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Analysis of the Effect of the Expansion of Bamboo Forest on Forest Plant Communities

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The expansion of bamboo forests due to climate change and neglect has raised concerns about declining forest biodiversity and the loss of ecosystem services. In this study, we investigated the characteristics of bamboo forest expansion and its effects on vegetation structure in a bamboo forest near Fukuoka City, Japan. A total of 15 sites were surveyed for vegetation and light conditions within the bamboo forest and adjacent to natural forests outside of it. The results revealed that high culm density in bamboo forests leads to extreme changes in light intensity and quality, which is unfavorable for plant germination and growth, resulting in low plant species diversity. Consequently, the understory vegetation was dominated by only certain plants with strong shade tolerance. Under these conditions, there were fewer bamboo shoots. Bamboo invades natural forests by extending its underground canopy beyond the resource-advantaged bamboo forest. In doing so, it grows bamboo shoots and encroaches on the tree canopy in a short period of time. This invasion strategy gradually simplifies the hierarchical forest structure and reduces species diversity.

Key words: words: Expansion of bamboo forest, Harvest bamboo shoot, Light environment, *Phyllostachys pubescens*, Shade tolerance

INTRODUCTION

In Korea and Japan, bamboo forests were developed by planting species such as *Phyllostachys pubescens* and *Phyllostachys bambusoides* to harvest bamboo shoots in May and June, as well as to obtain bamboo. However, these bamboo forests are now being neglected due to their decreased utilization compared to the past (Manabo *et al.*, 2020). *P. pubescens*, the species primarily harvested for bamboo shoots, is commonly found across various regions of Japan. It can grow to a height of approximately 12 m, with thick culms reaching diameters of about 20 cm. It features luxuriant branches and leaves in the upper part and is characterized by its ability to expand through asexual reproduction via rhizomes. Consequently, rhizomes extend into adjacent forests, producing bamboo shoots and thereby expanding the bamboo forest area (Takenaka *et al.*, 2017). Specifically, the diffusion process of bamboo into forest areas follows a survival strategy that includes: ① growth and spread of rhizomes into adjacent forest areas, ② generation of bamboo shoots from rhizomes within these areas, ③ the shoots reaching the upper canopy layer where light conditions are favorable, and ④ the newly grown bamboos occupying the canopy layer (Okutomi *et al.*, 1996; Yoo *et al.*, 2017). According to Takenaka *et al.* (2017), the distribution expansion of bamboo forests is significantly influenced by average temperature. It is predicted that a 4°C increase in average temperature could shift the distribution areas of *P. pubescens* and *P. bambusoides* forests up to 500 km northward from their current locations. The expansion rates of *P. pubescens* forests were recorded as 3.0 m/year in the shrub forests southwest of Tokyo, 2.5 m/year in abandoned cultivated lands, and 1.8 m/year in deciduous broadleaf forests (Okutomi *et al.*, 1996). These rates tend to decrease in areas with developed canopy layers. Additionally, the expansion rate is higher on slopes and flatlands, and lower on ridges and steep slopes (Hayashi and Yamada, 2008). Rhizomes infiltrate areas adjacent to bamboo forests where canopies are relatively sparse and environmental conditions are favorable, quickly reaching the canopy layers and expanding the bamboo forests.

The encroachment of bamboo forests into adjacent forests alters the species composition and structure of plant communities. There have been numerous reports of bamboos with large cross–sectional areas at breast height and high culm densities, which have degraded the light environment in the understory, leading to reduced species diversity (Manabo *et al.*, 2020). Concerns arise that accelerated expansion of bamboo forests due to climate change and neglect could simplify the layered architecture, diminish plant species diversity, and reduce ecosystem services (Okutomi *et al.*, 1996; Suzuki, 2008; Kodani and Esaki, 2012; Takenaka *et al.*, 2017; Manabo *et al.*, 2020). Similar patterns are expected in the southern regions of Korea, where bamboo forests are predominantly found. Thus, this study aims to examine the vegetation and light environment of a *P. pubescens* bamboo forest near Fukuoka, Japan, to understand the characteristics of bamboo forest expansion and its impact on plant communities.

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MATERIALS AND METHODS

Selection of study site and general overview

The study site is the whole area of Mt. Tachibana and Shikanoshima in Fukuoka, Japan, where bamboo forests are widely distributed (Fig. 1). This area was developed by planting *P. pubescens* native to China in the past to use bamboo shoots and culms. This area has a warm and humid climate with an average annual temperature of 17.3°C, an average temperature of the coldest month of 6.9°C, and an average temperature of the warmest month of 28.4°C. Due to the influence of the Kuroshio Warm Current, winters are mild, and summers are hot and humid. Therefore, this area is a typical warm–temperate climate zone, where evergreen broad-leaved forests are widely distributed. The study site is mainly adjacent to evergreen broad–leaved forests of *Castanopsis sieboldii*, *Machilus thunbergii*, *Cinnamomum camphora*, etc. Survey plot 11 was surveyed in Shikanoshima, and the remaining survey plots were surveyed in Mt. Tachibana. In survey plots 1 to 11, species composition, the numbers of culms and bamboo shoots of *P. pubescens* generated were surveyed in bamboo forests. Survey plots 12 to 15 were surveyed by installing the survey plots consecutively from the outskirts of the bamboo forest to the natural forest. Through the foregoing, this study attempted to find out changes in species composition and growth of *P. pubescens* due to the expansion of bamboo forests into natural forests.

The altitudes above sea level of the survey plots range from 100 to 140 meters. Consequently, the differences are not substantial, and there will be minimal changes in species composition across survey plots due to variations in altitude.

