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**Original article**

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## **Species-area relationships of fragmented lucidophyllous forests in Japan**

**Hiroaki ISHIDA and Tamotsu HATTORI**

*Institute of Natural and Environmental Sciences, University of Hyogo/Division of Ecological Restoration, Museum of Nature and Human Activities, Hyogo, Yayoigaoka 6, Sanda 669-1546, Japan*

### **Abstract**

We have undertaken a comparison of small fragmented lucidophyllous (evergreen broad-leaved) forests in four regions of Japan to elucidate regional differences in the relationship between the number of lucidophyllous forest species and the forest area (species-area relationship). For all regions, both the species-log area and log species-log area models were well fit to the species-area relationships, and there were no marked differences in goodness-of-fit between the two models. The slope of the regression for the species-area relationships was similar among the four regions. However, there were clear regional differences in species richness. We found that these differences greatly reflected the regional differences in temperature. The species-area relationship for large areas of forest was analyzed by combining the data for the small forests and the data for the large forests for each of two regions. The results showed that the log species-log area model was better suited than the species-log area model for representing the species-area relationship for large areas of forest.

**Key words:** Fragmented forest, Lucidophyllous forest, Regional difference, Species-area relationship, Species richness

### **Introduction**

Studies on fragmented forests or isolated forests have increased considerably since the latter half of the 1970s. Many of these studies have shown that the number of plant species is highly dependent on the area occupied by the fragmented forests (e.g., Usher, 1979; Peterken and Game, 1984; Dzwonko and Loster, 1988, 1989; Zacharias and Brandes, 1990; Hattori et al., 1994; Grashof-Bokdam, 1997; Murakami and Morimoto, 2000; Hill and Curran, 2003). Also, the relationship between species richness and forest area in fragmented forests (species-area relationship) has been observed to differ between regions, even among the same forest types (Peterken and Game, 1984; Dzwonko and Loster, 1989; Ishida et al., 2002). According to

Peterken and Game (1984) and Dzwonko and Loster (1989), while the species-log area model (Gleason, 1922) and the log species-log area model (Arrhenius, 1921) are both suitable for representing the species-area relationship of fragmented forests under conditions of limited spatial scales, the log species-log area model more accurately represents the species-area relationship for large areas of forest. This condition might hold for various types of fragmented forests.

Lucidophyllous (evergreen broad-leaved) forests occur in warm-temperate to subtropical regions with considerable rainfall. Lucidophyllous forests are one of the representative natural forest types in Japan. However, despite having once covered much of the basal zone west of the Tohoku region, many of the native lucidophyllous forests in Japan have been

destroyed by human activities since the Jomon Era. At present, the few extant lucidophyllous forests are restricted to areas such as islands, the southern part of the Kyushu region, and the precincts of shrines and temples, most of which are small in size and isolated.

We previously reported species-area relationships of small fragmented lucidophyllous forests preserved within the precincts of shrines and temples in four regions of Japan (Ishida et al., 1998, 2001; Hattori and Ishida, 2000). In the present study, we have used the data of these previous studies to undertake a comprehensive comparison of fragmented lucidophyllous forests in the four regions for the sake of elucidating regional differences in species-area relationships and their underlying causes. Furthermore, by also considering new data obtained for large fragmented lucidophyllous forests, we sought to ascertain whether the species-log area model or log species-log area model was better suited to representing the species-area relationship for large areas of forest. Clarifying these points is likely to be essential for ascertaining the characteristics of the species-area relationship of fragmented lucidophyllous forests and for identifying the physical extent of the area necessary for maintaining the species richness of lucidophyllous forests. We believe that the results of the present study will be useful in elucidating the ecological features of fragmented lucidophyllous forests and will contribute to the way in which information is collected and applied to their preservation.

### Study regions

The present study examined fragmented lucidophyllous forests in the following four regions:

#### 1) Central Miyazaki

Central Miyazaki is located in the central part of Miyazaki Prefecture (31°50'N-32°9'N and 131°3'E-131°26'E). In this region, 38 small lucidophyllous forests (size: 0.0030 to 7.84 ha) and one large lucidophyllous forest (45.0 ha) were surveyed, dominated mainly by *Quercus gilva*, *Persea thunbergii*, and *Castanopsis cuspidata* var. *cuspidata*. The lucidophyllous forests surveyed are located 6.0 to 37.3 km from the coastline at elevations ranging from 10 to 250 m for the small lucidophyllous forests, and 180 to 480 m for the large forest. The large forest is on the slope of

mountains in the upper reaches of the Ayaminami River, and is located about 3 km south of Mt. Ohmori. The annual mean temperature as measured at a meteorological station within this study region (31°57'N and 131°18'E, elevation 10 m) is 17.1°C, with a mean temperature for the coldest month (MTCM) of 7.1°C and an annual rainfall of 2435 mm (Meteorological Agency, 1958, 1959). Hattori and Ishida (2000) provide a detailed description of the small lucidophyllous forests surveyed.

