the lianas and trees on the steep slopes, possibly due to the heterogeneity in anthropogenic
398 disturbances, grazing effects, and soil conditions across the study site. Although the consistent patterns
399 identified for both lianas and trees across different spatial scales reinforce the robustness of our findings at
400 the community level, it is important to note that the species-specific patterns observed in the 40 quadrats
401 located across 23 ha were not always in line with those from the one-hectare plot; this discrepancy suggests
402 potential biases in species-level patterns resulting from the design of the current study. A more
403 comprehensive understanding of the drivers affecting the abundance, distribution, and coexistence of
404 woody plant species in this region would benefit from further long-term monitoring. Given that our study
405 did not assess soil factors such as water and nutrient availability, nor did it examine tree-liana and liana-

406 liana interactions at the species level, further investigation into these soil conditions and woody plant
407 communities on steep slopes would be valuable in elucidating the determinants of liana abundance and the
408 size-dependent distribution patterns in such areas. Because lianas are known to proliferate in forests that
409 have experienced large-scale disturbances, further research focusing on the liana and tree communities
410 within secondary forests, particularly in temperate zones where knowledge is limited compared to the
411 tropical zones, is crucial to understand, and predict the liana abundance and distribution in forests.

412

413 **References**

- 414 Allen BP, Pauley EF, Sharitz RR (1997) Hurricane Impacts on Liana Populations in an Old-Growth
415 Southeastern Bottomland Forest. *J Torrey Bot Soc* 124:34-42. <https://doi.org/10.2307/2996596>
- 416 Allen BP, Sharitz RR, Goebel PC (2005) Twelve years post-hurricane liana dynamics in an old-growth
417 southeastern floodplain forest. *For Ecol Manag* 218:259-269.
418 <https://doi.org/10.1016/j.foreco.2005.08.021>
- 419 Ando M, Yokota H-o, Shibata E (2004) Why do sika deer, *Cervus nippon*, debark trees in summer on Mt.
420 Ohdaigahara, central Japan. *Mamm Study* 29:73-83. <https://doi.org/10.3106/mammalstudy.29.73>
- 421 Bürkner P-C (2017) brms: An R package for Bayesian multilevel models using Stan. *Journal of Statistical*
422 *Software* 80:1-28.
- 423 Carrasco-Urra F, Gianoli E (2009) Abundance of climbing plants in a southern temperate rain forest: host
424 tree characteristics or light availability? *J Veg Sci* 20:1155-1162. [https://doi.org/10.1111/j.1654-](https://doi.org/10.1111/j.1654-1103.2009.01115.x)
425 [1103.2009.01115.x](https://doi.org/10.1111/j.1654-1103.2009.01115.x)
- 426 Chiatante D, Scippa SG, Di Iorio A, Sarnataro M (2002) The Influence of Steep Slopes on Root System
427 Development. *J Plant Growth Regul* 21:247-260. <https://doi.org/10.1007/s00344-003-0012-0>
- 428 DeWalt SJ, Schnitzer SA, Alves LF, Bongers F, Burnham RJ, Cai Z, Carson WP, Chave J, Chuyong GB,

429 Costa FRC, Ewango CEN, Gallagher RV, Gerwing JJ, Amezcua EG, Hart T, Ibarra-Manríquez G,
430 Ickes K, Kenfack D, Letcher SG, Macia MJ, et al. (2015). Biogeographical patterns of liana
431 abundance and diversity. In SA Schnitzer, F Bongers, RJ Burnham, FE Putz (Eds.), *Ecology of Lianas*
432 (pp. 131-146). John Wiley & Sons, Ltd. <https://doi.org/10.1002/9781118392409.ch11>

433 Ferry B, Morneau F, Bontemps J-D, Blanc L, Freycon V (2010) Higher treefall rates on slopes and
434 waterlogged soils result in lower stand biomass and productivity in a tropical rain forest. *J Ecol*
435 98:106-116. <https://doi.org/10.1111/j.1365-2745.2009.01604.x>

436 Ganskopp D, Vavra M (1987) Slope use by cattle, feral horses, deer, and bighorn sheep. *Northwest Sci* 61.

437 Gelman A, Carlin JB, Stern HS, Dunson DB, Vehtari A, Rubin DB. (2014). *Bayesian data analysis* (2).
438 CRC press Boca Raton, FL.