In survey plots 1 to 11, canopy layers were mostly dominated by *P. pubescens*, while trees such as *Machilus thunbergii*, *Ilex integra*, *Eurya japonica*, *Aucuba japonica*, etc. appeared in parts of understory layers and shrub layers. On the other hand, in survey plots 12 to 15, *P. pubescens* and *Quercus serrata* competed with each other in the canopy layer, and various tree species *Eurya japonica*, *Machilus thunbergii* and *Ligustrum japonicum* were present.

Due to this vegetation structure, except for survey plot 7, the Photosynthetic relative Photon Flux Density (rPPFD), which indicates the brightness of forest floors in plots 1 to 11, was low (ranging from 0.98 to 4.14%), whereas the rPPFD of survey plots 12 to 15 was relatively high (ranging from 3.09 to 6.80%).

Survey and analysis methods

A total of 15 points were selected in the study site, and survey plots (size 10 m × 10 m) were installed at the points to survey vegetation. The trees that appeared in the survey plots were divided into a canopy layer and an understory layer, and the tree species names and diameters at breast height by individual were surveyed. For the shrub layers, 5 m × 5 m survey plots were installed overlapping in the survey plots, and the crown widths (long side x short side) by individual were surveyed. The numbers of culms and bamboo shoots of *P. pubescens* generated and altitudes above sea level, slope orientations, and gradients, which are environmental factors, were surveyed by survey plot.

To compare the relative dominance of individual tree species, Importance Percentages (IPs) and Mean Importance Percentages (MIPs) were calculated. The IPs (Brower and Zar, 1977) were calculated with (relative density + relative coverage)/2, and considering the sizes of the individuals, the MIPs were obtained with (canopy layer IP × 3 + understory layer IP × 2 + shrub layer IP × 1)/6, which was given weights by crown layer (Park, 1985). Based on the MIP data, TWINSPAN classification analysis (Hill, 1979) was conducted to summarize vegetation survey data that extract identified spe-

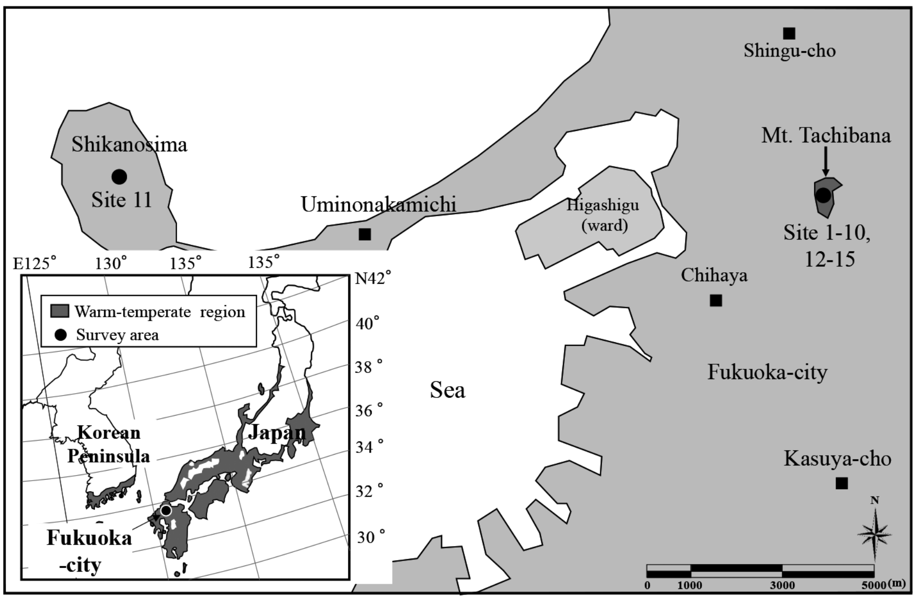

Fig. 1. Surveyed Sites Map of Mt. Tachibana and Shikanosima in Fukuoka.

cies and classify them into groups with similar species compositions. Vegetation categorization was attempted by grouping 15 vegetation survey data into several plant communities. The vegetation survey data grouped with this analysis were integrated and vegetation structures and stand dynamics (Harcombe and Marks, 1978) were identified through analysis of IPs and diameter at breast height (DBH).

To evaluate the light environments in the forest by survey plot, PPFD was measured at a height of 2 m above the ground surface using a photosynthetic photon flux density (PPFD) sensor (SQ–110, Apogee), and this value was shown as the relative photosynthetic photon flux density (rPPFD) value of full light, which is a state where sunlight is unblocked. Using a spectrometer (SPIC–200, EVERFINE), the spectrum, illumination, and solar radiation were measured at 1 m, 2 m, 4 m, 6 m, 8 m, and 10 m heights from the ground surface.

RESULTS

Classification analysis

The 15 survey plots were simplified as they were grouped into four communities (groups) of survey plots with similar characteristics through TWINSPAN analysis (Fig. 2). The identified species indirectly represent the characteristics of the location environments of the study plots. At level 1, the identified species in the right group was *Quercus serrata*, but in the left group, no identified species was extracted. Again, at Level 2, community I included plots 3 to 5 with *Castanopsis sieboldii* as the identified species, and community Ⅱ included survey plots 1, 2, and 6 to 11 with *Machilus thunbergii* as the identified species. Meanwhile, in the right group, survey plots 12 and 14 were grouped into community Ⅲ with *Dendropanax morbifera* as the identified species. Survey plots 13 and 15 were grouped into community Ⅳ, and no identified species was extracted. The survey plots (S1~11) belonging to communities I and Ⅱ were surveyed in the bamboo forest, and showed a community structure in which the canopy layer was dominated by bamboo species and some tree species appeared in the understory and shrub layers. In contrast, since communities Ⅲ and Ⅳ are where bamboo forests and natural forests are adjacent, *P. pubescens* and *Q. serrata* appeared together in the canopy layer, and relatively diverse tree species appeared in the arborescent and shrub layers. The identified species of community I was *C. sieboldii*, and this species is reported to mainly appear in dry and barren areas of ridges and slopes (Kang *et al.*, 2022). Because the gradient of community I is steep, ranging from 23 to 41°, community I is judged to have less soil moisture and is more barren than community Ⅱ. The identified species of community Ⅲ was *D. morbifera*, which has strong shade tolerance, and the forest floor appears be darker than that of community Ⅳ. Overall, it is considered that the TWINSPAN analysis reflected the species composition and location environment characteristics of the survey plots so that the survey plots were clearly grouped into four communities. Therefore, focusing on the four communities, the characteristics of vegetation structure, light environment, species diversity, and bamboo shoot development were identified as follows.

