The University of Osaka
Institutional Knowledge Archive

Title	The elevational distribution of Fagus crenata regeneration at low elevations in the Shirakami Mountains, a World Natural Heritage site in Japan
Author(s)	Inomata, Tatsuki; Saeki, Ikuyo
Citation	Journal of Forest Research. 2023, 29(3), p. 214-220
Version Type	AM
URL	https://hdl.handle.net/11094/104767
rights	© 2023 The Japanese Forest Society.
Note	

The University of Osaka Institutional Knowledge Archive : OUKA

https://ir.library.osaka-u.ac.jp/

The University of Osaka

Title: The elevational distribution of *Fagus crenata* regeneration at low elevations in the Shirakami Mountains, a World Natural Heritage site in Japan

Tatsuki INOMATA[1,†], Ikuyo SAEKI[2,3,*]

1 Agro-biological Resource Sciences, University of Tsukuba, 1-1-1 Tennodai, Tsukuba, Ibaraki 305-8571, Japan
2 Faculty of Life and Environmental Sciences, University of Tsukuba, 1-1-1 Tennodai, Tsukuba, Ibaraki 305-8571, Japan
3 Makino Herbarium, Tokyo Metropolitan University, 1-1 Minami-osawa, Hachioji, Tokyo 192-0397, Japan

[†] Present address: Graduate School of Agriculture and Life Science, Hirosaki University, 3 Bunkyo-cho, Hirosaki, Aomori 036-8561, Japan
* Author for correspondence: Ikuyo SAEKI (saeki.ikuyo.ge@u.tsukuba.ac.jp)

Ikuyo SAEKI: ORCiD: 0000-0003-3252-6819

Article Type: Original Article
Number of Tables: 1
Number of Figures: 5
Number of Supplementary Information files: 2 tables, 3 figures

ABSTRACT

The Shirakami Mountains are a World Natural Heritage site because of their vast beech (*Fagus crenata*) forests and high diversity of flora and fauna. As global warming progresses, the area suitable for *F. crenata* growth is expected to shift from low to higher elevations. However, no studies have examined the current elevational distribution of the species' regeneration. Here, we investigated the amount of *F. crenata* regeneration in the Shirakami Mountains and compared this amount among different elevations. Our nine study sites covered forests ranging from 269 m to 662 m, which covers the low to middle parts of the elevational distribution of *F. crenata*. At each site, we established three 20 m × 20 m plots and conducted a tree census. We approximated the regeneration density as a function of the diameter at breast height (*DBH*) distribution of *F. crenata* at each site using a power function: $density = a\ DBH^b$. We found that *a* and *b* decreased and increased, respectively, as elevation decreased. Generalized linear mixed model analysis also indicated that decreasing elevation significantly decreased the number of seedlings of *F. crenata*. These results suggest decreasing regeneration at low elevation. Although it is difficult to identify the main causes of this pattern, we predict that regeneration may become even poorer if climate warming continues. Long-term monitoring along elevational clines will help us track the detailed effects of global warming on the beech forests.

Keywords: Cool-temperate forest, Global warming, Japanese beech, Vegetation, World Natural Heritage site

INTRODUCTION

The Shirakami Mountains were designated a World Natural Heritage site in 1993 under criterion ix, "ecosystem," because of their vast forests of beech (*Fagus crenata* Blume) and the high diversity of flora and fauna. The forest covers 16 971 ha of Japan's Aomori and Akita prefectures and provides indispensable ecosystem services for local people, such as supplying many natural products, recharging water resources, and preventing surface erosion. Many animals live in the Shirakami Mountains, including notable species such as the serow (*Capricornis crispus* Temminck), Japanese dormouse (*Glirulus japonicus* Schinz), black woodpecker (*Dryocopus martius* Linnaeus), and golden eagle (*Aquila chrysaetos* Linnaeus).

Recent data suggest that the mean temperature in the Shirakami Mountains has been continuously increasing, accompanied by decreasing snowfall (Fig. S1). Because of this change, the area that is unsuitable for the growth of *F. crenata* is likely to be expanding at lower elevations. Indeed, many studies have shown that tree species are changing their distribution toward the poles and higher elevations (Walther et al. 2002; Penuelas et al. 2007; Beckage et al. 2008; Harsch et al. 2009; Feeley et al. 2011; Shimazaki et al. 2011; Koide et al. 2017, 2022; Gatti et al. 2019). Wason & Dovciak (2017) suggested that distribution of American beech (*Fagus grandifolia* Ehrh.) is likely expanding upslope, although other factors, such as land-use changes, may mask species range shifts caused by changing climate. In Germany, the growth of European beech (*Fagus sylvatica* L.) has decreased at lower elevations but increased at higher elevations (Dulamsuren et al. 2017). In Japan, the relative abundance of evergreen broadleaved trees increased near the colder boundaries of their range, coinciding with a decrease in the relative abundance of deciduous broadleaved trees (Suzuki et al. 2015). A similar

change was observed at the colder edge of the distribution of deciduous broadleaved forest communities, in which the abundance of deciduous trees is increasing, accompanied by decreasing abundance of boreal coniferous species.

According to models of the potential impacts of climate change on canopy tree species in Japan, Matsui et al. (2018) predicted that the beech-dominated forest type will be replaced mostly by oak-dominated forest types. Their size-based species distribution model also implies that the potential habitat of juvenile *F. crenata* would be lost at warmer and snowless sites (Koide et al. 2016). In the Shirakami Mountains, a previous study based on ecological niche modeling predicted that the area suitable for *F. crenata* will decrease to nearly 0% within the World Natural Heritage area by 2100 as current global warming progresses (Matsui et al. 2007). These predictions suggest that *F. crenata* forest will gradually decline at the lower boundary of its distribution but will expand its range toward higher elevations. However, no studies in the Shirakami Mountains have examined the current elevational distribution of its regeneration.

Here, we investigated the amount of *F. crenata* regeneration in the Shirakami Mountains and compared this amount among different elevations. We paid particular attention to the lower boundary of *F. crenata*'s distribution because that area may no longer be a suitable habitat for *F. crenata* in the near future due to current warming. In addition, we compared the pattern of regeneration with those of *Magnolia obovata* Thunb. and *Acer pictum* Thunb. subsp. *mayrii*, which are canopy tree species frequently associated with *F. crenata* in the Shirakami Mountains. The comparison allows us to understand whether the pattern observed in *F. crenata* is common to the other species.

METHODS

Study species

Fagus crenata is one of the dominant tree species in the cool-temperate zone of the Japanese archipelago. It is a shade-tolerant, late-successional tree species and develops a significant seedling bank on the forest floor (Nakashizuka 1987; Koike 1988). Seedlings cannot grow rapidly under a closed canopy (Nakashizuka 1987) and have low survival rates under dwarf bamboo (Abe et al. 2002). Beech forest in Japan is unique due to its high understory coverage by dwarf bamboo. Thus, gap formation and the death of dwarf bamboo are important to promote *F. crenata* regeneration because these changes improve light conditions and decrease seed predation by rodents (Abe et al. 2001, 2005). *Fagus crenata* exhibits synchronized seed production, and its masting cycles affect the number of seed predators (Kon et al. 2005).

Study sites

The study was conducted in the northern part of the Shirakami Mountains in Aomori Prefecture, Japan (Fig. 1). Beech forests in Japan are classified into the Japan Sea type and the Pacific Ocean type, which are distinguished primarily by maximum snow depth, with the separation at 50 cm (Shimano 2006). The Shirakami Mountains belong to the Japan Sea type, which has greater snowfall.

We selected nine study sites in the Shirakami Mountains, and established three 20 m × 20 m plots at each site, for a total of 27 plots (Fig. 1; Table S1). The elevation of the study sites ranges from 269 m asl (Lake Juniko site) to 662 m asl (Tsugaru Pass site). All plots were located in forests with closed canopies within the cool-temperate deciduous broadleaved forest zone. Matsui et al. (2007) found that the lower elevation boundary for beech forests in the Shirakami Mountains was 260 m, and the upper was

1070 m. Therefore, the elevation range of our study sites covers the low to middle parts of the elevational distribution of *F. crenata* in the Shirakami Mountains. Matsui et al. (2007) predicted the lower boundary of the potential distribution of *F. crenata* as 43 m based on the warmth index (Kira 1948). The area near this boundary has been disturbed by deforestation. Microtopography of the study sites was similar, with flat to gently sloped terrain.

Tree census

Our tree census was conducted from August to September 2021 at the 27 plots. We recorded the diameter at breast height (*DBH*, the diameter at a height of 1.3 m) of all trees in each plot. For individuals with $DBH < 2$ cm and ≥ 1.3 m in height, we recorded only the number of individuals. Hereafter, we call these individuals "saplings." In addition, we selected one corner of each 20 × 20 m plot described above and counted the number of seedlings of *F. crenata* by walking within the plot, along the edge, until the total area examined reached 25 m^2 (typically, a transect that covered 1 m × 25 m). Seedlings were defined as individuals shorter than 1.3 m in height. We determined the coverage by dwarf bamboo within each plot at 10% intervals since this species is known to affect *F. crenata* regeneration (Nakashizuka & Numata 1982).

Data Analyses

We summarized the data from the tree census (see Tables S2a-i) and analyzed the relationships between the amount of *F. crenata* regeneration and elevation. First, we calculated the juvenile-to-canopy tree (*J/C*) ratio, where *J* represents the number of juvenile trees in the plot, which we defined as trees with $DBH < 10$ cm and ≥ 1.3 m in

height, and *C* represents the number of canopy trees, which we defined as trees with DBH ≥ 30 cm (Shimano & Okitsu 1994). The ratio therefore indicates the relative proportion of juvenile trees of *F. crenata*. In this method, a higher *J/C* ratio means better regeneration. For this analysis, we pooled the data from the three plots at each site. The ratio was also calculated for *M. obovata* and *A. pictum* subsp. *mayrii*.