439 Gerwing JJ, Schnitzer SA, Burnham RJ, Bongers F, Chave J, DeWalt SJ, Ewango CEN, Foster R, Kenfack
440 D, Martínez-Ramos M, Parren M, Parthasarathy N, Pérez-Salicrup DR, Putz FE, Thomas DW (2006)
441 A Standard Protocol for Liana Censuses. *Biotropica* 38:256-261. [https://doi.org/10.1111/j.1744-](https://doi.org/10.1111/j.1744-7429.2006.00134.x)
442 [7429.2006.00134.x](https://doi.org/10.1111/j.1744-7429.2006.00134.x)

443 Heydari M, Cheraghi J, Omidipour R, Rostaminia M, Kooch Y, Valkó O, Carcaillet C (2023) Tree dieback,
444 woody plant diversity, and ecosystem driven by topography in semi-arid mountain forests:
445 Implication for ecosystem management. *J Environ Manag* 339:117892.

446 <https://doi.org/10.1016/j.jenvman.2023.117892>

447 Ichihashi R, Tateno M (2011) Strategies to balance between light acquisition and the risk of falls of four
448 temperate liana species: to overtop host canopies or not? *J Ecol* 99:1071-1080.
449 <https://doi.org/10.1111/j.1365-2745.2011.01808.x>

450 Joseph M (2016) Exact sparse car models in stan. *Stan Official Website*. [https://mc-](https://mc-stan.org/users/documentation/case-studies/mbjoseph-CARStan.html)
451 [stan.org/users/documentation/case-studies/mbjoseph-CARStan.html](https://mc-stan.org/users/documentation/case-studies/mbjoseph-CARStan.html) Accessed 28 Jun 2023

452 Koike S, Masaki T (2019) Characteristics of fruits consumed by mammalian frugivores in Japanese
453 temperate forest. *Ecol Res* 34:246-254. <https://doi.org/10.1111/1440-1703.1057>

454 Kusumoto B, Enoki T, Kubota Y (2013) Determinant factors influencing the spatial distributions of
455 subtropical lianas are correlated with components of functional trait spectra. *Ecol Res* 28:9-19.
456 <https://doi.org/10.1007/s11284-012-0993-x>

457 Kusumoto B, Enoki T, Watanabe Y (2008) Community structure and topographic distribution of lianas in a
458 watershed on Okinawa, south-western Japan. *J Trop Ecol* 24:675-683.
459 <https://doi.org/10.1017/s0266467408005452>

460 Ladwig LM, Meiners SJ (2010) Spatiotemporal dynamics of lianas during 50 years of succession to
461 temperate forest. *Ecology* 91:671-680.

462 Ladwig LM, Meiners SJ (2010) Liana host preference and implications for deciduous forest regeneration.
463 *The Journal of the Torrey Botanical Society* 137:103-112. <https://doi.org/10.3159/09-ra-041.1>

464 Ladwig LM, Meiners SJ. (2014). The role of lianas in temperate tree communities. In SA Schnitzer, F
465 Bongers, RJ Burnham, FE Putz (Eds.), *Ecology of Lianas* (pp. 188-202). John Wiley & Sons, Ltd.
466 <https://doi.org/10.1002/9781118392409.ch15>

467 Lai HR, Hall JS, Turner BL, Breugel M (2017) Liana effects on biomass dynamics strengthen during
468 secondary forest succession. *Ecology* 98:1062-1070. <https://doi.org/10.1002/ecy.1734>

469 Ledo A, Schnitzer SA (2014) Disturbance and clonal reproduction determine liana distribution and maintain
470 liana diversity in a tropical forest. *Ecology* 95:2169-2178.