Analysis of tree species by IP and DBH

In community I, *P. pubescens* was the most dominant in the canopy layer with the importance percentage (IP) at 92.13% and had the highest density with the number of culms at 187 (with a culm density of 62.3 per 100 m²). In the understory layer, the species appeared were sparse as one *Machilus japonica* and one *Ilex integra* appeared, and in the shrub layer, quite a few species, such as *C. sieboldii*, *Symplocos kuroki*, *Cinnamomum japonicum*, *M. thunbergii*, and *Daphniphyllum teijsmanni* appeared. As with the abovementioned community, in community Ⅱ surveyed in the bamboo forest, the IP of *P. pubescens* was high at 98.99%, and the number of culms was 396 with the next highest density (with a culm density of 49.5 per 100 m²). The understory layer and the shrub layer were dominated by several limited tree species with strong shade tolerance, such as *M. thunbergii*, *Eurya japonica*, *Neolitsea sericea*, and *Aucuba japonica*. Looking at the analysis of diameter at breast height (DBH) by community, 186 individuals of *P. pubescens* with DBHs (diameter at breast height) not lower than 7 cm appeared in community I. In community Ⅱ too, 396 individuals of *P. pubescens* appeared in the DBH range of 7 to 22 cm. Because the overwhelming appearance of *P. pubescens* in the canopy layer darkened the forest floor, the layered architecture could not be developed, and evergreen broad-leaved tree species with strong shade tolerance were distributed only in the shrub layer.

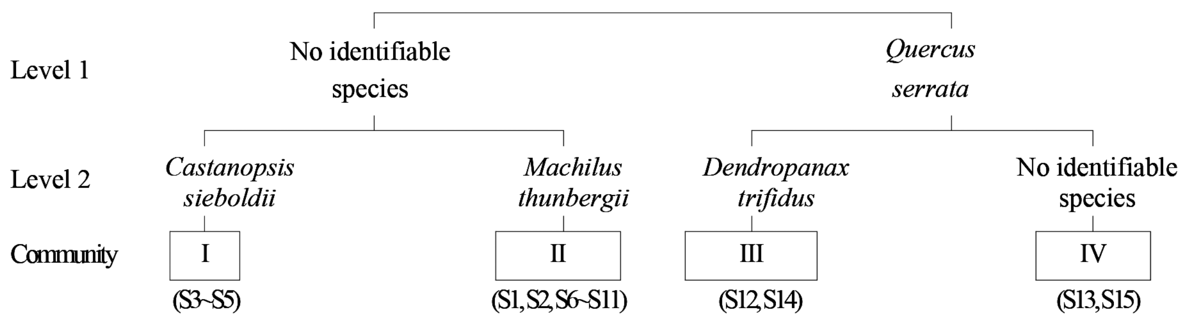

Fig. 2. The dendrogram of classification by TWINSPAN (Two–Way Indicator Species Analysis) in the survey site.

Meanwhile, in community Ⅲ surveyed in an area adjacent to a bamboo forest and a natural forest, the IP of *P. pubescens* was 67.60% (with a culm density of 14 per 100 m^2) and that of *Q. serrata* was 32.40% in the canopy layer. In the understory layer, *Eurya japonica* dominated with an IP of 61.89%, followed by *Ligustrum lucidum* at 18.30%. Additionally, *Lyonia ovalifolia* ssp. *Neziki* accounted for 12.51% of the understory vegetation.

In the shrub layer, *Ligustrum lucidum*, *Neolitsea sericea*, *M. thunbergii*, *Daphniphyllum teijsmanni*, etc. were found through surveys. Community Ⅳ showed a similar vegetation structure to community Ⅲ. The powers of *P. pubescens* (IP 43.15%) and *Q. serrata* (45.84%) were similar to each other, and *Symplocos kuroki* and *Pinus desiflora* appeared together. In the understory layer and shrub layer, tree species similar to those in community Ⅲ appeared and dominated. The culm density here is 10 per 100 m^2, which is lower than that of the other three areas, and it seems that various tree species appear because the forest is bright. In community Ⅲ, 29 individuals of *P. pubescens* were distributed in the DBH range of 2 to 17 cm and 6 individuals of *Q. serrata* were distributed in the DBH range of 7 to 37, so that they are in competition with each other. In community Ⅳ, 68 individuals of *Eurya japonica*, *Ligustrum lucidum*, *L. ovalifolia* ssp. *neziki*, and *M. thunbergii* were distributed in the DBH range of 2 to 22 cm, forming an understory layer and a shrub layer. The aspects of community Ⅳ were similar to those of community Ⅲ.