Second, we examined the shape of the *DBH* class distribution (Shimano 2000) of *F. crenata*. We constructed this distribution for each site by compiling the data from the three study plots with 5 cm class intervals. We transformed the data into a double logarithmic graph, and calculated the coefficients *a* and *b* for the power function $density = a\ DBH^b$. We subsequently compared the parameter values among the sites. When the proportion of small trees increases, *a* and *b* increase and decrease, respectively. In constructing the *DBH* class distribution, we included the sapling data in the lowest *DBH* class (i.e., 1 to 6 cm). We then quantified the relationships between the obtained values of *a* and *b* and the site's elevation by using a linear model. We did not conduct this analysis for *M. obovata* and *A. pictum* subsp. *mayrii* due to their small sample sizes.

Finally, we analyzed the relationships between elevation and the number of *F. crenata* seedlings and saplings by using a generalized linear mixed model (GLMM). In these analyses, the response variable was the number of seedlings or saplings, and the explanatory variables were elevation, coverage by dwarf bamboo, and the *BA* of *F. crenata*, excluding individuals with DBH <30 cm in each plot. *BA* of *F. crenata* with DBH ≥30 cm was included in the model as an indicator of the size of the seed source. We modeled the error distribution as a Poisson distribution with a log-link function. Site was treated as a random effect. The explanatory variables were standardized before the analyses. We selected the best-fit models using Akaike's information criterion (*AIC*); the

model with the smallest *AIC* was selected as the best model. We also selected models with a similarly good fit (i.e., models whose *AIC* differed by < 2 from the best model). For references, we performed the same analyses for *M. obovata* and *A. pictum* subsp. *mayrii*. For these species, we used the number of saplings in each plot as the response variable. We conducted the GLMM analyses using version 4.1.2 of the R software (R Core Team 2021) and the packages lme4 (https://cran.r-project.org/web/packages/lme4/index.html), lmerTest (https://cran.r-project.org/web/packages/lmerTest/index.html), and MuMIn (https://cran.r-project.org/web/packages/MuMIn/index.html).

RESULTS

Stand structure

In the tree census, *F. crenata* was the dominant tree species at all of our study sites; its *BA* was the largest at 22 out of 27 plots (Table S2). The average *F. crenata BA* was 31.90 m²/ha, and ranged from 13.67 m²/ha (TGB site, average of three plots) to 55.46 m²/ha (LJ site). *Acer pictum* sub*sp. mayrii* and *M. obovata* had the second- and third-largest *BA*s, respectively. Other major associated tree species included *Aesculus turbinata* Blume, *Quercus crispula* Blume, and *Tilia japonica* (Miq.) Simonk. (Fig. 2). At two of the low-elevation sites (LJ and BGSNT), the proportions of *A. pictum* subsp. *mayrii* and *M. obovata* were relatively high in the sapling population. The coverage by dwarf bamboo averaged 22%, with values ranging from 10 to 80% (Fig. S2).

Relationship between elevation and *F. crenata* regeneration

The *F. crenata J/C* ratio was relatively low at the low-elevation sites, although the

relationship was not statistically significant (Fig. 3a; $p = 0.21$). The highest *J/C* ratio (15.7) was recorded at the TGB site (elevation 559 m). In our analysis of the shape of the *DBH* class distribution for *F. crenata*, the *a* parameter increased slowly with increasing elevation, but the increase was only marginally significant ($R^2 = 0.42$; $p = 0.06$; Fig. 4, Fig. S3). In contrast, the *b* parameter decreased significantly with increasing elevation ($R^2 = 0.47$; $p = 0.04$).

According to the GLMM analyses, the number of *F. crenata* seedlings was best explained by the model that included elevation and the *BA* of *F. crenata* canopy trees (Table 1). The full model that included elevation, coverage by dwarf bamboo, and the *BA* of *F. crenata* canopy trees provided a comparably good fit (i.e., *AIC* differed by < 2 units). For the number of *F. crenata* saplings, the two models with comparable values of *AIC* provided comparably good fits: both included coverage by dwarf bamboo (significantly negative) and the *BA* of *F. crenata* canopy trees (significantly negative) as explanatory variables. Elevation was also included in the second model.

Comparisons of the regeneration patterns with *M. obovata* and *A. pictum* subsp. *mayrii*

The *J/C* ratio of *M. obovata* (Fig. 3b) showed a similar trend to that of *F. crenata*, but there was a marginally significant positive relationship ($p = 0.10$). That is, the *J/C* ratio decreased with decreasing elevation. In contrast, *A. pictum* subsp. *mayrii*, showed no significant relationship with elevation (Fig. 3c; $p = 0.44$). In the GLMM analysis, elevation was not significantly related to sapling numbers for *M. obovata* and *A. pictum* subsp. *mayrii* (Table 1). However, the number of *M. obovata* saplings was significantly positively related to the *BA* of canopy trees, and the number of *A. pictum* subsp. *mayrii* saplings was significantly negatively related to the coverage by dwarf bamboo and to

the *BA* of canopy trees.

DISCUSSION

In the present study, we examined the relationship between elevation and regeneration of *F. crenata*. In the GLMM analysis, elevation was selected in one or several best-fit models as an explanatory variable for number of seedlings and saplings of *F. crenata* (Table 1). *Fagus crenata* regeneration was limited at lower elevations as compared to that at middle elevation range, suggesting a clear effect of elevation on the number of seedlings. Moreover, the power analysis of DBH-class distribution indicates that parameters *a* and *b* decrease and increase, respectively, with decreasing elevation (Fig. 4), though the increasing trend of parameter *a* was marginally significant. Parameters *a* and *b* represent tree density and decreasing density when tree size is doubled, respectively. Thus, the results suggest that the tree density was higher and the density increased more sharply as DBH class decreased at high elevation sites than that at low elevation. Shimano (2006) demonstrated that the population parameters of *F. crenata* differed markedly between the Pacific and Japan Sea populations; the latter had much better regeneration than the former. Our data demonstrated that elevational differences also existed in the forests of the Shirakami Mountains. Additionally, the J/C ratio tended to be low at the low-elevation sites (Fig. 3) although the relationship was not statistically significant due to the high variation.

The elevational pattern of plant distribution and associated changes of species composition have been studied for tree species in other countries. In a Spanish study (Penuelas et al. 2007), the relative abundance of European beech (*F. sylvatica*) at the lower limit of the vertical distribution was half that at the center and upper limit of the

species' distribution. The authors suggested that the result was likely due to current global warming. Furthermore, holm oak (*Quercus ilex* L.) in small size classes showed very high recruitment at the lower limit of the distribution of *F. sylvatica*, which suggests that the forest's composition appears to be changing from beech to oak. On the other hand, Benavides et al. (2015) showed that *F. sylvatica* had an unexpectedly high density of juveniles at lower elevations, suggesting that there may be other reasons for this phenomenon that were not linked to climate change, such as changes of land-use practices and disturbance regimes. With the limited information from our study, we are unable to determine whether the decreased *F. crenata* regeneration at lower elevations in the Shirakami Mountains may be caused by current global warming or not. To identify the major causes of this pattern, it will be important to examine the effects of other potential factors, such as anthropogenic disturbance. We should also consider aspects of the species' life history, such as changes in flower and seed production (e.g., masting) and in its interactions with other organisms, such as the frequency and severity of damage caused by insects and seed predators as a function of elevation. Although it is difficult to determine how much the current warming has contributed to this trend, our data agree with previous predictions that the distribution of *F. crenata* near the low-elevation boundary will shift toward higher elevations as the climate warms (Matsui et al. 2007) and that potential juvenile habitat will be lost at the warmer and snowless sites (Koide et al. 2016). Our results also suggest that if the climate continues to warm in the future, *F. crenata* regeneration will decrease at lower elevations, where it may be replaced by other species.

In the GLMM analyses, we found a significant positive effect of the *F. crenata BA* on the number of seedlings (Table 1). This may be because *F. crenata* trees with a large

BA have wide canopies and can therefore produce large numbers of seeds. In the models for saplings, however, the *BA* of *F. crenata* had a significant negative effect on the number of saplings in both models, which was the opposite of the result for seedlings. This may be caused by shading by the large mature trees, which would decrease the growth of saplings because *F. crenata* needs the high light levels that occur in canopy gaps for successful regeneration (Nakashizuka & Numata 1982; Nakashizuka 1987). We hypothesize that the negative effects caused by shading would also be important for the growth of seedlings, but that their numbers would be high because of the abundant seed production by the large trees right after seedling establishment. In the selected models for the number of saplings, the coefficient for the coverage by dwarf bamboo was negative (Table 1). This indicates that dwarf bamboo inhibits the growth of seedlings, which agrees with previous studies (Peters et al. 1992; Abe et al. 2002).