471 Leicht-Young SA, Pavlovic NB, Frohnapple KJ, Grundel R (2010) Liana habitat and host preferences in
472 northern temperate forests. *For Ecol Manag* 260:1467-1477.
473 <https://doi.org/10.1016/j.foreco.2010.07.045>

474 Liu Q, Sterck FJ, Medina-Vega JA, Sha L, Cao M, Bongers F, Zhang J, Poorter L (2021) Soil nutrients,
475 canopy gaps and topography affect liana distribution in a tropical seasonal rain forest in southwestern
476 China. *J Veg Sci* 32. <https://doi.org/10.1111/jvs.12951>

477 Londré RA, Schnitzer SA (2006) The distribution of lianas and their change in abundance in temperate

478 forests over the past 45 years. *Ecology* 87:2973-2978. <https://doi.org/10.1890/0012->
479 [9658\(2006\)87\[2973:TDOLAT\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[2973:TDOLAT]2.0.CO;2)

480 Makimoto K (2019) State of Japan's Forests and Forest Management — 3rd Country Report of Japan to
481 the Montreal Process —. *Forestry Agency, Japan*.

482 Masaki T, Hata S, Ide Y (2015) Heterogeneity in soil water and light environments and dispersal limitation:
483 what facilitates tree species coexistence in a temperate forest? *Plant Biology* 17:449-458.
484 <https://doi.org/10.1111/plb.12253>

485 Michel NL, Douglas Robinson W, Sherry TW. (2014). Liana-bird relationships: a review. In SA Schnitzer,
486 F Bongers, RJ Burnham, FE Putz (Eds.), *Ecology of Lianas* (pp. 362-397). John Wiley & Sons, Ltd.
487 <https://doi.org/10.1002/9781118392409.ch25>

488 Mori H, Kamijo T, Masaki T (2016) Liana distribution and community structure in an old-growth temperate
489 forest: the relative importance of past disturbances, host trees, and microsite characteristics. *Plant*
490 *Ecol* 217:1171-1182. <https://doi.org/10.1007/s11258-016-0641-6>

491 Mori H, Masaki T, Tsunamoto Y, Naoe S (2020) Survival rate and environmental response of current-year
492 seedlings of the temperate liana *Wisteria floribunda* across a heterogeneous environment. *J Plant*
493 *Res* 133:193-203. <https://doi.org/10.1007/s10265-019-01163-1>

494 Mori H, Ueno S, Matsumoto A, Kamijo T, Tsumura Y, Masaki T (2018) Large contribution of clonal
495 reproduction to the distribution of deciduous liana species (*Wisteria floribunda*) in an old-growth
496 cool temperate forest: evidence from genetic analysis. *Ann Bot* 121:359-336.
497 <https://doi.org/10.1093/aob/mcx153>

498 Nabe-Nielsen J (2001) Diversity and distribution of lianas in a neotropical rain forest, Yasuní National Park,
499 Ecuador. *J Trop Ecol* 17:1-19. <https://doi.org/10.1017/s0266467401001018>

500 Nakashizuka T, Katsuki T, Tanaka H (1995) Forest canopy structure analyzed by using aerial photographs.
501 *Ecol Res* 10:13-18. <https://doi.org/10.1007/bf02347651>

502 Naoe S, Tayasu I, Sakai Y, Masaki T, Kobayashi K, Nakajima A, Sato Y, Yamazaki K, Kiyokawa H, Koike
503 S (2019) Downhill seed dispersal by temperate mammals: a potential threat to plant escape from
504 global warming. *Sci Rep* 9:14932. <https://doi.org/10.1038/s41598-019-51376-6>

505 Nesheim I, Økland RH (2007) Do vine species in neotropical forests see the forest or the trees? *J Veg Sci*
506 18:395-404. <https://doi.org/10.1111/j.1654-1103.2007.tb02552.x>

507 Ohashi H, Hoshino Y, Oono K (2007) Long-term changes in the species composition of plant communities
508 caused by the population growth of Sika deer (*Cervus nippon*) in Okutama, Tokyo. (in Japanese with
509 English summary). *Vegetation Science* 24:123-151. <https://doi.org/10.15031/vegsci.24.123>

510 Okitsu S (2014) Changes in Green Spaces and Their Management in Tokyo with Reference to the Tama
511 Area (In Japanese with English summary). *Journal of Geography (Chigaku Zasshi)* 123:211-222.
512 <https://doi.org/10.5026/jgeography.123.211>

513 Poulsen JR, Koerner SE, Miao Z, Medjibe VP, Banak LN, White LJT (2017) Forest structure determines
514 the abundance and distribution of large lianas in Gabon. *Global Ecol. Biogeogr.* 26:472-485.
515 <https://doi.org/10.1111/geb.12554>

516 Putz FE (1984) The natural history of lianas on Barro Colorado Island, Panama. *Ecology* 65:1713-1724.
517 <https://doi.org/https://doi.org/10.2307/1937767>

518 Putz FE, Chai P (1987) Ecological studies of lianas in Lambir national park, Sarawak, Malaysia. *J Ecol*
519 523-531.

