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The Importance of Large Trees in Shrine Forests for the Conservation of Epiphytic Bryophytes in Urban Areas

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1. Introduction

1.1. Shrine forests

Shrines in Japan are often surrounded by forests known as *chinju-no-mori* (shrine forests; Figure 1). Previous studies have shown that shrine forests contribute to the conservation of biodiversity, particularly in urban areas where green area is severely limited, although these forests are often fragmented by the city matrix. For example, shrine forests promote the diversity of birds [1, 2], trees [3], grasses [4], and ferns [5]. These forests can thus be regarded as important for biodiversity in urban areas.

1.2. Bryophytes in shrine forests

Shrine forests are also important habitats for bryophytes in urban areas [6-10]. Oishi [8] found approximately 30–60 epiphytic bryophyte species, including endangered species, on tree bark in several shrine forests.

Bryophytes are unique among plants in that they lack vascular bundles and cuticle layers on their leaves (Figure 2); they absorb water and nutrients through their leaf surfaces instead of through roots [11]. This character allows bryophytes to grow on tree bark where soils are scarce; some bryophytes strongly prefer to grow on tree bark [10]. Thus, tree bark is an important habitat for bryophytes.



Figure 1. Shrine forests: Left: Nakaragi shrine and its shrine forest, Kyoto prefecture; Right: Enlarged view of the shrine forest



Figure 2. *Plagiomnium actum* (left) and a leaf section (right). As the leaf section shows, the body structure of bryophytes is very simple and lacks vascular bundles.

1.3. Environmental factors for bryophytes in shrine forests

Several studies have examined epiphytic bryophytes in fragmented forests, including shrine forests. Oishi [8] showed that species richness in fragmented forests is strongly affected by patch size and maintenance. In fragmented forests, the forest edge dries more quickly because of its greater exposure to strong wind and light intensity (edge effects); therefore, patch size is closely connected with drought stress [12-13], which impacts bryophyte diversity [8]. This drought stress causes severe damage to species vulnerable to desiccation, such as bryophytes on tree bases [8-9]. In another study, Hylander et al. [14] found that bryophytes on convex forms (e.g., logs, tree bases, and mesic ground) are more vulnerable to desiccation than those on concave forms.

Conversely, some bryophytes prefer to grow at sunny sites. For these species, maintenance such as tree cutting or trimming is necessary to increase light intensity in the forest interior [8]. Previous studies [6-10] have partly revealed the effects of environmental conditions on

bryophytes; however, the effects of forest structure on these species have not been sufficiently addressed.

To understand the relationship between forest structure and bryophyte diversity, we focused on the diameter at breast height (DBH) of trees in shrine forests for the following reasons. First, large trees in shrine forests are often regarded as sacred and are preferentially preserved. Second, DBH is deeply related to bryophyte diversity because the nature of tree bark changes with DBH, thereby impacting bryophyte diversity [15-18]. Therefore, revealing the relationship between DBH and epiphytic bryophyte diversity is useful for understanding the effects of shrine forests on these species.

2. Objective

In this study, we examined the role of shrine forests in the conservation of epiphytic bryophytes. Based on our results, we discuss the effective conservation methods for epiphytic bryophytes in fragmented forests.

3. Methods

3.1. Study site

The study was conducted at a shrine forest of the Shimogamo Shrine, Kyoto, Japan (Figure 3). This shrine may have been founded before 8th century [19] and is designated a World Heritage Site. The shrine forest is known as the "Tadasu-no-mori" and covers approximately 12.4 ha. One of the dominant trees is *Aphananthe aspera* (Thunb.) Planch, of which the forest contains more than 300 individuals. However, the numbers of *Celtis sinensis* Pers. and *Cinnamomum camphora* (L.) J. Presl have recently increased [20]. The dynamics of the trees in this forest have been reported by Tabada et al. [20-23].

3.2. Bryophyte survey

In 2006, we surveyed the epiphytic bryophyte flora at the study site. We recorded the occurrence of species and their cover on each *A. aspera* individual. The DBH of *A. aspera* was measured in 2002 by one of the authors. The average DBH was 161.5 ± 82.4 cm (mean \pm standard deviation), the maximum was 420.0 cm, and the smallest was 27.0 cm. To understand the relationship between bryophyte diversity and DBH, we analyzed the changes in bryophyte life forms and reproductive strategies in addition to those of species richness and cover.