The *J/C* ratio of *M. obovata* showed a similar pattern to *F. crenata* in its relationships between elevation and regeneration, although the relationship was only marginally significant for *M. obovata* (Fig. 3b). This may be because *M. obovata* has a similar vertical distribution (i.e., 200 to 920 m; Matsui et al. 2007) to *F. crenata* in the Shirakami Mountains, and the young populations in low-elevation areas may also suffer from high mortality caused by current warming or other anthropogenic factors. Our result agrees with Koide et al. (2022), who demonstrated that *M. obovata* shifted to colder sites by comparing juvenile and adult temperature ranges. However, in the models selected by our GLMM analyses, the *M. obovata BA* had a significant positive effect on the number of saplings of *M. obovata*; this effect was the opposite of the relationship for *F. crenata*. This may be partially due to the sprouting ability of *M. obovata*, because we often observed young stems of *M. obovata* originating from the

base of large trees. In contrast, the effect of dwarf bamboo was small and not significant in the selected models (Table 1). This may also be due to the high sprouting ability of *M. obovata* because sprouting stems have a high growth rate and are less sensitive to competition from dwarf bamboo. For *A. pictum* subsp. *mayrii*, the coverage of the site by dwarf bamboo and the *BA* of canopy-size individuals significantly affected its number of saplings, as was the case for *F. crenata* (Table 1). However, there was no significant relationship with elevation. This may be because its lowest elevation boundary (i.e., 0 m according to Matsui et al. 2007) is much lower than that of our study area.

In the low-elevation areas, the major species that were co-dominant with *F. crenata* in the understory layer were *A. pictum* subsp. *mayrii, M. obovata, A. turbinata*, and *Pterocarya rhoifolia* Sieb. et Zucc. (Fig. 2). Matsui et al. (2018) predicted that *F. crenata* is likely to be replaced by *Quercus* spp., but our data demonstrated that other tree species may also actively regenerate and compete with *F. crenata*. The species composition under a gap may be different from the ones we found, and additional research will be needed to clarify the mechanisms of species turnover.

The regeneration patterns we obtained in this study were based on 27 plots with closed canopies. We must therefore caution readers that *F. crenata* regeneration may be more vigorous than would be predicted based on our results if canopy gaps are created by large disturbances (Nakashizuka & Numata 1982; Nakashizuka 1987; Shimano 2006). The *J/C* ratios in our study (0.2 to 15.7) were smaller than those (1.2 to 19.4) reported by Shimano (2006) because Shimano focused on well-regenerated areas in canopy gaps. In addition, the regeneration could differ from our results even at the same site, since *F. crenata* forests have a mosaic structure (Yamamoto et al. 1995; Ida 2000;

Henbo et al. 2004). Conversely, it is possible that other species may become even more vigorous than *F. crenata* in canopy gaps. Considering the mechanisms involved in *F. crenata* gap dynamics, our plot size may have been too small to detect all of this variation following disturbances.

CONCLUSIONS

Our results suggest that *F. crenata* regeneration is poorer at the lower boundary of its vertical distribution than in the middle of its distribution range. If the climate continues to warm in the future, *F. crenata* regeneration at lower elevations may worsen. It is beyond the scope of our study to examine how much current warming has contributed to the observed regeneration patterns. The decreased regeneration at lower elevations may also be shaped by other factors, such as variation in anthropogenic disturbance or stand history. To more accurately predict the effects of climate change, long-term monitoring studies will be helpful because they provide a better understanding of chronological patterns of turnover and growth rates of the target species. Several monitoring projects are currently underway in the Shirakami Mountains. They are being conducted at a limited number of sites, mainly within the World Natural Heritage site area. We propose that such activities be extended to a wider elevational range, including sites outside the World Natural Heritage site area. Monitoring at low elevations will be especially important because these sites are likely to have been most strongly affected by recent global warming due to the decreased amount of beech regeneration. In addition, these areas are located close to local communities and tourist spots. Participation of citizens in forest monitoring activities would increase public interest in the conservation of beech forests and in the challenges being created by climate change.

Such educational activities for *F. crenata*, a symbol of this World Natural Heritage site, will strengthen the relationships between local people and the ecosystems of the Shirakami Mountains.

ACKNOWLEDGMENTS

We thank Prof. K. Shimano (Osaka Sangyo University), Prof. K. Ishida (Hirosaki University), Prof. Y. Ishikawa (Shirakami Research Center for Environmental Sciences), Prof. T. Kamijo (University of Tsukuba), Prof. T. Matsui (University of Tsukuba, Forestry and Forest Products Research Institute), Mr. W. Komatsu and the members of the Laboratory of Silviculture and Nature Conservation, University of Tsukuba, for their many useful comments and field assistance on our research. We are also grateful to the staff of the Shirakami-Sanchi World Heritage Conservation Center (Nishimeya), the Tsugaru District Forest Office of the Forestry Agency, and the Nature Protection Division of the Aomori Prefectural Government for their assistance in applying for permission to conduct our study. Comments from four anonymous reviewers helped with improving our manuscript.

DECLARATION OF INTEREST STATEMENT

The authors report there are no competing interests to declare.

REFERENCES

Abe M, Izaki J, Miguchi H, Masaki T, Makita A, Nakashizuka T. 2002. The effects of Sasa and canopy gap formation on tree regeneration in an old beech forest. J Veg Sci. 13:565-574.

Abe M, Miguchi H, Honda A, Makita A, Nakashizuka T. 2005. Short-term changes affecting regeneration of Fagus crenata after the simultaneous death of Sasa kurilensis. J Veg Sci. 16:49-56.

Abe M, Miguchi H, Nakashizuka T. 2001. An interactive effect of simultaneous death of dwarf bamboo, canopy gap, and predatory rodents on beech regeneration. Oecologia. 127:281-286.

Beckage B, Osborne B, Gavin DC, Pucko C, Siccama T, Perkins T. 2008. A rapid upward shift of a forest ecotone during 40 years of warming in the Green Mountains of Vermont. Proc Natl Acad Sci U.S. Am. 105:4197-4202.

Benavides R, Escudero A, Coll L, Ferrandis P, Gouriveau F, Hodar JA, Ogaya R, Rabasa SG, Granda E, Santamaria BP, et al. 2015. Survival vs. growth trade-off in early recruitment challenges global warming impacts on Mediterranean mountain trees. Perspect Plant Ecol Evol Syst. 17:369-378.

Dulamsuren C, Hauck M, Kopp G, Ruff M, Leuschner C. 2017. European beech responds to climate change with growth decline at lower, and growth increase at higher elevations in the center of its distribution range (SW Germany). Trees Struct Funct. 31:673-686.

Feeley KJ, Silman MR, Bush MB, Farfan W, Cabrera KG, Malhi Y, Meir P, Revilla NS, Quisiyupanqui MNR, Saatchi S. 2011. Upslope migration of Andean trees. J Biogeogr. 38:783-791.

Gatti RC, Callaghan T, Velichevskaya A, Dudko A, Fabbio L, Battipaglia G, Liang JJ. 2019. Accelerating upward treeline shift in the Altai Mountains under last-century climate change. Sci Rep. 9. 7678.

Harsch MA, Hulme PE, McGlone MS, Duncan RP. 2009. Are treelines advancing? A

global meta-analysis of treeline response to climate warming. Ecol Lett. 12:1040-1049.

Henbo Y, Itaya A, Nishimura N, Yamamoto SI. 2004. Long-term canopy dynamics in a large area of temperate old-growth beech (Fagus crenata) forest: analysis by aerial photographs and digital elevation models. J Ecol. 92:945-953.

Ida H. 2000. Treefall gap disturbance in an old-growth beech forest in southwestern Japan by a catastrophic typhoon. J Veg Sci. 11:825-832.

Kira T. 1948. On the altitudinal arrangement of climatic zones in Japan: A contribution to the rational land utilization in cool highlands. Agricultural Sci North Temperate Reg. 2:143-173. (in Japanese with English title)

Koide D, Higa M, Nakao K, Ohashi H, Tsuyama I, Matsui T, Tanaka N. 2016. Projecting spatiotemporal changes in suitable climate conditions to regenerate trees using niche differences between adult and juvenile trees. Eur J For Res. 135:125-136.

Koide D, Yoshida K, Daehler C.C., Mueller-Dombois D. 2017. An upward elevation shift of native and non-native vascular plants over 40 years on the island of Hawai'i. J Veg Sci. 28:939-950.

Koide D, Yoshikawa T, Ishihama F, Kadoya T. 2022. Complex range shifts among forest functional types under the contemporary warming. Glob Chang Biol. 28:1477-1492.

Koike T. 1988. Leaf Structure and Photosynthetic Performance as Related to the Forest Succession of Deciduous Broad-Leaved Trees (Symposium: Adaptive significance of leaf expansion and branchings in trees). Plant Species Biol. 3:77-87.

Kon H, Noda T, Terazawa K, Koyama H, Yasaka M. 2005. Evolutionary advantages of mast seeding in Fagus crenata. J Ecol. 93:1148-1155.

Matsui T, Tanaka N, Yagihashi T. 2007. Predicting Changes in Suitable Habitats for Beech (Fagus crenata Blume) Forests under Climate Warming in Shirakami Mountains World Natural Heritage Area, Northern Japan. J Jap For Soc. 89:7-13. (in Japanese with English summary)

Matsui T, Nakao K, Higa M, Tsuyama I, Kominami Y, Yagihashi T, Koide D, Tanaka N. 2018. Potential impact of climate change on canopy tree species composition of cool-temperate forests in Japan using a multivariate classification tree model. Ecol Res. 33:289-302.

Nakashizuka T. 1987. Regeneration dynamics of beech forests in Japan. Vegetatio. 69:169-175.

Nakashizuka T, Numata M. 1982. Regeneration process of climax beech forest I. Structure of a beech forest with the undergrowth of *Sasa*. Jap J Ecol. 32:57-67.

Penuelas J, Ogaya R, Boada M, Jump AS. 2007. Migration, invasion and decline: changes in recruitment and forest structure in a warming-linked shift of European beech forest in Catalonia (NE Spain). Ecography. 30:829-837.