Characteristics of light environments

When the rPPFD, illuminance, and solar radiation of the four communities were compared, communities I and Ⅱ with higher IPs of *P. pubescens* and larger numbers of culms in the canopy layer showed relatively lower values than communities Ⅲ and Ⅳ. In particular, rPPFD, which measured only photosynthetic effective light, was the lowest in community I (Fig. 3). This is because the number of culms of *P. pubescens* in the canopy layer affected the amount of light. The numbers of culms of *P. pubescens* in the canopy layer were the largest in community I with an average of 62.3 per 100 m^2, followed by community Ⅱ with 49.5, community Ⅲ with 14.5, and community Ⅳ with 10.0. On the other hand, community Ⅳ, in which *P. pubescens*, *Q. serrata*, etc. show a structure for competing with each other in the canopy layer tended to have the highest PPFD, illuminance, and solar radiation. As stated in various literature (*e.g.* Suzuki, 2014; Kodani and Esaki, 2012), the amount of light entering the lower layer of this bamboo forests will be significantly reduced, greatly effecting the decline of species diversity and the simplification of layered architectures (Manabo *et al.*, 2020).

Looking at the spectra according to the heights by community, community I had decreased solar radiation in most wavelength bands regardless of the measurement height, and the patterns were similar (Fig. 4). Community Ⅱ showed a tendency for solar radiation to increase in the far–red light wavelength range of 700 to 750 nm. This may be because the far–red light wavelength, which has leaf penetrability, penetrated the canopy layer of *P. pubescens* in community Ⅱ, which had a smaller number of culms of *P. pubescens* bamboo shoots than community I. In the previous comparison of rPPFD, community I had the lowest PPFD, and the spectrum also showed consistent results with extremely reduced solar radiation in all wavelength bands. Under such a light environment, if the amount of photosynthesis of plants is reduced due to the lack of light resulting in slow plant growth, or the plants lose competition to receive light competition, the plants may die or specialized in only certain plants with strong shade tolerance. In addition, here, red light (600~700 nm, R) and far–red light (700~750 nm, FR) will be drastically reduced, or the R/FR ratio will become different from that of natural forests, adversely affecting physiological functions such as breaking the rhythm of flowering and photoperiod and inhibiting seed germination.

Meanwhile, communities Ⅲ and Ⅳ showed similar spectral patterns, and as the measurement height decreased, solar radiation in most wavelength bands decreased. However, as the height (Community Ⅲ: 8 m, Community Ⅳ: 10 m) increased, a spectral pattern similar to that of open space was shown. Unlike the previously mentioned communities I and Ⅱ, these communi-

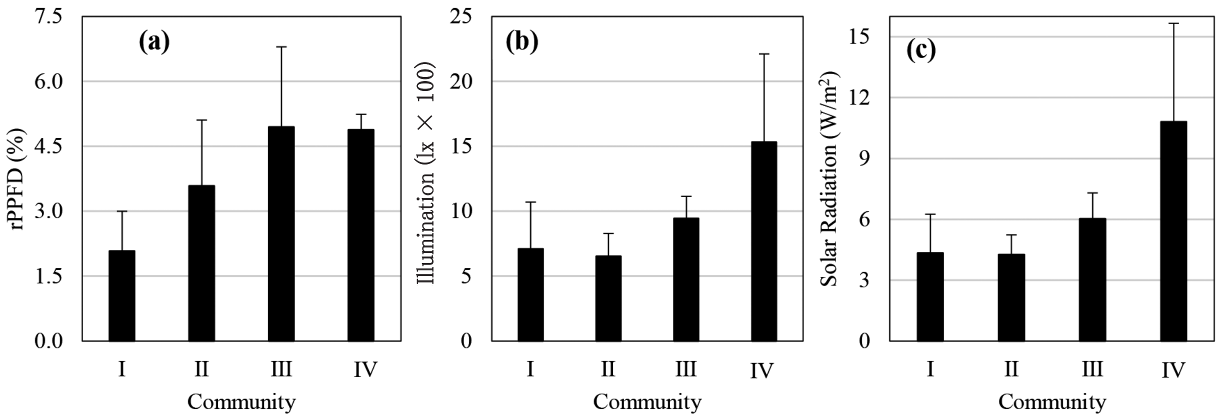

Fig. 3. Comparison of relative photosynthetic photon flux density (rPPDF) (a), illumination (b), and solar radiation (c) by each the community.

ties may have shown this pattern because they had a community structure in which *P. pubescens*, *Q. serrata*, etc. were mixed in the canopy layer. However, the spectral patterns of the two communities appear to have differed by height depending on the tree species and tree heights that appear by layer.

Species diversity and bamboo shoot generation

Looking at the differences in species diversity indexes by community, it could be seen that species diversity indexes were higher in communities Ⅲ and Ⅳ than in communities Ⅰ and Ⅱ (Fig. 5a). Also, the amount of bamboo shoots generated appears to vary according