3.3. Bryophyte life form

Bryophytes change their forms according to light intensity and humidity [24]. For example, in sunny and dry environments, bryophytes maintain water content in their bodies by forming contact mats similar to cushions [24]. Conversely, in dark and humid environments, bryo-

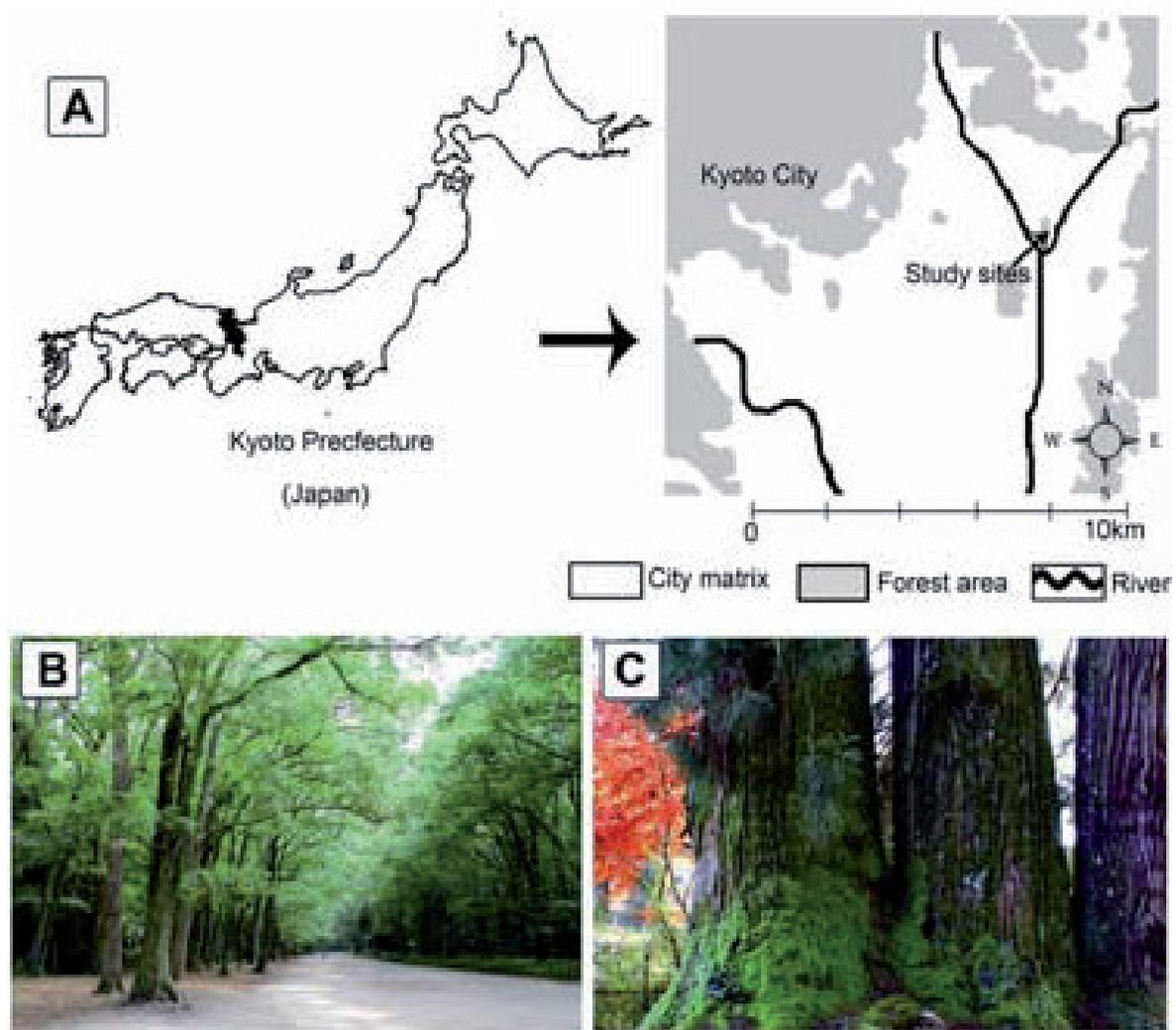


Figure 3. Study site (Tadasu-no-mori, Shimogamo Shrine). A. Location of the study site, revised from Fig. 1 in Oishi [9]; B. Tadasu-no-mori forest; C. Bryophytes on tree trunks

phytes increase photosynthetic efficiency by forming flat mats similar to fans [24]. Therefore, bryophyte life forms are useful for evaluating habitat environmental conditions, and several studies have used them for this purpose [8-10, 25-26].