Peters R, Nakashizuka T, Ohkubo T. 1992. Regeneration and development in beech dwarf bamboo forest in Japan. For Ecol Manag. 55:35-50.

R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. [Accessed 27 September 2022]. https://www.R-project.org/.

Shimano K. 2000. A power function for forest structure and regeneration pattern of pioneer and climax species in patch mosaic forests. Plant Ecol. 146:207-220.

Shimano K. 2006. Differences in beech (Fagus crenata) regeneration between two types of Japanese beech forest and along a snow gradient. Ecol Res. 21:651-663.

Shimano K, Okitsu S. 1994. Regeneration of natural *Fagus crenata* forests around Kanto District. Jap J Ecol. 44:283-291. (in Japanese with English summary)

Shimazaki M, Sasaki T, Hikosaka K, Nakashizuka T. 2011. Environmental dependence of population dynamics and height growth of a subalpine conifer across its vertical distribution: an approach using high-resolution aerial photographs. Glob Chang Biol. 17:3431-3438.

Suzuki SN, Ishihara MI, Hidaka A. 2015. Regional-scale directional changes in abundance of tree species along a temperature gradient in Japan. Glob Chang Biol. 21:3436-3444.

Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin JM, Hoegh-Guldberg O, Bairlein F. 2002. Ecological responses to recent climate change. Nature. 416:389-395.

Wason JW, Dovciak M. 2017. Tree demography suggests multiple directions and drivers for species range shifts in mountains of Northeastern United States. Glob Chang Biol. 23:3335-3347.

Yamamoto S, Nishimura N, Matsui K. 1995. Natural disturbance and tree species coexistence in an old-growth beech - Dwarf bamboo forest, southwestern Japan. J Veg Sci. 6:875-886.

TABLE

Table 1. Characteristics of the best-fit models for predicting the number of seedlings and saplings of *Fagus crenata* and the number of saplings of *Magnolia obovata* and *Acer pictum* subsp. *mayrii* in the Shirakami Mountains, Japan, as a function of three explanatory variables: the site's elevation, coverage by dwarf bamboo, and basal area (*BA*) of individuals with DBH ≥ 30 cm. The analyses were performed with generalized linear mixed models. The table shows the models with the lowest values of Akaike's information criterion (*AIC*) and models with values that differ by < 2 units from that value; Δ*AIC* represents the difference in *AIC* compared to the model with the lowest *AIC*. The models were constructed based on the results of the tree censuses in 27 plots (each 20 m × 20 m) at the nine study sites. Significance: ***, $p<0.001$; **, $p<0.01$; *, $p<0.05$ (based on *t*-statistics using Satterthwaite's method).

Response variable	Intercept	Elevation	Coverage by dwarf bamboo	*BA* of conspecific trees with DBH ≥ 30 cm	*AIC*	Δ*AIC*
Number of seedlings of *F. crenata*	0.54	1.62***		0.74***	145.9	
	0.54	1.58*	0.15	0.75***	147.6	1.72
Number of saplings of *F. crenata*	0.36		-0.65***	-1.19***	147.6	
	0.37	0.27	-0.66***	-1.18***	149.4	1.83

Number of saplings of *M. obovata*	-1.14	1.22		0.92***	101.6	
	-1.16	1.25	-0.08	0.92***	103.5	1.95
Number of saplings of *A. pictum* subsp. *mayrii*	-2.38		-1.06*	-2.82*	76.6	
	-2.36	-0.21	-1.07*	-2.82*	78.6	1.95

FIGURES

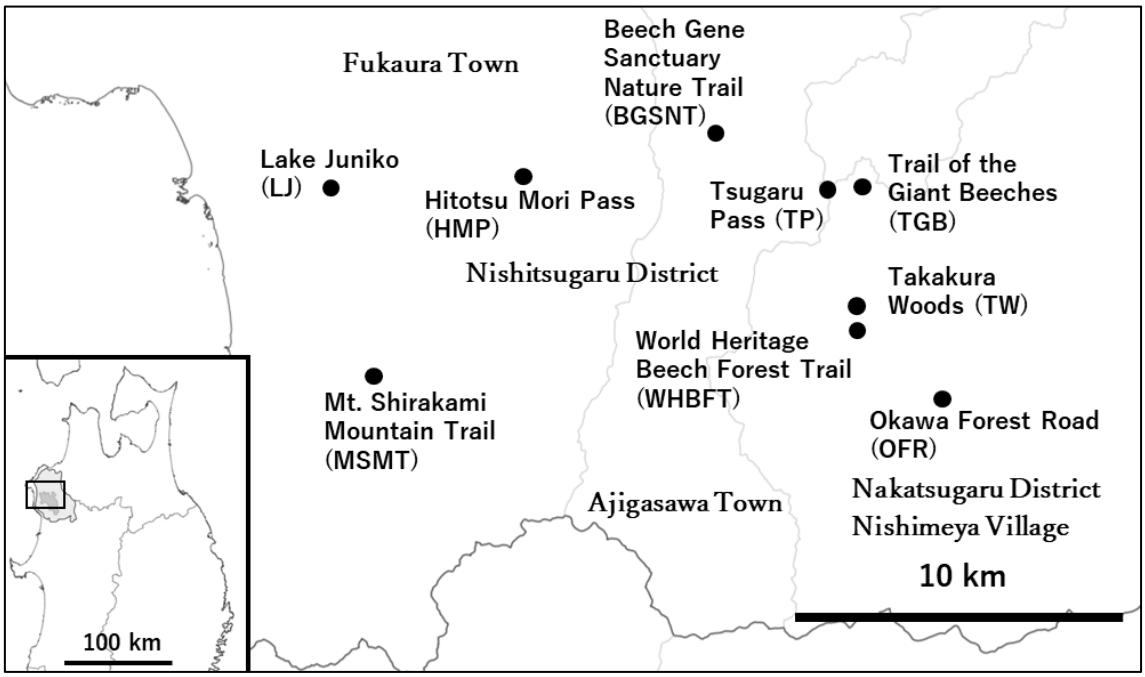

Fig. 1 Map of Northern Tohoku, Japan (small map) and map of northern Aomori Prefecture, showing the nine *Fagus crenata* study sites (large map). The dark and light gray areas in the small map indicate the World Natural Heritage area and the Shirakami Mountains, respectively. The light lines in the large map are municipal boundaries. The gray dotted lines in the large map are latitude and longitude. The base map was created from geographic data provided by the Geospatial Information Authority of Japan (https://maps.gsi.go.jp/#8/39.846504/140.789795/&base=blank&ls=blank&disp=1&vs=c0g1j0h0k0l0u0t0z0r0s0m0f1).

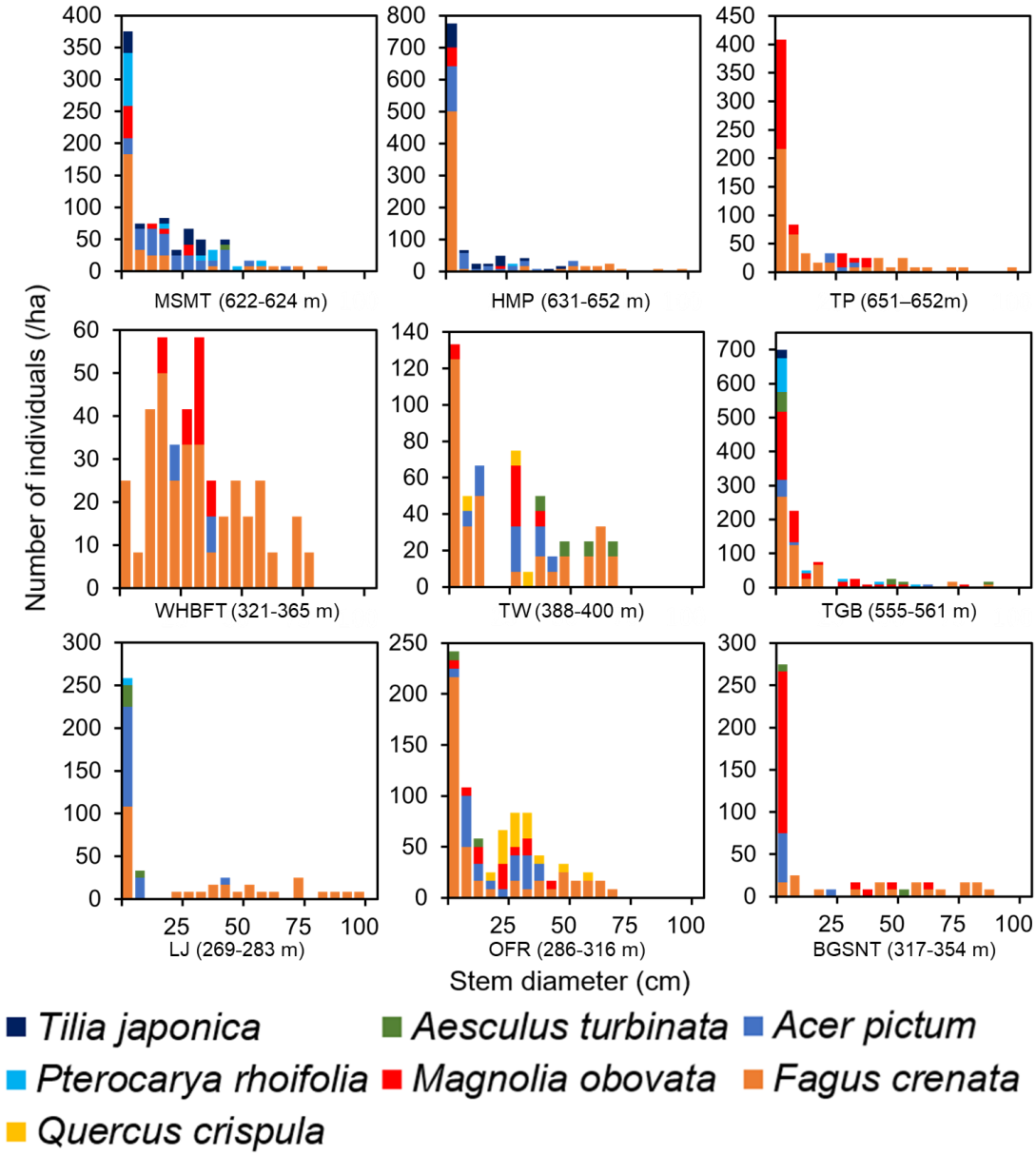

Fig. 2 Stem-diameter distribution of major tree species in forests dominated by *Fagus crenata* at nine study sites in Shirakami Mountains, Japan. Abbreviations below the *x*-axis represent the site and elevation range. Figure 1 and Table S1 define the abbreviations for the site names.