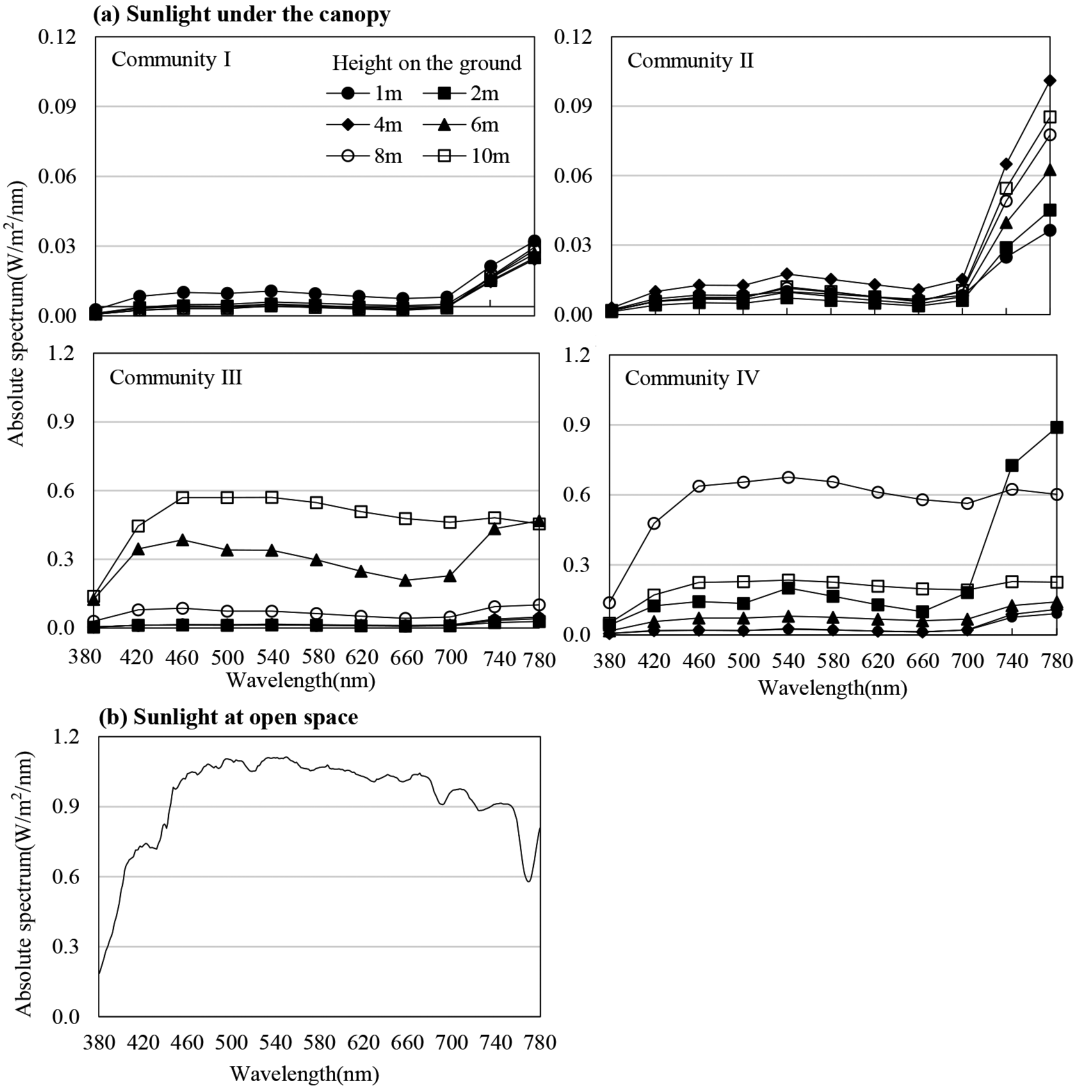

Fig. 4. Comparison of spectra between each the community (a) and open space (b).

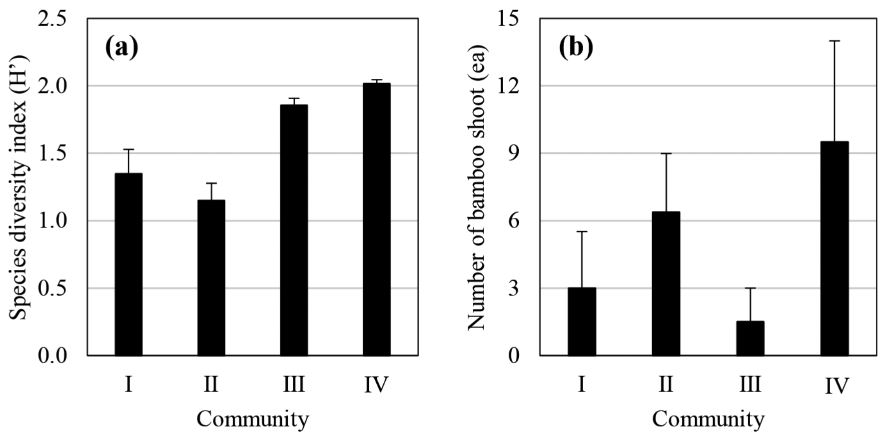

Fig. 5. Species diversity indices (a) and number of bamboo shoot occurrences (b) for each community.

to the light environment in the lower layer, and except for community Ⅲ, the amount of bamboo shoots generated increased as the light amount increased (Fig. 5b). Based on the foregoing, it seems that the light environment affects the power expansion characteristics of bamboo. What can be inferred from this result is that the larger the number and size of the culms of *P. pubescens* in the canopy layer, the smaller the number of species and individuals in the lower layer due to the decrease in the amount of light entering the lower layer and the change in light quality leading to the decrease in the species diversity index (H'). The amount of bamboo shoots generated was larger in natural forest areas with good light conditions than in bamboo forests with smaller amounts of light, which means that this area is more advantageous for the expansion of bamboo forests.

DISCUSSION

In the results of this study, when the density of the culms of *P. pubescens* forest was high, the amount of light in the forest floor decreased and the light quality changed extremely, which was unfavorable for plant germination and growth, leading to a decrease in plant species diversity. Therefore, only certain plants with strong shade tolerance were distributed in the lower layer vegetation leading to a simple layered architecture. It was found that under such forest floor conditions, the generation of the bamboo shoots of *P. pubescens* also decreased.