#### 2) Southern Tsushima

Southern Tsushima is located in the southern part of Tsushima Island (34°6'N-34°28'N and 129°11'E-129°23'E). Eighteen small lucidophyllous forests (size: 0.023 to 4.40 ha) and one large lucidophyllous forest (70.0 ha), dominated mainly by *C. cuspidata* var. *sieboldii*, were surveyed in this region. The surveyed forests are located 0.1 to 3.3 km from the coastline at elevations ranging between 10 to 120 m for the small lucidophyllous forests, and 120 to 559 m for the large forest. The large forest is on the northern slope of Mt. Tatera. A mean annual temperature of 15.1°C, MTCM of 4.5°C and an annual rainfall of 2109 mm were recorded at a meteorological station within this study region (34°12'N and 129°17'E, elevation 21 m). Ishida et al. (2001) present a detailed description of the small lucidophyllous forests surveyed.

#### 3) Southeastern Hyogo

Southeastern Hyogo is located at 34°41'N-35°0'N and 134°37'E-135°27'E. Twenty-nine small lucidophyllous forests (size: 0.025 to 16.4 ha) were surveyed in this region. The surveyed forests are all dominated by *Castanopsis cuspidata* var. *cuspidata*, and located 6.5 to 31.8 km from the coastline at an elevation ranging from 70 to 300 m. An annual mean temperature of 13.9°C, a MTCM of 2.4°C and an annual rainfall of 1303 mm were recorded by a meteorological station within this study region (34°53'N and 135°13'E, elevation 157 m). See Ishida et al. (1998) for a detailed description of the surveyed forests.

#### 4) Northern Kyoto

Northern Kyoto is located at 35°25'N-35°41'N and 134°49'E-135°18'E. The 18 small lucidophyllous forests (size: 0.010 to 2.10 ha) surveyed are dominated mainly by *C. cuspidata* var. *sieboldii*, and

are located 0.35 to 20.8 km from the coastline at elevations ranging between 5 to 125 m. An annual mean temperature of 14.2°C, MTCM of 3.3 °C and an annual rainfall of 1942 mm were recorded at a meteorological station within the study region (35°32'N and 135°12'E, elevation 1 m). Comprehensive details concerning the surveyed forests are given by Ishida et al. (2001).

## Methods

The flora of each forest were investigated to prepare a species list for the lucidophyllous forest species (lucidophyllous elements). Lucidophyllous elements were considered as consisting primarily of shade-tolerant species capable of growing under the closed canopy of lucidophyllous forests and excluded pioneer species (e.g., *Aralia elata*, *Mallotus japonicus*, *Fagara ailanthoides*, *Rhus javanica*, *Euscaphis japonica*, *Fagara mantchurica*), species with strong habitat preferences for the forest edge, treefall gaps, or secondary forests (e.g., *Quercus serrata*, *Pinus densiflora*, *Carpinus tschonoskii*, *Rhus trichocarpa*, *Styrax japonicus*, *Albizia julibrissin*, *Callicarpa mollis*, *Akebia trifoliata*, *Wisteria floribunda*, *Lonicera japonica*), planted species, and escapees. Lucidophyllous elements were classified according to the classification system developed by Hattori and Minamiyama (2001).

We compiled species lists on walks through as many parcels of forest as possible (no regular survey route was employed). Walks were more oriented toward including as many topographically diverse areas as possible with all selected forests visited mainly from May to November. Very small forests (< 0.5 ha) were visited once or twice by one or more surveyors (maximum four), while larger forests were visited more than three times by more than three surveyors (maximum eight). We also recorded epiphytes that had fallen to the ground. Each visit was conducted for as long as it took before it became difficult to add new species to the list. The lists for the large lucidophyllous forests were supplemented by available data from other researchers (Itow and Nakanishi, 1994; Kodate et al., 2002; Hattori et al., 2003a). We therefore concluded that the plant surveys were almost complete and that under-recording would have no significant effect on the analysis of the species-area

relationship. The study period spanned from 1982 to 1999 in central Miyazaki, from 1997 to 1999 in southern Tsushima, from 1994 to 1995 in southeastern Hyogo and from 1995 to 1999 in northern Kyoto.

The area of each forest was calculated from topographical maps, aerial photographs, and surveys conducted in the forests. When stands markedly disturbed by human activities were encountered within the forest, their areas were excluded from the forest area.

In order to analyze the relationship between the number of lucidophyllous elements and the forest area, simple regression analyses were conducted using the species-log area and log species-log area models. These models are expressed by the following formulas:

$$S = c + z \log A$$

$$\log S = c + z \log A$$

where  $S$  is the number of species,  $A$  is the area of the forest under consideration, and  $c$  and  $z$  are constants.

## Results and Discussion

### Comparison of species-area relationships

Table 1 shows the results of simple regression analyses on the species-area relationship of small lucidophyllous forests, while Figure 1 shows the regression curves for each model in each region. For all regions, both models fit well, and there were no marked differences in goodness-of-fit between the two models.