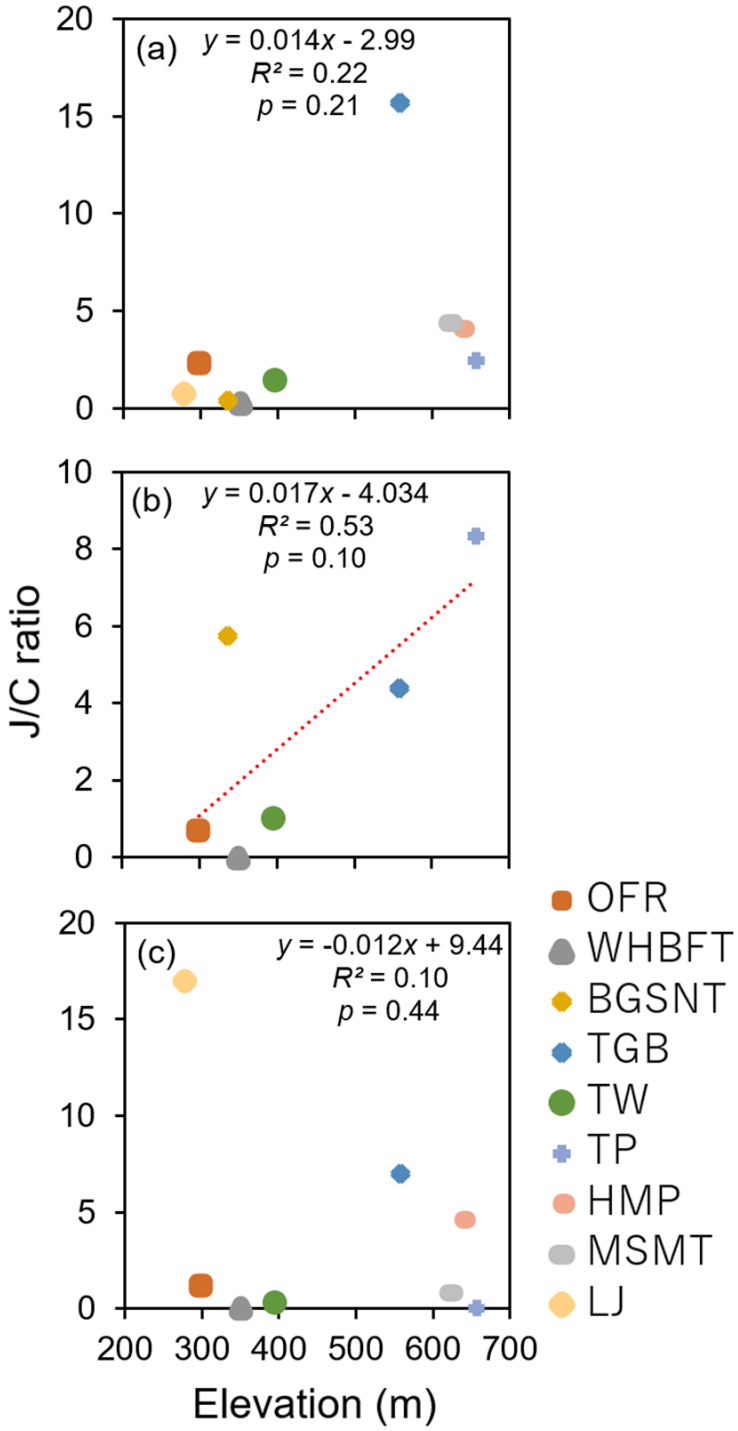

Fig. 3 Relationship between the juvenile-to-canopy tree (*J/C*) ratio for (a) *Fagus crenata,* (b) *Magnolia obovata*, and (c) *Acer pictum* subsp. *mayrii*. Note that the *y*-axis scale differs among the species. Site names are defined in Figure 1 and Table S1.

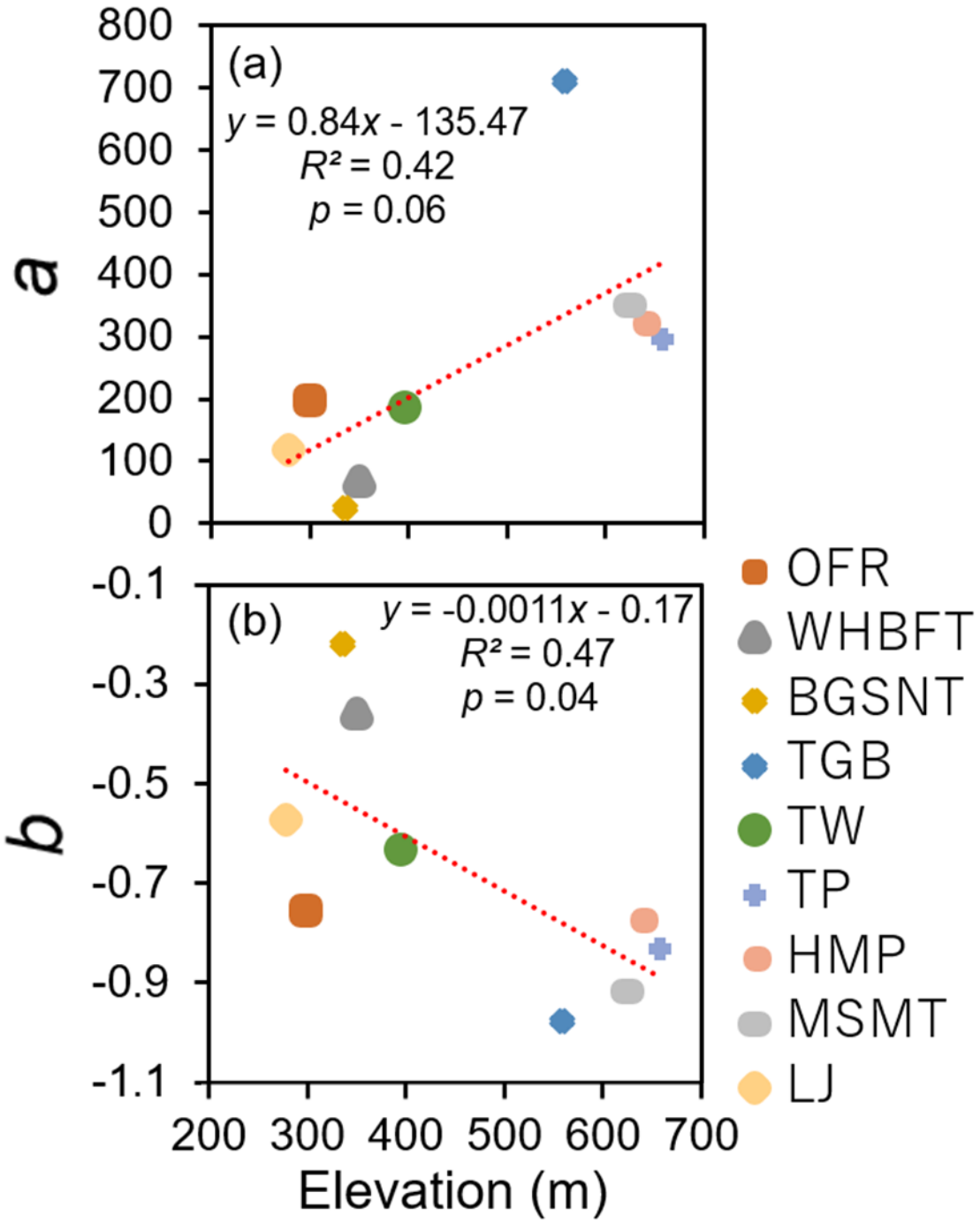

Fig. 4 Relationships between elevation and the values of the *a* (a) and *b* (b) parameters in the power function constructed based on the *DBH* class distribution of *Fagus crenata*: *density* = $a\ DBH^b$. Site names are defined in Figure 1 and Table S1.

SUPPLEMENTAL ONLINE MATERIAL

Table S1 List of study sites, plot information (three plots per site) and abundance of *Fagus crenata*.