3.4. Reproductive strategy

Bryophytes have two main reproductive strategies: sexual reproduction by spores and asexual reproduction by gemmae, fragile body parts, etc [27]. Sexual reproduction may be further classified into monoicous and dioicous types. Monoicous bryophytes have both antheridia and archegonia on the same shoot, while dioicous bryophytes have these organs on different shoots. Therefore, monoicous bryophytes have more opportunities for fertilization than do dioicous ones. Bryophytes with asexual reproduction can also reproduce more frequently than dioicous species. We hypothesized that this difference in reproductive frequency would affect the habitat preferences of bryophytes.

4. Analysis

4.1. DBH and bryophyte diversity

First, we compared the DBH values of trees with and without epiphytic bryophytes using the *t*-test to reveal the characteristics of trees with bryophytes. We then examined the effects of DBH on the diversity at both the community and species levels. The flow chart of this study is presented as Figure 4.

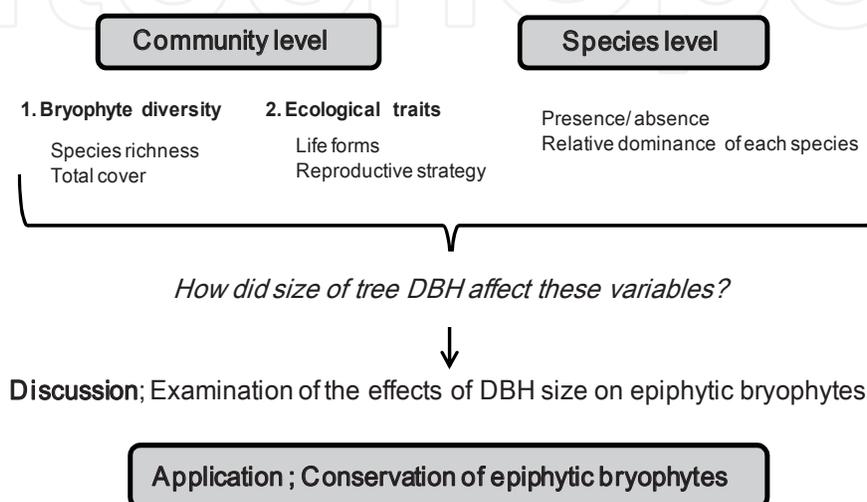


Figure 4. Flow chart of this study

4.2. Community level

The relationships between bryophyte diversity (total species richness and cover) and the DBH of *A. aspera* were examined using Pearson's product-moment correlation coefficients. Additionally, we examined the correlations of DBH with both the richness of the life forms and the species richness of each life form. The life forms recorded at the study site were short turfs (t), small cushions (cu), dendroids (D), rough mats (Rm), smooth mats (Sm), thalloid mats (Th), thread-like forms (Tl), wefts (W), and fans (F). These forms were classified according to the system of Bates [24]. Finally, we examined the correlation of DBH with the ratio of the species richness of dioicous species (RD_i). This ratio was calculated as follows:

$$RD_i = \text{species richness of dioicous bryophytes} / \text{total species richness}$$

The value of RD_i therefore increases with the dominance of dioicous species.

4.3. Species level

To understand the preferences of each species for DBH, we examined the changes in the relative dominance of each species (RDo) as DBH increased. To clarify the relationship between RDo and DBH, the *A. aspera* trees with epiphytic bryophytes were evenly divided into three categories (small, medium, and large). The relative dominance was calculated as follows:

$RDo = \text{cover of each species on trees of one category (small, medium, or large)} / \text{total cover of the species}$

This analysis was conducted for species that occurred more than 10 times at the study site.

5. Results

5.1. Presence/absence of bryophytes

Bryophytes were found on 181 of the 313 *A. aspera* trees at the study site. We compared the DBH of trees with and without bryophytes using the *t*-test. The DBH values of trees with bryophytes were significantly higher than those without bryophytes ($t = -5.4$, $d.f. = 311$, $p < 0.01$; Figure 5). In the following analysis, we examined the relationships between tree DBH and bryophyte diversity in trees with bryophytes.