Bamboo is an individual that grew as numerous ramets consisting of culms and rhizomes were connected underground, and forms a large–scale network community (clone). Bamboo has such a survival strategy because of its long–period monocarpy characteristics (Suyama *et al.*, 2010; Park and choi, 2017). It is known that the flowering cycle of bamboos in cool–temperate regions is between 30 years and 120 years, but the cycle is not clear (Janzen, 1976). The fact that the cause of this flowering is a certain gene (aka genetic clock) that is expressed periodically according to the biological clock rather than the influence of external environmental factors is being converged with recent study findings (Park and Choi, 2017). Since bamboos do not bloom every year to produce seeds, sexual reproduction is disadvantageous for survival. The asexual reproduction strategy to form a single individual and large-scale genet by extending rhizomes underground to create bamboo shoots in appropriate environments thereby expanding the individual is more advantageous for survival (Kikuzawa, 1988). Along with this survival strategy, bamboos have a unique physiological characteristic called physiological integration (Stuefer *et al.*, 1996; Li *et al.*, 1998). Bamboos, which are a clonal plant, have an excellent ability to expand areas using rhizomes and adaptability. This is said to be because the physiological integration function of bamboos, with which rhizomes exchanges resources and assimilation products with each other, effectively utilizes resources in forest floor environments where the distribution of resources such as nutrient salt, light, and moisture is uneven (Stuefer *et al.*, 1996). Thanks to this unique physiological mechanism, bamboo forests are believed to be expanding faster than other plant communities.

Due to this unique characteristic of the survival strategy, if photosynthetic products (energy) are invested in a bamboo forest to generate bamboo shoots and extend culms into the canopy layer, the culms must compete with existing culms to receive light, so that energy recovery through photosynthesis becomes disadvantageous, Therefore, the foregoing is inefficient. Extending rhizomes toward the outskirts (towards natural forests) rather than inside the bamboo forest to make bamboo shoots thereby creating culms is advantageous in terms of survival strategy. That is, expanding the power (bamboo shoots) into the natural forest to receive resource supply from outside is more effective than competing for resources such as the amount of light and soil salts in the bamboo forest. Due to the survival strategy as such, bamboo forests expand their power by infiltrating into adjacent natural forests with rhizomes, and deteriorate the light environment in the forest floor, simplifying the layered architecture and reducing species diversity. Another strength of bamboo is that their tolerance to strong winds and heavy snows is excellent. Bamboo's stems and branches are highly elastic and flexible, so that bamboos do not break easily even in strong winds such as typhoons or heavy snows. On the other hand, under such weather conditions, the branches and leaves of trees in the crown layer break, causing mechanical damage to neighboring trees (Okutomi *et al*, 1996; Isagi and Tori, 1997). If this process is repeated frequently, the trees gradually become weaker than the bamboo and die, creating gaps in the forest that are favorable for the growth of bamboo shoots, leading to the expansion of the bamboo forest.

Along with an asexual reproduction strategy to extend rhizomes underground thereby expanding the individual, bamboos have a unique a unique physiological mechanism for physiological integration with which rhizomes exchange resources and assimilation products with each other. Utilizing such characteristics, bamboos extend rhizomes to the outskirts of the bamboo forest, where resource supply is advantageous, to invade natural forests. Since bamboo shoots generated in natural forests are connected to rhizomes, bamboos have a power expansion strategy to receive photosynthetic products to reach the canopy layer in a short period of time, encroaching on the canopy layer. As the cross–sectional area at breast height and density of bamboos gradually increase through this strategy, existing trees die as they fall behind in the competition to receive light, leading to the simplification of the layered architecture. The light environment in the lower layer of the bamboo forest becomes extremely poor, becoming unfavorable for plant germination and growth, so that only specialized plant species with strong shade tolerance grow, reducing species diversity. If the density of culms in a bamboo forest is too high, bamboos will have disadvantages in competition with existing plants and securing resources, so that they will expand their power to the outskirts of the bamboo forest. Therefore, in order to prevent the expansion of bamboo forests, measures to appropriately reduce the culm density are necessary.

AUTHOR CONTRIBUTIONS

S. G. Park designed the study, performed the histological experiments, analyzed the data and wrote the paper. H. J. Bang supervised the work, wrote the paper. All authors assisted in editing of the manuscript and approved the final version.

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Table 1. Overview of physical characteristics and vegetation by the survey site

Community		I			II				
Plot number		S3	S4	S5	S1	S2	S6	S7	S8
The survey sites		Mt. Tachibana			Mt. Tachibana				
Location (GPS)		N30.40.8 E130.27.58	N30.40.8 E130.27.58	N30.40.9 E130.27.43	N30.40.5 E130.27.58	N30.40.6 E130.27.58	N30.40.29 E130.27.21	30.40.7 E130.27.45	N30.40.7 E130.27.46
Altitude (m)		130	130	150	129	130	160	160	160
Aspect (°)		112	112	112	90	72	26	10	90
Slope (°)		41	40	23	27	27	5	10	30
rPPFD (%) of ground layer		1.35	0.98	3.91	2.03	2.96	4.14	13.92	1.12
Major plant communities†		Pp	Pp, Cc	Pp, Ii	Pp, Ej	Pp, Ej	Pp, Mt	Pp, Mt	Pp
Number of species		7	13	13	7	9	12	12	3
Number of bamboo shoots		–	1	8	2	8	18	17	–
Canopy	Height(m)	14.6	14.6	11.3	14.6	13	13	13	20
	Mean DBH(cm)	9.9	10.7	11.3	11.2	10.0	11.0	9.5	11.7
	Major plant†	Pp	Pp	Pp	Pp	Pp	Pp	Pp	Pp
Understory	Mean DBH(cm)	–	2.0	9.0	9.0	3.5	13.8	4.2	–
	Major plant†	–	Mj	Ii	Ej	Ej	Mt, Ej	Mt	–
Shrub	Major plant†	Cs, Lj	Sk	Cs	Cy	Mja	Ns	Ej	Mt, Ns

Table 1. (Continued)