Site (Abbreviation)	Latitude	Longitude	Elevation (m)	Coverage of dwarf bamboo (%)	Stem density of all species with *DBH* > 2.0 cm (/ha)	*BA* of all species with *DBH* > 2.0 cm (m^2)	Stem density of *F. crenata* with *DBH* > 2.0 cm (/ha)	*BA* of *F. crenata* with *DBH* > 2.0 cm (m^2)	*No. of seedlings of F. crenata (/ha)*	*No. of saplings of M. obovata (/ha)*	*No. of saplings of A. pictum (/ha)*
Okawa Forest Road (OFR)	N 40°29'38.64"	E 140°11'55.25"	294	10	875	42.98	400	25.39	800	0	0
	N 40°30'18.29"	E 140°12'08.35"	286	10	1350	50.84	175	14.73	800	0	0
	N 40°29'52.64"	E 140°12'03.86"	316	10	875	57.93	225	38.58	800	0	0
World Heritage Beech Forest Trail (WHBFT)	N 40°31'14.13"	E 140°10'18.75"	321	10	500	40.89	250	28.09	400	0	0
	N 40°31'11.15"	E 140°10'14.61"	365	10	300	49.11	200	47.52	9200	0	0
	N 40°31'11.38"	E 140°10'11.13"	365	10	850	40.77	575	38.78	4800	0	0
Beech Gene Sanctuary Nature Trail (BGSNT)	N 40°34'26.12"	E 140°07'16.19"	317	10	800	64.06	200	41.34	400	275	25
	N 40°34'28.87"	E 140°07'16.92"	336	10	1050	46.11	175	45.64	0	0	75
	N 40°34'28.68"	E 140°07'13.72"	354	10	675	26.75	100	25.03	0	0	50
Trail of the Giant Beeches (TGB)	N 40°33’45.93”	E 140°10’25.03”	561	20	1425	43.45	450	3.50	3600	25	25
	N 40°33’39.97”	E 140°10’16.88”	559	20	2350	51.47	450	13.55	1200	0	0
	N 40°33’41.13”	E 140°10’14.51”	555	20	1350	44.24	50	23.96	8000	0	125
Takakura Woods (TW)	N 40°31'32.30"	E 140°10'25.46"	400	10	725	42.76	350	33.23	2000	0	0
	N 40°31'31.40"	E 140°10'20.41"	398	10	750	54.65	100	22.42	0	0	0

	N 40°31'29.90"	**E 140°10'17.10"**	**388**	**10**	**800**	**39.82**	**325**	**28.90**	**2400**	**25**	**0**
Tsugaru Pass (TP)	**N 40°33'27.10"**	**E 140°09'40.76"**	**651**	**20**	**975**	**42.34**	**225**	**41.64**	**23200**	**0**	**0**
	N 40°33'26.96"	**E 140°09'39.81"**	**662**	**30**	**2700**	**41.72**	**475**	**30.49**	**20000**	**0**	**0**
	N 40°33'27.31"	**E 140°09'38.73"**	**659**	**20**	**3175**	**39.52**	**400**	**24.42**	**9600**	**325**	**0**
Hitotsu Mori Pass (HMP)	**N 40°33'58.87"**	**E 140°03'03.55"**	**652**	**70**	**475**	**58.02**	**125**	**37.17**	**0**	**75**	**0**
	N 40°33'58.14"	**E 140°03'01.64"**	**635**	**40**	**1450**	**57.64**	**500**	**35.96**	**400**	**0**	**25**
	N 40°33'59.85"	**E 140°03'00.75"**	**631**	**10**	**2200**	**55.04**	**325**	**44.47**	**400**	**0**	**175**
Mt. Shirakami Mountain Trail (MSMT)	**N 40°30'32.01"**	**E 139°59'36.57"**	**624**	**10**	**1175**	**50.23**	**125**	**10.67**	**0**	**100**	**50**
	N 40°30'31.74"	**E 139°59'36.38"**	**627**	**20**	**700**	**49.35**	**225**	**31.16**	**800**	**0**	**0**
	N 40°30'29.95"	**E 139°59'36.53"**	**622**	**10**	**1175**	**48.51**	**350**	**8.25**	**0**	**50**	**0**
Lake Juniko (LJ)	**N 40°33'45.54"**	**E 139°58'57.27"**	**283**	**80**	**1125**	**53.27**	**225**	**50.90**	**0**	**0**	**0**
	N 40°33'38.30"	**E 139°58'56.09"**	**269**	**60**	**550**	**107.48**	**200**	**78.01**	**0**	**0**	**225**
	N 40°33'36.67"	**E 139°58'54.14"**	**283**	**40**	**475**	**42.25**	**300**	**37.49**	**0**	**0**	**100**

Table S2
a. Species composition at the Okawa Forest Road (OFR) site (*DBH*≥2 cm)

Plot No.	**1**		**2**		**3**	
Elevation (m)	**294 m**		**286 m**		**316 m**	
Species	**Stem density (/ha)**	***BA* (m²/ha)**	**Stem density (/ha)**	***BA* (m²/ha)**	**Stem density (/ha)**	***BA* (m²/ha)**
Fagus crenata	**400**	**25.39**	**175**	**14.73**	**225**	**38.58**
Quercus crispula	**50**	**3.00**	**225**	**20.93**	**100**	**6.01**
Acer pictum* subsp. *mayrii	**150**	**8.99**	**325**	**11.09**	**25**	**1.52**
Magnolia obovata	**25**	**3.19**	**25**	**0.09**	**225**	**9.70**
Dead tree	**50**	**1.68**	**125**	**3.65**	**125**	**2.02**
Aesculus turbinata	**50**	**0.35**				
Acer amoenum* var. *matsumurae	**25**	**0.02**	**325**	**0.29**		
Styrax obassia	**25**	**0.23**				
Acer sieboldianum	**25**	**0.05**	**25**	**0.01**	**25**	**0.04**
Aria alnifolia	**25**	**0.07**				
Padus grayana			**125**	**0.05**	**25**	**0.01**
Viburnum furcatum	**50**	**0.02**			**75**	**0.03**
Lindera umbellata* var. *membranacea					**25**	**0.01**
Clethra barbinervis					**25**	**0.01**
total	**875**	**42.98**	**1350**	**50.84**	**875**	**57.9**

b. Species composition at the World Heritage Beech Forest Trail (WHBFT) site (*DBH*≥2 cm)

Plot No.	**1**		**2**		**3**	
Elevation (m)	**321 m**		**365 m**		**365 m**	
Species	**Stem density (/ha)**	***BA* (m²/ha)**	**Stem density (/ha)**	***BA* (m²/ha)**	**Stem density (/ha)**	***BA* (m²/ha)**
Fagus crenata	**250**	**28.09**	**200**	**47.52**	**575**	**38.78**
Magnolia obovata	**125**	**8.66**	**25**	**1.45**		
Acer pictum* subsp. *mayrii	**50**	**4.09**				
Acer sieboldianum			**25**	**0.02**	**125**	**1.40**
Dead tree	**25**	**0.01**			**75**	**0.55**
Vitis coignetiae	**25**	**0.03**	**50**	**0.12**		
Clethra barbinervis					**50**	**0.02**
Lindera umbellata* var. *membranacea					**25**	**0.01**
Acer amoenum* var. *matsumurae	**25**	**0.01**				
total	**500**	**40.89**	**300**	**49.11**	**850**	**40.77**

c. Species composition at the Beech Gene Sanctuary Nature Trail (BGSNT) site (*DBH*≥2 cm)

Plot No.	**1**		**2**		**3**	
Elevation (m)	**317 m**		**336 m**		**354 m**	
Species	**Stem density (/ha)**	***BA* (m²/ha)**	**Stem density (/ha)**	***BA* (m²/ha)**	**Stem density (/ha)**	***BA* (m²/ha)**
Fagus crenata	**200**	**41.34**	**175**	**45.64**	**100**	**25.03**
Magnolia obovata	**400**	**17.13**				
Aesculus turbinata	**25**	**5.49**				
Acer pictum* subsp. *mayrii	**25**	**0.02**			**25**	**0.90**
Padus grayana			**50**	**0.04**	**75**	**0.64**
Viburnum furcatum	**125**	**0.05**	**275**	**0.17**	**175**	**0.07**
Lindera umbellata* var. *membranacea			**300**	**0.12**	**275**	**0.11**
Magnolia salicifolia			**125**	**0.07**	**25**	**0.01**
Clethra barbinervis			**100**	**0.06**		
Acer sieboldianum	**25**	**0.03**	**25**	**0.01**		
total	**800**	**64.06**	**1050**	**46.11**	**675**	**26.75**

d. Species composition at the Trail of the Giant Beeches (TGB) site (*DBH*≥2 cm)

Plot No.	**1**		**2**		**3**	
Elevation (m)	**561m**		**559m**		**555m**	
Species	**Stem density (/ha)**	***BA* (m²/ha)**	**Stem density (/ha)**	***BA* (m²/ha)**	**Stem density (/ha)**	***BA* (m²/ha)**
Magnolia obovata	**450**	**14.81**	**600**	**24.16**	**125**	**2.10**
Fagus crenata	**450**	**3.50**	**450**	**13.55**	**50**	**23.96**
Aesculus turbinata	**100**	**20.53**	**25**	**5.09**	**75**	**4.28**
Pterocarya rhoifolia	**50**	**4.22**			**125**	**7.94**
Acer pictum* subsp. *mayrii			**50**	**7.60**		
Salix dolichostyla					**25**	**3.20**
Dead tree	**25**	**0.01**	**150**	**0.17**	**75**	**1.94**
Clethra barbinervis			**250**	**0.18**	**250**	**0.16**
Lindera umbellata* var. *membranacea	**75**	**0.03**	**300**	**0.19**	**50**	**0.07**
Magnolia salicifolia	**100**	**0.14**	**75**	**0.08**	**75**	**0.04**
Viburnum furcatum	**50**	**0.03**	**175**	**0.14**	**125**	**0.06**
Chengiopanax sciadophylloides					**75**	**0.20**
Padus grayana			**150**	**0.16**	**50**	**0.02**
Kalopanax septemlobus	**25**	**0.10**				
Vitis coignetiae	**25**	**0.01**			**100**	**0.09**
Euonymus oxyphyllus	**75**	**0.08**	**25**	**0.01**		
Acer japonicum					**50**	**0.08**
Toxicodendron orientale			**25**	**0.07**		
Fraxinus lanuginosa					**25**	**0.06**
Corylus sieboldiana			**50**	**0.04**		
Acer sieboldianum					**50**	**0.03**
Cornus controversa			**25**	**0.02**		
Weigela hortensis					**25**	**0.01**
total	**1425**	**43.45**	**2350**	**51.47**	**1350**	**44.24**

e. Species composition at the Takakura Woods (TW) site (*DBH*≥2 cm)