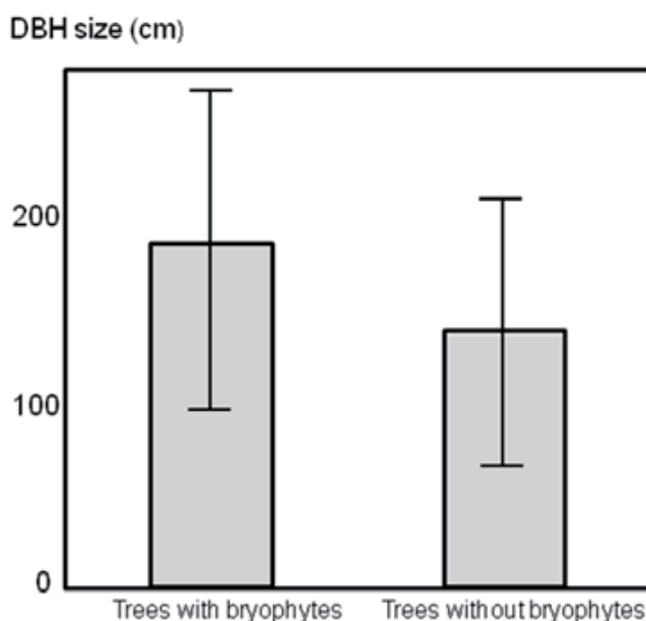


Figure 5. Comparison of DBH between trees with/without epiphytic bryophytes

5.2. Bryophyte flora

We found 42 bryophyte species (28 mosses and 14 liverworts) on the *A. aspera* trees, including two endangered species [*Leskeella pusilla* (Mitt.) Nog. and *Hypnodontopsis apiculata* Z. Iwats. & Nog.]. Figure 6 displays several species found at the study site. The most frequently observed species was *Trocholejeunea sandvicensis* (Gottsche) Mizut. (73 times), followed by *Metzgeria lindbergii* Schiffn. (64 times), *Rhynchostegium pallidifolium* (Mitt.) A. Jaeger (62 times), *Macvicaria ulophylla* (Steph.) S. Hatt. (58 times), and *Frullania parvistipula* Steph. (58 times). The species with the largest total cover was *T. sandvicensis*, followed by *R. pallidifolium*, *M. lindbergii*,

Rhynchostegium inclinatum (Mitt.) A. Jaeger, and *M. ulophylla*. The complete species list is presented in the Appendix.



Figure 6. Several bryophyte species found at the study site

5.3. Bryophyte diversity

The relationships between the species richness/cover and DBH were examined using Pearson's product-moment correlation coefficients. Both species richness and bryophyte cover were significantly and positively correlated with DBH (Table 1).

Variables	Pearson's product-moment correlation coefficients
Species richness	0.22**
Cover	0.28**
Life forms	
Life form richness	0.19*
Short turfs	-0.05
Small cushions	0.07
Dendroids	0.20**
Rough mats	0.17*
Smooth mats	0.14
Thalloid mats	0.18*
Thread-like forms	0.14
Wefts	0.14
Fans	-0.05
Ratio of the species richness of Dioicous species	0.25**

**; $p < 0.01$, *; $p < 0.05$

Table 1. Relationships between bryophyte diversity and DBH

6. Life forms and reproductive strategy

The Pearson's product-moment correlation coefficients between DBH and life form diversity are shown in Table 1. The richness of life forms also increased with increasing DBH. The species richness of dendroids, rough mats, and thalloid mats were significantly and positively correlated with DBH. RDi was also significantly and positively correlated with DBH.

7. Preference of each species for large trees

Bryophytes were observed on 181 *A. aspera* trees, which were divided into three categories based on DBH (small, medium, and large) containing 60, 60, and 61 trees, respectively. The changes in the relative dominance of each species are shown in Figure 7. As seen in the figure, the bryophyte species could be classified into four types based on dominance pattern. Type 1 (three species) preferred to grow on trees with small DBH, type 2 (three species) on trees with

middle DBH, and type 3 (nine species) on trees with large DBH. Type 4 (five species) grew almost exclusively on trees with large DBH.