520 Putz FE, Romero C, Sist P, Schwartz G, Thompson I, Roopsind A, Ruslandi R, Medjibe V, Ellis P (2022)
521 Sustained Timber Yield Claims, Considerations, and Tradeoffs for Selectively Logged Forests. *PNAS*
522 *Nexus*. <https://doi.org/10.1093/pnasnexus/pgac102>

523 Putz FE, Cayetano DT, Belair EP, Ellis PW, Roopsind A, Griscom BW, Finlayson C, Finkral A, Cho PP,
524 Romero C (2023) Liana cutting in selectively logged forests increases both carbon sequestration and
525 timber yields. *For Ecol Manag* 539:121038. <https://doi.org/10.1016/j.foreco.2023.121038>

526 Putz FE, Holbrook NM. (1991). Biomechanical studies of vines. In FE Putz, HA Mooney (Eds.), *The*
527 *Biology of Vines* (pp. 73-98). Cambridge University Press.
528 <https://doi.org/10.1017/CBO9780511897658.005>

529 QGIS Development Team. (2023). *QGIS Geographic Information System*. QGIS Association.
530 <https://www.qgis.org>

531 R Core Team. (2021). *R: A Language and Environment for Statistical Computing*. R Foundation for
532 Statistical Computing. <https://www.R-project.org/>

533 Roeder M, Slik JW, Harrison RD, Paudel E, Tomlinson KW (2015) Proximity to the host is an important
534 characteristic for selection of the first support in lianas. *J Veg Sci* 26:1054-1060.
535 <https://doi.org/https://doi.org/10.1111/jvs.12316>

536 Saremi H, Kumar L, Stone C, Turner R, Melville G (2014) Impact of local slope and aspect assessed from
537 LiDAR records on tree diameter in radiata pine (*Pinus radiata* D. Don) plantations. *Ann For Sci* 71.
538 <https://doi.org/10.1007/s13595-014-0374-4>

539 Schnitzer SA (2005) A mechanistic explanation for global patterns of liana abundance and distribution. *Am*
540 *Nat* 166:262-276.

541 Schnitzer SA, Mangan SA, Dalling JW, Baldeck CA, Hubbell SP, Ledo A, Muller-Landau H, Tobin MF,

542 Aguilar S, Brassfield D, Hernandez A, Lao S, Perez R, Valdes O, Yorke SR (2012) Liana abundance,
543 diversity, and distribution on Barro Colorado Island, Panama. *PLoS One* 7:e52114.
544 <https://doi.org/10.1371/journal.pone.0052114>

545 Schnitzer SA, Dalling JW, Carson WP (2000) The impact of lianas on tree regeneration in tropical forest
546 canopy gaps: evidence for an alternative pathway of gap-phase regeneration. *J Ecol* 88:655-666.

547 Schnitzer SA (2018) Testing ecological theory with lianas. *New Phytol* 220:366-380.
548 <https://doi.org/10.1111/nph.15431>

549 Schnitzer SA, Bongers F (2011) Increasing liana abundance and biomass in tropical forests: emerging
550 patterns and putative mechanisms. *Ecol Lett* 14:397-406. [https://doi.org/10.1111/j.1461-](https://doi.org/10.1111/j.1461-0248.2011.01590.x)
551 [0248.2011.01590.x](https://doi.org/10.1111/j.1461-0248.2011.01590.x)

552 Schnitzer S, Bongers F, Burnham RJ, Putz FE (2015) *Ecology of lianas*. Wiley-Blackwell, Oxford, UK.

553 Schnitzer SA, DeFilippis DM, Visser M, Estrada-Villegas S, Rivera-Camaña R, Bernal B, Pérez S, Valdéz
554 A, Valdéz S, Aguilar A, Dalling JW, Broadbent EN, Almeyda Zambrano AM, Hubbell SP, Garcia-
555 Leon M (2021) Local canopy disturbance as an explanation for long-term increases in liana
556 abundance. *Ecol Lett* 24:2635-2647. <https://doi.org/10.1111/ele.13881>

557 Shitara T, Suzuki S, Nakamura Y (2021) Phytosociological study of *Betula costata* forests in central Honshu,

558 Japan. *Vegetation Science* 38:49-66.

559 Stan Development Team (2022) RStan: the R interface to Stan. R package version 2.21.7. <https://mc->

560 [stan.org/](https://mc-stan.org/).