Community		II			III		IV	
Plot number		S9	S10	S11	S12	S14	S13	S15
The survey sites		Mt. Tachibana		Shikanosima	Mt. Tachibana		Mt. Tachibana	
Location (GPS)		N30.40.10 E130.27.46	N30.40.10 E130.27.46	N33.40.27 E130.18.11	N33.39.59 E130.27.57	N33.39.52 E130.27.48	N33.40.0 E130.27.58	N33.39.53 E130.27.49
Altitude (m)		140	140	140	120	110	110	100
Aspect (°)		36	36	242	279	294	273	294
Slope (°)		5	5	8	17	30	17	15
rPPFD (%) of ground layer		2.04	1.21	1.28	3.09	4.52	6.80	5.24
Major plant communities†		Pp, Aj	Pp	Pp, Mt	Pp, Qs, Ej	Pp, Qs, Ej	Pp, Qs, Ej	Pp, Qs, Ej
Number of species		3	5	8	11	13	12	10
Number of bamboo shoots		5	-	1	3	-	5	14
Canopy	Height(m)	15	15	15	16	14	11	12
	Mean DBH(cm)	10.1	10.7	11.0	14.8	9.6	14.0	15.8
	Major plant†	Pp	Pp	Pp	Pp, Qs	Pp, Qs	Pp, Qs	Pp, Qs
Understory	Mean DBH(cm)	-	-	5.7	6.0	5.9	6.9	5.3
	Major plant	-	-	Mt	Ej, Mt, Lj	Ej, Lj	Ej, Lj	Ej, Lj
Shrub	Major plant†	Aj	Mt	Aj	Dt, Mt, Lj	Ns, Lj, Ic	Ns, Sk	Sh, Ns

†Aj: *Aucuba japonica*, Cc: *Cinnamomum camphora*, Cs: *Castanopsis sieboldii*, Cy: *Cinnamomum yabunikkei*, Dt: *Dendropanax trifidus*, Ej: *Eurya japonica*, Ic: *Ilex crenata*, Ii: *Ilex integra*, Lj: *Ligustrum japonicum*, Lj: *Ligustrum japonicum*, Mj: *Machilus japonica*, Mj: *Machilus japonica*, Mja: *Maesa japonica*, Mt: *Machilus thunbergii*, Ns: *Neolitsea sericea*, Ns: *Neolitsea sericea*, Pp: *Phyllostachys pubescens*, Qs: *Quercus serrata*, Sh: *Stauntonia hexaphylla*, Sk: *Symplocos kuroki*

Table 2. Importance percentage (IP) and diameter at breast height (DBH) distribution of major woody species for each community in the survey site

Com. (Area, m^2)	Species \ Layer	C[†]	U	S	M	DBH (number of individuals)									
						Shrub	D_1[‡]	D_2	D_3	D_4	D_5	D_6	D_7	D_8	D_9
I (300)	*Phyllostachys pubescens*	92.13	–	–	54.40	–	1	–	5	141	40	–	–	–	–
	Myrica rubra	4.81	–	–	2.40	–	–	–	–	–	–	–	–	–	–
	Cinnamomum camphora	3.06	–	0.60	1.63	1	–	–	–	–	–	–	–	–	1
	Machilus japonica	–	50.00	0.81	11.25	1	–	1	–	–	–	–	–	–	–
	Ilex integra	–	50.00	–	11.11	–	–	–	2	–	–	–	–	–	–
	Symplocos kuroki	–	–	11.68	2.40	2	–	–	–	–	–	–	–	–	–
	Neolitsea sericea	–	–	6.20	1.03	4	–	–	–	–	–	–	–	–	–
	Ligustrum japonicum	–	–	9.54	2.22	6	–	–	–	–	–	–	–	–	–
	Machilus thunbergii	–	–	7.09	1.18	8	–	–	–	–	–	–	–	–	–
	Castanopsis sieboldii	–	–	21.88	4.42	11	–	–	–	–	–	–	–	–	–
	Ficus erecta	–	–	0.84	0.14	1	–	–	–	–	–	–	–	–	–
	Daphniphyllum teijsmannii	–	–	5.10	0.85	5	–	–	–	–	–	–	–	–	–
	Cinnamomum yabunikkei	–	–	10.07	1.84	7	–	–	–	–	–	–	–	–	–
	Aucuba japonica	–	–	2.82	0.47	2	–	–	–	–	–	–	–	–	–
	Maesa japonica	–	–	6.19	1.03	2	–	–	–	–	–	–	–	–	–
	Quercus glauca	–	–	5.39	1.35	1	–	–	–	–	–	–	–	–	–
	Dendropanax trifidus	–	–	6.82	1.46	4	–	–	–	–	–	–	–	–	–
	Ardisia crispa	–	–	1.07	0.18	1	–	–	–	–	–	–	–	–	–
	Daphne kiusiana	–	–	3.28	0.55	4	–	–	–	–	–	–	–	–	–
	Sasa borealis	–	–	0.67	0.11	1	–	–	–	–	–	–	–	–	–
II (800)	*Phyllostachys pubescens*	98.99	–	–	58.72	–	–	12	248	136	–	–	–	–	–
	Styrax japonicus	0.59	–	–	0.44	–	–	–	–	–	–	1	–	–	–
	Zanthoxylum ailanthoides	0.42	–	–	0.21	–	–	–	–	–	–	–	–	–	–
	Machilus thunbergii	–	42.66	24.15	14.36	20	–	5	–	–	–	–	–	–	–
	Eurya japonica	–	37.63	5.24	8.71	11	–	3	1	–	–	–	–	–	–
	Neolitsea sericea	–	7.05	16.47	4.80	36	1	1	–	–	–	–	–	–	–
	Actinodaphne lancifolia	–	5.80	0.57	1.32	3	–	2	–	–	–	–	–	–	–
	Ficus erecta	–	3.90	–	0.81	–	–	1	–	–	–	–	–	–	–
	Ligustrum japonicum	–	1.50	5.12	1.17	12	–	1	–	–	–	–	–	–	–
	Castanopsis sieboldii	–	1.44	3.81	1.04	4	–	1	–	–	–	–	–	–	–
	Lyonia ovalifolia ssp. *neziki*	–	–	0.62	0.10	1	–	–	–	–	–	–	–	–	–
	Maesa japonica	–	–	2.98	0.50	1	–	–	–	–	–	–	–	–	–
	Symplocos kuroki	–	–	0.85	0.14	4	–	–	–	–	–	–	–	–	–
	Ilex integra	–	–	0.85	0.14	2	–	1	–	–	–	–	–	–	–
	Trachelospermum asiaticum	–	–	0.12	0.02	1	–	–	–	–	–	–	–	–	–
	Stauntonia hexaphylla	–	–	0.36	0.06	1	–	–	–	–	–	–	–	–	–
	Ficus oxyphylla	–	–	0.91	0.15	5	–	–	–	–	–	–	–	–	–
	Xylosma japonica	–	–	0.47	0.08	1	–	–	–	–	–	–	–	–	–
	Cinnamomum yabunikkei	–	–	9.78	1.63	19	–	–	–	–	–	–	–	–	–
	Aucuba japonica	–	–	24.41	5.05	27	–	–	–	–	–	–	–	–	–
	Daphniphyllum teijsmannii	–	–	0.47	0.08	1	–	–	–	–	–	–	–	–	–
	Quercus glauca	–	–	2.37	0.40	5	–	–	–	–	–	–	–	–	–
	Fatsia japonica	–	–	0.45	0.07	1	–	–	–	–	–	–	–	–	–