Plot No.	**1**		**2**		**3**	
Elevation (m)	**400 m**		**398 m**		**388 m**	
Species	**Stem density (/ha)**	***BA* (m²/ha)**	**Stem density (/ha)**	***BA* (m²/ha)**	**Stem density (/ha)**	***BA* (m²/ha)**
Fagus crenata	**350**	**33.23**	**100**	**22.42**	**325**	**28.90**
Aesculus turbinata			**100**	**22.15**		
Acer pictum* subsp. *mayrii	**25**	**2.56**	**75**	**3.01**	**125**	**8.03**
Magnolia obovata	**25**	**1.35**	**75**	**5.37**	**25**	**1.71**
Quercus crispula	**50**	**3.29**	**25**	**0.11**		
Dead tree	**50**	**1.62**	**50**	**0.43**	**75**	**0.86**
Acer japonicum	**175**	**0.69**	**25**	**0.05**	**75**	**0.24**
Styrax obassia			**25**	**0.97**		
Clethra barbinervis			**50**	**0.02**	**125**	**0.06**
Magnolia salicifolia	**50**	**0.03**	**25**	**0.01**		
Lindera umbellata* var. *membranacea			**75**	**0.03**		
Viburnum furcatum			**25**	**0.01**	**50**	**0.02**
Padus grayana			**25**	**0.02**		
Euonymus oxyphyllus			**50**	**0.02**		
Corylus sieboldiana			**25**	**0.02**		
total	**725**	**42.76**	**750**	**54.65**	**800**	**39.82**

f. Species composition at the Tsugaru Pass (TP) site (*DBH*≥2 cm)

Plot No.	**1**		**2**		**3**	
Elevation (m)	**651 m**		**662 m**		**659 m**	
Species	**Stem density (/ha)**	***BA* (m²/ha)**	**Stem density (/ha)**	***BA* (m²/ha)**	**Stem density (/ha)**	***BA* (m²/ha)**
Fagus crenata	**225**	**41.64**	**475**	**30.49**	**400**	**24.42**
Magnolia obovata			**350**	**8.30**	**100**	**4.22**
Acer pictum* subsp. *mayrii			**25**	**1.31**	**75**	**4.16**
Acer japonicum			**75**	**0.25**	**875**	**4.29**
Magnolia salicifolia	**325**	**0.29**	**900**	**0.67**	**500**	**0.45**
Dead tree	**175**	**0.21**	**425**	**0.44**	**250**	**0.34**
Fraxinus lanuginosa					**25**	**0.92**
Clethra barbinervis	**175**	**0.16**			**275**	**0.28**
Viburnum furcatum	**50**	**0.04**	**350**	**0.19**	**375**	**0.20**
Lindera umbellata* var. *membranacea					**175**	**0.17**
Padus grayana			**100**	**0.08**	**50**	**0.02**
Hamamelis japonica					**25**	**0.04**
Chengiopanax sciadophylloides	**25**	**0.01**			**25**	**0.01**
Sorbus commixta					**25**	**0.01**
total	**975**	**42.34**	**2700**	**41.72**	**3175**	**39.52**

g. Species composition at the Hitotsu Mori Pass (HMP) site (*DBH*≥2 cm)

Plot No.	**1**		**2**		**3**	
Elevation (m)	**652 m**		**635 m**		**631 m**	
Species	**Stem density (/ha)**	***BA* (m²/ha)**	**Stem density (/ha)**	***BA* (m²/ha)**	**Stem density (/ha)**	***BA* (m²/ha)**
Fagus crenata	**125**	**37.17**	**500**	**35.96**	**325**	**44.47**
Acer pictum* subsp. *mayrii	**100**	**15.41**	**200**	**5.14**	**350**	**3.32**
Tilia japonica	**25**	**3.28**	**150**	**9.43**	**175**	**3.30**
Dead tree	**100**	**1.07**	**150**	**4.35**	**250**	**0.31**
Acer japonicum	**50**	**0.92**	**200**	**1.16**	**800**	**2.60**
Pterocarya rhoifolia			**25**	**1.37**		
Magnolia obovata	**50**	**0.05**	**50**	**0.03**	**25**	**0.83**
Hydrangea petiolaris			**25**	**0.13**		
Dead liana	**25**	**0.11**	**25**	**0.01**		
Fraxinus lanuginosa					**150**	**0.10**
Sorbus commixta					**25**	**0.08**
Euonymus oxyphyllus			**75**	**0.04**	**25**	**0.01**
Viburnum furcatum			**50**	**0.02**	**50**	**0.02**
Chengiopanax sciadophylloides					**25**	**0.01**
total	**475**	**58.02**	**1450**	**57.64**	**2200**	**55.04**

h. Species composition at the Mt. Shirakami Mountain Trail (MSMT) site (*DBH*≥2 cm)

Plot No.	**1**		**2**		**3**	
Elevation (m)	**624 m**		**627 m**		**622 m**	
Species	**Stem density (/ha)**	***BA* (m²/ha)**	**Stem density (/ha)**	***BA* (m²/ha)**	**Stem density (/ha)**	***BA* (m²/ha)**
Fagus crenata	**125**	**10.67**	**225**	**31.16**	**350**	**8.25**
Acer pictum* subsp. *mayrii	**175**	**2.19**	**200**	**12.33**	**350**	**32.11**
Pterocarya rhoifolia	**300**	**18.99**			**25**	**0.01**
Tilia japonica	**250**	**12.00**	**50**	**3.57**		
Magnolia obovata	**25**	**0.44**	**50**	**2.09**	**25**	**1.43**
Aesculus turbinata					**25**	**3.17**
Kalopanax septemlobus	**50**	**2.77**				
Cornus controversa	**25**	**0.85**			**50**	**1.58**
Fraxinus lanuginosa	**25**	**1.50**			**75**	**0.31**
Dead tree	**50**	**0.56**	**25**	**0.02**	**100**	**0.54**
Phellodendron amurense					**25**	**0.79**
Acer japonicum	**75**	**0.07**	**75**	**0.08**	**125**	**0.19**
Vitis coignetiae	**25**	**0.13**	**25**	**0.02**		
Hydrangea petiolaris					**25**	**0.13**
Dead liana			**25**	**0.09**		
Hydrangea hydrangeoides	**25**	**0.05**				
Viburnum furcatum	**25**	**0.02**				
Euonymus oxyphyllus			**25**	**0.01**		
total	**1175**	**50.23**	**700**	**49.35**	**1175**	**48.51**

i. Species composition at the Lake Juniko (LJ) site (*DBH*≥2 cm)

Plot No.	**1**		**2**		**3**	
Elevation (m)	**283 m**		**269 m**		**283 m**	
Species	**Stem density (/ha)**	***BA* (m²/ha)**	**Stem density (/ha)**	***BA* (m²/ha)**	**Stem density (/ha)**	***BA* (m²/ha)**
Fagus crenata	**225**	**50.90**	**200**	**78.01**	**300**	**37.49**
Kalopanax septemlobus			**25**	**14.79**		
Cercidiphyllum japonicum			**50**	**13.96**		
Acer pictum* subsp. *mayrii	**25**	**0.06**	**25**	**0.07**	**75**	**3.48**
Acer japonicum	**775**	**1.89**	**50**	**0.06**	**25**	**0.03**
Dead tree	**50**	**0.22**	**25**	**0.04**	**25**	**1.07**
Styrax obassia			**75**	**0.42**		
Hydrangea hydrangeoides	**25**	**0.09**			**25**	**0.15**
Aesculus turbinata			**50**	**0.11**	**25**	**0.03**
Cornus controversa	**25**	**0.11**				
Stachyurus praecox			**25**	**0.01**		
Acer amoenum* var. *matsumurae			**25**	**0.01**		
total	**1125**	**53.27**	**550**	**107.48**	**475**	**42.25**