561 Takatsuki S (2009) Effects of sika deer on vegetation in Japan: A review. *Biol Conserv* 142:1922-1929.

562 <https://doi.org/10.1016/j.biocon.2009.02.011>

563 Takatsuki S, Ito TY (2009) Plants and Plant Communities on Kinkazan Island, Northern Japan, in Relation

564 to Sika Deer Herbivory. In McCullough DR, Takatsuki S, Kaji K (Eds.), *Sika Deer* (pp. 125-143).

565 Springer Japan. https://doi.org/10.1007/978-4-431-09429-6_9

566 Tsujino R, Noma N, Yumoto T (2004) Growth of the sika deer (*Cervus nippon yakushimae*) population in

567 the western lowland forests of Yakushima Island, Japan. *Mamm Study* 29:105-111.

568 <https://doi.org/10.3106/mammalstudy.29.105>

569 Valladares F, Gianoli E, Saldana A (2011) Climbing plants in a temperate rainforest understorey: searching

570 for high light or coping with deep shade? *Ann Bot* 108:231-239. <https://doi.org/10.1093/aob/mcr132>

571 Vivek P, Parthasarathy N (2015) Liana community and functional trait analysis in tropical dry evergreen

572 forest of India. *Journal of Plant Ecology* 8:501-512. <https://doi.org/10.1093/jpe/rtu031>

573 Webb CO, Peart DR (2000) Habitat associations of trees and seedlings in a Bornean rain forest. *J Ecol*

574 88:464-478. <https://doi.org/10.1046/j.1365-2745.2000.00462.x>

575 Wright A, Tobin M, Mangan S, Schnitzer SA (2015) Unique competitive effects of lianas and trees in a
576 tropical forest understory. *Oecologia* 177:561-569. <https://doi.org/10.1007/s00442-014-3179-0>

577 Wyka TP, Zadworny M, Mucha J, Żytkowiak R, Nowak K, Oleksyn J (2019) Biomass and nitrogen
578 distribution ratios reveal a reduced root investment in temperate lianas vs. self-supporting plants.
579 *Ann Bot* 124:777-790. <https://doi.org/10.1093/aob/mcz061>

580 Yamada H, Takatsuki S (2015) Effects of Deer Grazing on Vegetation and Ground-Dwelling Insects in a
581 Larch Forest in Okutama, Western Tokyo. *International Journal of Forestry Research* 2015:1-9.
582 <https://doi.org/10.1155/2015/687506>

583 Yohsuke K, Tamotsu S, Keiko T, Tohru M, Akira E, Naohiko N (2003) Classification of bird-dispersed
584 plants by fruiting phenology, fruit size, and growth form in a primary lucidophyllous forest: an
585 analysis, with implications for the conservation of fruit-bird interactions. *Ornithological Science* 2:3-
586 23. <https://doi.org/10.2326/osj.2.3>

587 Yonekura K, Kajita T (2003) BG Plants: Japanese name--scientific name index (YList). <http://ylist.info>
588

589 **Declarations**

590 **Funding**

591 This study was partly supported by the JSPS KAKENHI Grant-in-Aid for Early-Career Scientists
592 (21K14882).

593 **Conflicts of interest**

594 The authors declare no conflicts of interest associated with this manuscript.

595 **Ethics approval**

596 Not applicable.

597 **Consent to participate**

598 Not applicable.

599 **Consent for publication**

600 Not applicable.

601 **Availability of data and material**

602 The data that support the findings of this study will be submitted and openly available in Forest Research
603 and Management Organization Repository (<https://repository.ffpri.go.jp>).