Table 2. (Continued)

Com. (Area, m^2)	Species \ Layer	$C^{\dagger}$	U	S	M	DBH (number of individuals)									
						Shrub	$D_1^{\ddagger}$	D_2	D_3	D_4	D_5	D_6	D_7	D_8	D_9
Ⅲ (200)	*Phyllostachys pubescens*	67.60	–	–	33.80	–	–	1	26	2	–	–	–	–	–
	Quercus serrata	32.40	1.50	–	16.68	–	–	–	1	1	1	1	1	1	–
	Eurya japonica	–	61.89	1.36	20.85	1	–	27	12	3	1	–	–	–	–
	Ligustrum japonicum	–	18.30	22.74	9.89	10	–	6	3	2	–	–	–	–	–
	Lyonia ovalifolia ssp. *neziki*	–	12.51	–	4.17	–	–	6	4	–	–	–	–	–	–
	Machilus thunbergii	–	4.28	16.30	4.14	9	–	5	–	–	–	–	–	–	–
	Daphniphyllum teijsmannii	–	0.79	2.39	0.66	1	–	1	–	–	–	–	–	–	–
	Mallotus japonicus	–	0.78	–	0.26	–	–	1	–	–	–	–	–	–	–
	Symplocos kuroki	–	–	8.86	1.48	5	–	–	–	–	–	–	–	–	–
	Neolitsea sericea	–	–	19.45	3.24	11	–	–	–	–	–	–	–	–	–
	Stauntonia hexaphylla	–	–	2.03	0.34	1	–	–	–	–	–	–	–	–	–
	Dendropanax trifidus	–	–	13.97	2.33	4	–	–	–	–	–	–	–	–	–
	Ternstroemia gymnanthera	–	–	2.03	0.34	1	–	–	–	–	–	–	–	–	–
	Ilex crenata	–	–	5.11	0.85	4	–	–	–	–	–	–	–	–	–
	Actinodaphne lancifolia	–	–	5.78	0.96	2	–	–	–	–	–	–	–	–	–
Ⅳ (200)	*Phyllostachys pubescens*	43.15	–	–	21.57	–	–	–	20	–	–	–	–	–	–
	Quercus serrata	45.84	1.12	–	23.29	–	–	–	2	1	–	1	2	1	–
	Symplocos kuroki	7.15	0.72	23.30	7.70	12	–	1	–	–	–	1	–	–	–
	Pinus densiflora	3.84	–	–	1.92	–	–	–	–	–	–	–	–	–	–
	Eurya japonica	–	46.86	4.00	16.29	2	–	27	13	1	–	–	–	–	–
	Ligustrum japonicum	–	26.39	24.64	12.90	15	–	7	2	–	–	–	–	–	–
	Lyonia ovalifolia ssp. *neziki*	–	14.80	0.00	4.93	–	–	12	2	–	–	–	–	–	–
	Machilus thunbergii	–	4.60	13.11	3.72	2	–	1	2	–	–	–	–	–	–
	Mallotus japonicus	–	2.62	–	0.87	–	–	–	–	–	–	–	–	–	–
	Ficus erecta	–	2.13	1.42	0.95	1	–	–	–	–	–	–	–	–	–
	Neolitsea sericea	–	0.74	28.52	5.00	20	–	–	–	–	–	–	–	–	–
	Stauntonia hexaphylla	–	–	1.42	0.24	1	–	–	–	–	–	–	–	–	–
	Daphniphyllum teijsmannii	–	–	2.60	0.43	2	–	–	–	–	–	–	–	–	–
	Machilus thunbergii	–	–	0.99	0.16	1	–	–	–	–	–	–	–	–	–

†C: Importance percentage (IP) in canopy layer, U: Importance percentage in understory layer, S: Importance percentage in shrub layer, M: Mean importance percentage

‡$D_1<2$(cm), $2\le D_2<7$, $7\le D_3<12$, $12\le D_4<17$, $17\le D_5<22$, $22\le D_6<27$, $27\le D_7<32$, $32\le D_8<37$, $37\le D_9<42$