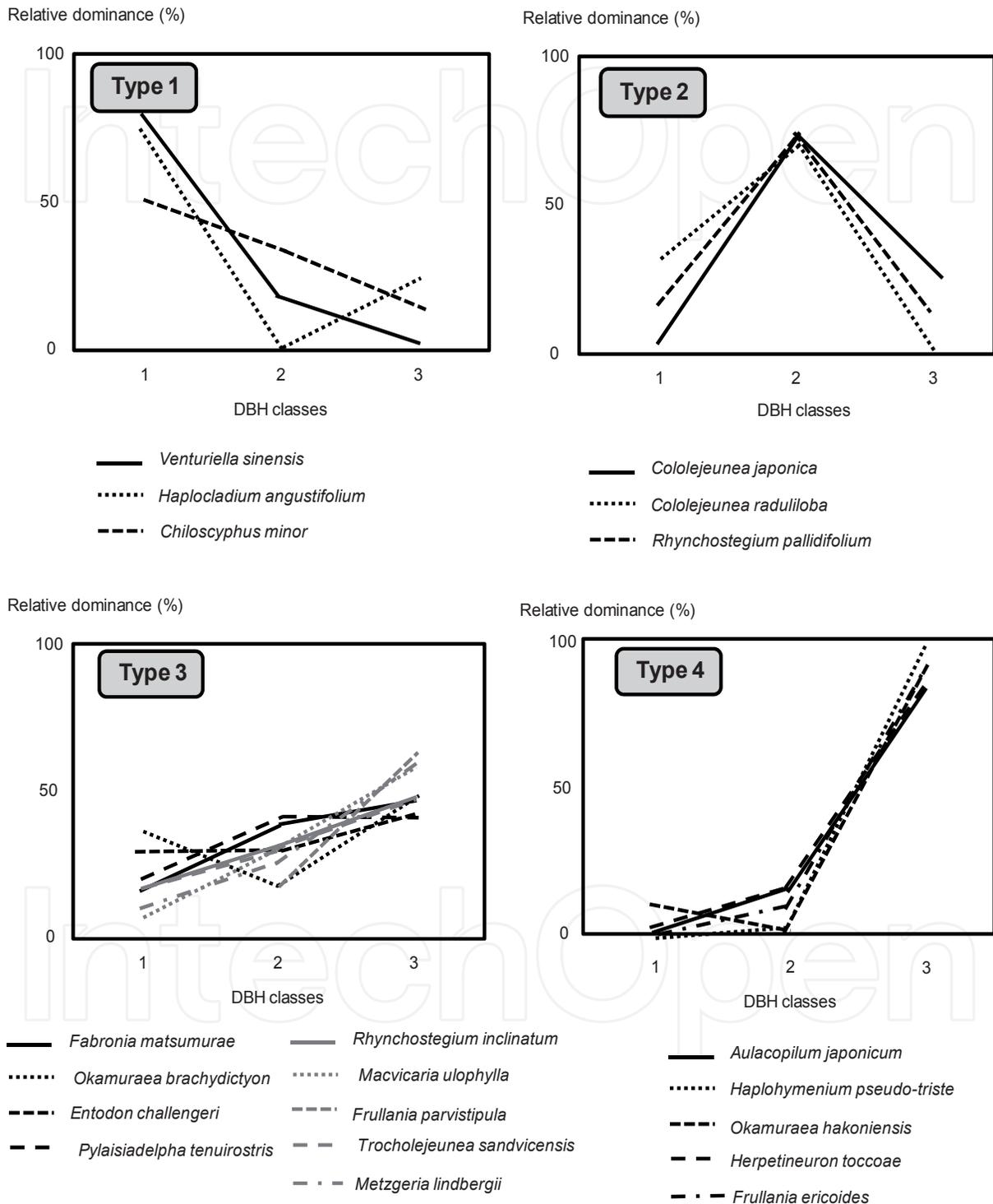


Figure 7. Relationships between the dominance of each species and DBH. DBH class; 1=small, 2=medium, 3=large. The classification of species into types 1–4 is as follows: Type 1: prefer to grow on trees with small DBH, Type 2: prefer to grow on trees with medium DBH, Type 3: prefer to grow on trees with large DBH, Type 4: almost exclusively grow on trees with large DBH

8. Discussion

8.1. Bryophyte diversity

We found 42 species on the bark of *A. aspera* alone (313 trees), while Oishi [8-10] found 57 species on the bark of all trees at the site. Approximately, two-thirds of the epiphytic bryophytes at the study site (containing more than 3000 total trees) were found on *A. aspera*, which indicates the high diversity of bryophytes on this species.