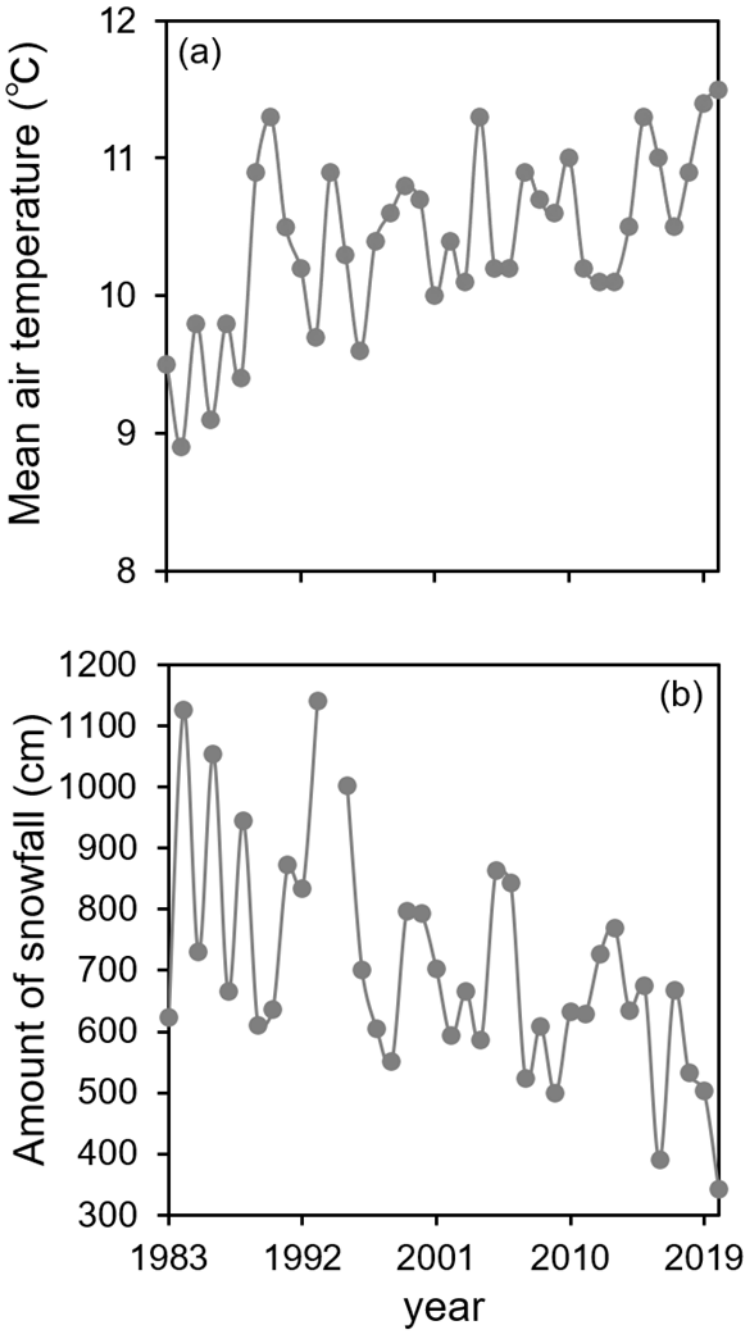

Figure S1 Mean (a) air temperature and (b) amount of snowfall in Hirosaki City, Aomori Prefecture, Japan, from 1983 to 2020. Data was obtained from the Japanese Meteorological Agency (Hirosaki City meterological station 2022; 40° 36.7 N, 140° 27.3 E.)
(https://www.data.jma.go.jp/obd/stats/etrn/view/annually_a.php?prec_no=31&block_no=0166&year=&month=&day=&view=).

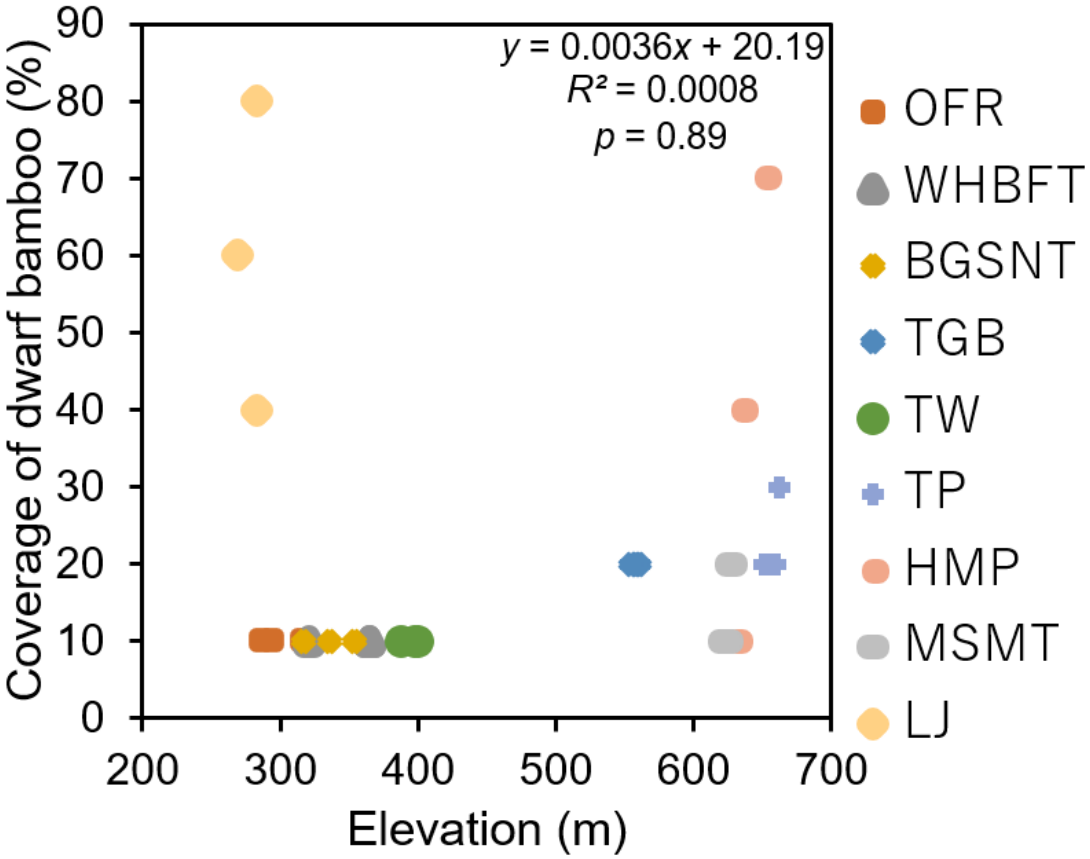

Figure S2. Relationships between coverage of the site by dwarf bamboo and elevation.

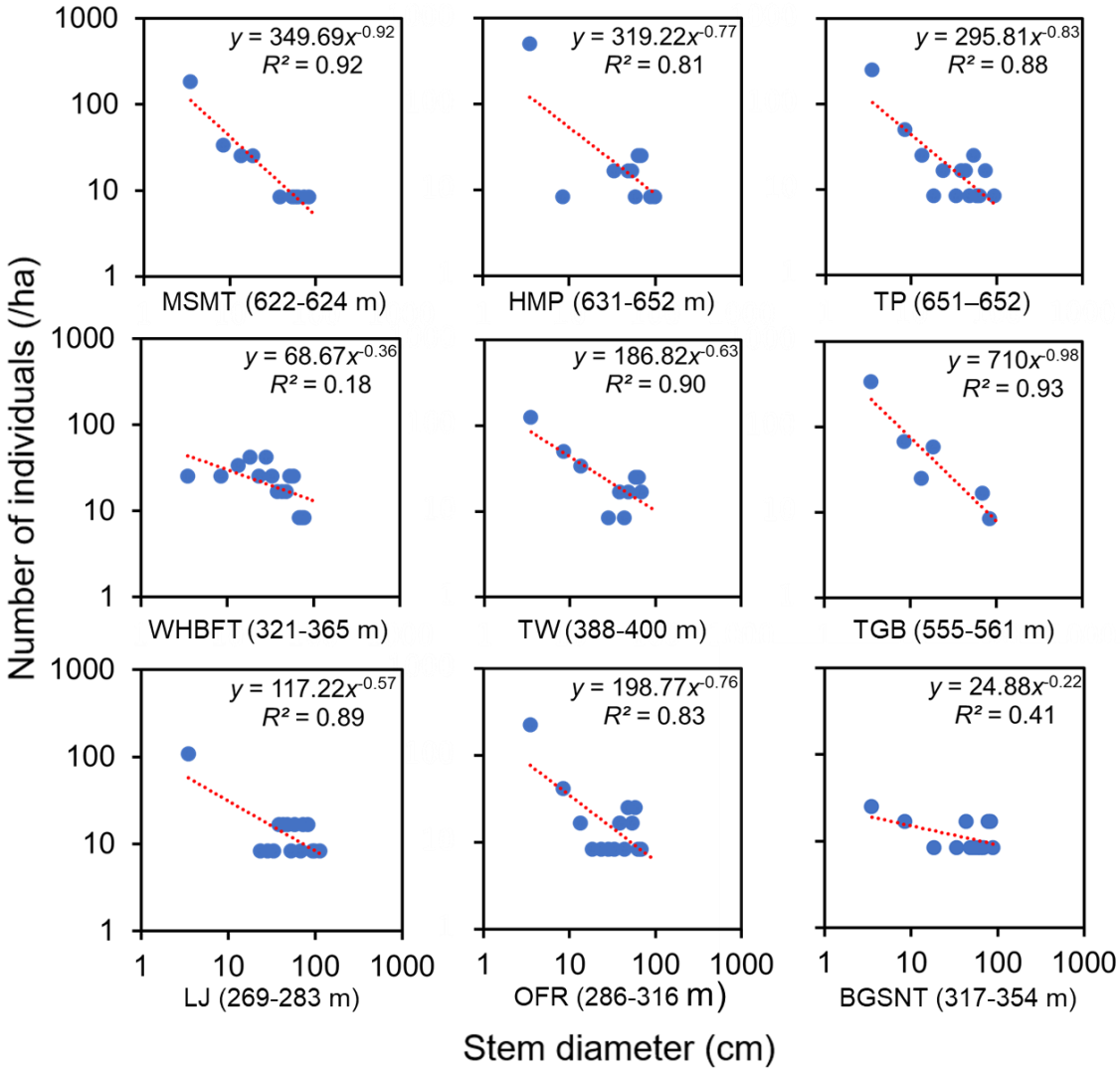

Fig. S3 Double logarithmic graphs used to calculate the coefficients *a* and *b* for the power function *density* = *a DBH*^{b} based on the DBH class distribution of *Fagus crenata*.