604 **Code availability**

605 Not applicable.

606 **Authors' contributions**

607 All authors contributed to the study conception and design. Material preparation, data collection and
608 analysis were performed by IN and HM. The first draft of the manuscript was written by HM and all authors
609 commented on previous versions of the manuscript. All authors read and approved the final manuscript.

610

611 **Figure Captions**

612 **Fig. 1** Map of the study area. Solid red lines represent the one-hectare plot and closed circles represent the
613 40 quadrats, each measuring 10 m x 10 m. Contour lines are at 10 m intervals.

614 **Fig. 2** Posterior distribution of the explanatory variables in liana species in the one-hectare plot. The thick
615 line indicates the median of the posterior distribution. The thin and dashed lines indicate 95% and 80%
616 credible intervals (CIs), respectively. The significance of the variables is shown with a filled background.

617 Species names are abbreviated as follows: Aa, *Actinidia arguta* var. *arguta*; Ap, *Actinidia polygama*; Co,
618 *Celastrus orbiculatus* var. *orbiculatus*; Hp, *Hydrangea petiolaris*; At, *Akebia trifoliata*; Br, *Berchemia*
619 *racemosa*; Vc, *Vitis coignetiae*.

620 **Fig. 3** Marginal posterior means (solid lines) of the species-specific effects of the variables in (a) lianas and

621 (b) trees in the one-hectare plot. Colors of the solid lines indicate the significance levels (95% and 80%
622 credible intervals (CI)). Shaded area in (a) and (b) indicate the 95% CI of the species-wide average of the
623 lianas and trees, respectively. Note that the x-axis for the trees is shown as log-transformed (see Methods).

624 **Fig. 4** Posterior distribution of the explanatory variables in liana species in the 10 m x 10 m quadrats (N=40).
625 The thick line indicates the median of the posterior distribution. The thin and dashed lines indicate
626 95% and 80% credible intervals (CIs), respectively. The significance of the variables is shown with a
627 filled background. Species names are abbreviated as follows: Aa, *Actinidia arguta* var. *arguta*; Vc, *Vitis*
628 *coignetiae*; Co, *Celastrus orbiculatus* var. *orbiculatus*; Br, *Berchemia racemosea*; Hp, *Hydrangea*
629 *petiolaris*; Ap, *Actinidia polygama*; Sr, *Schisandra repanda*.

630 **Fig. 5** Marginal posterior means (solid lines) of the species-specific effects of the variables in (a) lianas and
631 (b) trees in the 10 m x 10m quadrats (N=40). Colors of the solid lines indicate the significance levels (95%
632 and 80% credible intervals (CI)). Shaded area in (a) and (b) indicate the 95% CI of the species-wide average
633 of the lianas and trees, respectively. Note that the x-axis for the trees is shown as log-transformed (see
634 Methods).

635

636 **Supplementary Information**

637 **Fig S1.** Photographs of the study site.

638 **Fig. S2.** Histogram of the stem diameter of the lianas and trees in the study plot.

639 **Fig. S3.** Posterior distribution of overall-species effects of liana occurrence probability in linear mixed
640 model which does not account for liana size dependency.

641 **Fig. S4.** Posterior distribution of overall-species effects and species-specific effects on liana
642 occurrence probability in linear mixed models analyzed with different size classes.

643 **Fig S5.** Medians and SD of CI derived from 100 repeated estimates of the model of liana occurrence
644 probability.

645 **Fig S6.** Medians and SD of CI derived from 100 repeated estimates of the model of tree occurrence
646 probability.

647 **Fig. S7.** Marginal posterior means of the species-specific effects of the variables on liana occurrence
648 probability in the one-hectare plot, with the variable D_l was set as missing for all individuals.

649 **Fig. S8.** Scatter plots for liana density and tree density, and host tree DBH and tree density based on 5 m
650 x 5 m grids in the one-hectare plot.

651 **Fig S9.** Effects of canopy gap, slope angle, and curvature on occurrence probability in tree species in the
652 one-hectare plot.

653 **Fig S10.** Effects of slope angle, curvature, and elevation on occurrence probability in tree species in

654 the 10 m x 10 m quadrats (N = 40).

655 **Table S1** Summary of the environmental variables assessed in the 40 quadrats (10 m x 10 m). Mean values

656 are shown \pm one standard deviation (SD).

657

658