Notably, two endangered species (*L. pusilla* and *H. apiculata*) were found at the site. *L. pusilla*, which is classified as an endangered species on the red list of Kyoto prefecture [28], grows in large forests where desiccation stress is low [6]. Therefore, the large patch sizes of the study site support the occurrence of this species. *H. apiculata* is endemic to Japan and has severely limited habitat; therefore, this species is designated as “critically threatened” on the red list of Japan [29]. Why does this rare species grow at the study site? This species may be threatened by habitat losses caused by development [29]. As mentioned in the introduction, the study was conducted in an area that has long been preserved as a shrine forest. The preservation history of the study site likely contributed to the survival of this species.

8.2. Bryophyte diversity and DBH

Our results indicate that the diversity of both epiphytic bryophytes and life forms increased with DBH. Additionally, the relative dominance of 14 species (Types 3 & 4) increased with DBH; notably, five species (Type 4) occurred almost exclusively on large trees. These results indicate that the presence of large trees can increase the diversity of epiphytic bryophytes and are necessary for the conservation of these species. These relationships may be explained by (1) changes in tree bark and (2) the longer lives of large trees.

8.2.1. Changes in tree bark

The features of tree bark change with tree size: the bark surface of large trees has a higher moisture content and is rougher than that of small trees [30]. This higher moisture content can be important for bryophytes that grow in forms vulnerable to desiccation, such as fans, dendroids, and wefts [24], as reflected in the positive significant correlations of DBH with both the richness values of these life forms and total life form richness.

Furthermore, the rough bark surface of large trees may be more suitable for capturing bryophyte spores/gemmae than is the smooth surface of small trees. At our study site, the dominance of bryophytes with low reproductive frequency (dioicous species) increased with DBH. This result indicates that large trees are especially important for the establishment of bryophytes with low reproductive frequency due to their higher capture ability.

McGee & Kimmerer [31] showed that the occurrence and abundance of epiphytic bryophytes on large maple trees are likely regulated to a greater extent by factors such as dispersal or protonemal establishment than by the habitat requirements of mature gametophytes. Although we cannot directly apply the results of McGee & Kimmerer [31] to our study because

of differences in species and environmental conditions, their results suggest that changes in bark features more strongly affect dispersal or protonemal establishment than mature gametophytes.

8.2.2. Longer lives

Generally, larger trees live for longer periods than do small trees in similar environments, which provide comparatively more opportunities for bryophyte spore/gemma establishment. This effect may be partly reflected in the positive correlations between DBH and both the species richness and dominance of bryophytes with low reproductive frequency.

8.3. The significance of shrine forests

McGee & Kimmerer [17] described the importance of large trees for the conservation of epiphytic bryophytes in hardwood forests. This study shows that large trees can also contribute to the conservation of epiphytic bryophytes in shrine forests through their preferential bark features and longer lives. The effects of large trees are reflected in the changes of bryophyte life forms diversity and reproductive strategy according to DBH. In shrine forests, large trees are preferentially conserved because they are regarded as sacred. And, the management of shrine forests is effective for the conservation of epiphytic bryophytes.

Contrary to these results, several authors have reported that tree DBH does not strongly impact epiphytic bryophytes [32-33]. The possible explanations for the differences between this study and previous studies are as follow.

1. This study analyzed the epiphytic bryophytes on *A. aspera* alone. Therefore, other tree factors (e.g., bark pH) were relatively uniform, isolating the effects of DBH on epiphytic bryophytes.
2. The large differences of DBH in this study (minimum=27.0 cm, maximum=420.0 cm) clarified the effects of tree DBH on epiphytic bryophytes

8.4. History of shrine forests

This study also indicates that the long history of shrine forests contributes to the conservation of epiphyte diversity. Although this study did not gather sufficient data to examine the relationship between forest history and epiphytic bryophyte diversity, previous work has shown the importance of history for these species [18]. This conservation effect has also been reported in a fragmented forest in Kyoto city [34].

8.5. Epiphytic bryophytes and ecosystem

Epiphytic bryophytes play important roles in water storage [35, 36], nutrient cycling [37], and the retention of inorganic nitrogen [38] in forest ecosystems. These functions of epiphytic bryophytes have been examined not in urban forests but in tropical montane or old growth Douglas fir and western hemlock forests, in which epiphyte biomass is relatively high. The biomass of epiphytic bryophytes in urban forests is comparatively small; however, these

organisms may also be important in urban ecosystems. In particular, the role of bryophytes in water storage may contribute to the conservation of biodiversity, as the drought stress caused by edge effects is severe in fragmented urban forests [13].

9. Conclusion

The results of this study indicate that large trees in shrine forests can provide suitable habitats for epiphytic bryophytes and enhance their diversity in urban environments where green area is limited. These trees are especially effective for the conservation of species that are vulnerable to desiccation and/or have low reproductive frequency.

Epiphytic bryophytes are affected by environmental factors such as tree density [15, 33], past landscape structure [18, 34], bark type [39], silvicultural disturbance [40], air pollution [41], etc. By examining the influence of these factors on bryophytes in future studies, we can propose more effective methods for the conservation of these species. Furthermore, we should also examine the ecological roles of epiphytic bryophytes (e.g., water storage) in fragmented forests to understand the importance of their conservation.

Appendix

Appendix: Species list

The bryophyte nomenclature follows that reported by Iwatsuki [27].

Moss	Frequency	Cover (cm ²)
<i>Anomodon giraldii</i> Müll. Hal.	1	<100
<i>Aulacopilum japonicum</i> Broth.ex Card.	21	25000
<i>Brachymenium nepalense</i> Hook.	1	<100
<i>Brachythecium buchananii</i> (Hook.) A.Jaeger	1	<100
<i>Brachythecium populeum</i> (Hedw.) Schimp.	1	800
<i>Bryum capillare</i> Hedw.	4	<100
<i>Entodon challengerii</i> (Paris) Card.	30	30000
<i>Entodon sullivantii</i> (Müll. Hal.) Lindb.	1	400
<i>Fabronia matsumurae</i> Besch.	35	2600
<i>Haplocladium angustifolium</i> (Hampe & Müll.Hal.) Broth.	20	600

Moss	Frequency	Cover (cm ²)
<i>Haplocladium microphyllum</i> (Hedw.) Broth.	2	<100
<i>Haplohymenium pseudo-triste</i> (Müll. Hal.) Broth.	12	1700
<i>Haplohymenium triste</i> (Ces.) Kindb.	1	<100
<i>Herpetineuron toccoeae</i> (Sull. & Lesq.) Card.	34	20700
<i>Hypnodontopsis apiculata</i> Z.Iwats.& Nog.	1	<100
<i>Hypnum plumaeforme</i> Wilson	1	<100
<i>Leskeella pusilla</i> (Mitt.) Nog.	2	<100
<i>Neckera humilis</i> Mitt.	1	<100
<i>Okamuraea brachydictyon</i> (Card.) Nog.	15	<100
<i>Okamuraea hakoniensis</i> (Mitt.) Broth.	12	800
<i>Orthotricum consobrinum</i> Card.	3	<100
<i>Pylaisiadelphina tenuirostris</i> (Bruch & Schimp.) W.R.Buck	34	5700
<i>Rhynchostegium inclinatum</i> (Mitt.) A.Jaeger	35	41400
<i>Rhynchostegium pallidifolium</i> (Mitt.) A.Jaeger	62	53600
<i>Schwetschkea matsumurae</i> Besch.	2	400
<i>Sematophyllum subhumile</i> (Müll. Hal.) M.Fleisch.	1	2000
<i>Trachycystis microphylla</i> (Dozy & Mol.) Lindb.	1	<100
<i>Venturiella sinensis</i> (Vent.) Müll. Hal.	14	200
Liverwort		
<i>Acrolejeunea pusilla</i> (Steph.) Grolle & Gradst.	6	600
<i>Chiloscyphus minor</i> (Nees) J.J.Engel & R.M.Schust	37	4800
<i>Cololejeunea japonica</i> (Schiffn.) S.Hatt. ex Mizut.	18	800
<i>Cololejeunea raduliloba</i> Steph.	15	2600
<i>Frullania diversitexta</i> Steph.	1	<100
<i>Frullania ericoides</i> (Nees) Mont.	12	11500
<i>Frullania muscicola</i> Steph.	8	3210
<i>Frullania parvistipula</i> Steph.	58	35550
<i>Lejeunea japonica</i> Mitt.	2	2400

Moss	Frequency	Cover (cm ²)
<i>Lejeunea ulicina</i> (Tayl.) Gottsche, Lindenb.& Nees	1	<100
<i>Macvicaria ulophylla</i> (Steph.) S.Hatt.	58	38700
<i>Metzgeria lindbergii</i> Schiffn.	64	41500
<i>Radula constricta</i> Steph.	5	900
<i>Trocholejeunea sandvicensis</i> (Gottsche) Mizut.	73	59800

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