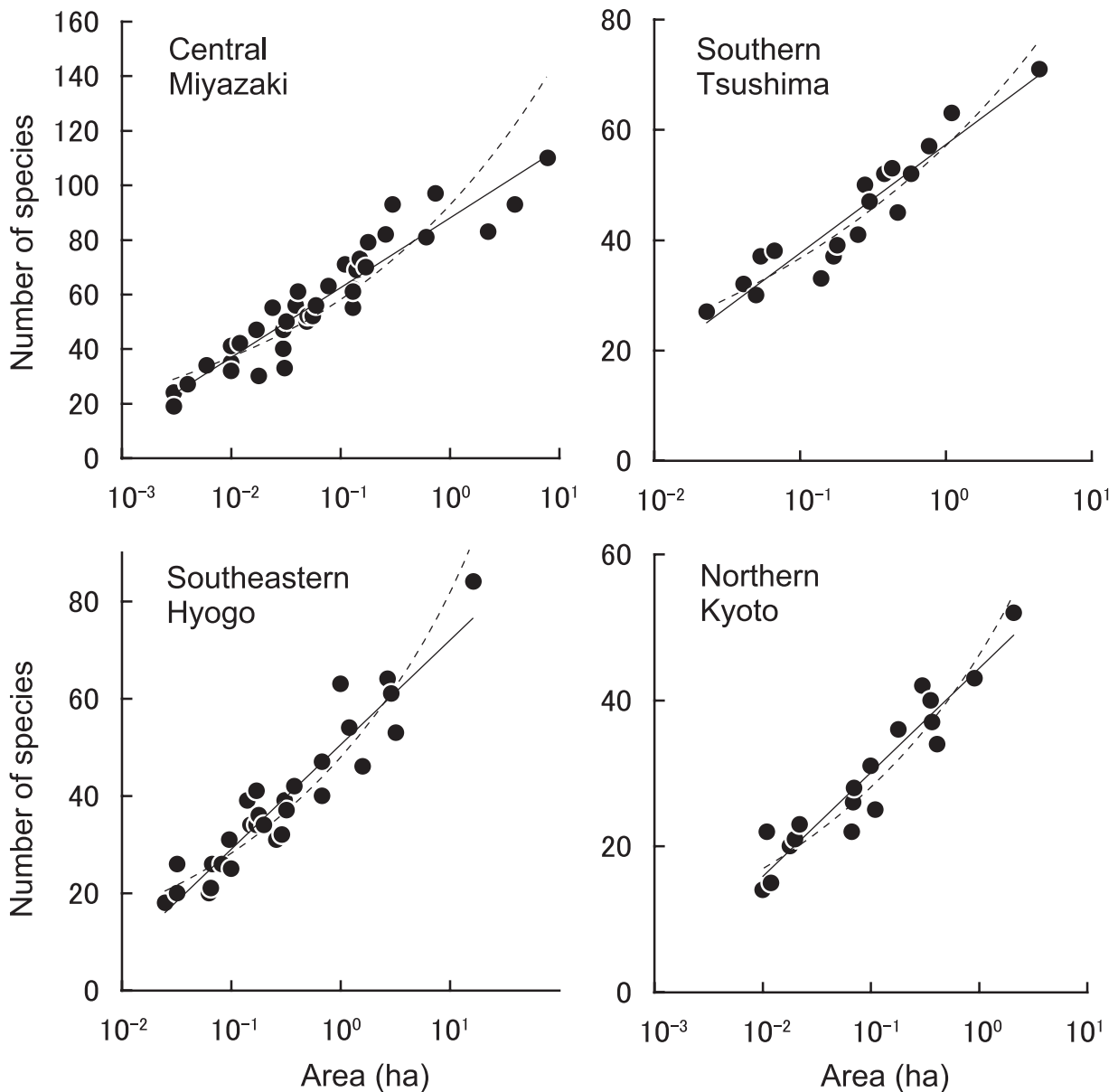
The slopes of the regression ( $z$  values) for the species-area relationships were compared among the four regions. With the species-log area model, the  $z$  value for central Miyazaki was the highest, followed by southeastern Hyogo, southern Tsushima and northern Kyoto, in order. However, with the log species-log area model, the  $z$  value for southeastern Hyogo was the highest, followed in decreasing order by northern Kyoto, central Miyazaki and southern Tsushima (Table 1). We then conducted statistical analyses of covariance (ANCOVA) to compare the differences in the observed  $z$  values for the two models among the four regions. The results showed that, with the species-log area model, there was a significant difference between northern Kyoto and

**Table 1.** Results of simple regression analyses on the relationship between the number of lucidophyllous elements ( $S$ ) and the forest area ( $A$ ; m<sup>2</sup>) in the small lucidophyllous forests in the four regions.

Region	$S = c + z \log A$			$\log S = c + z \log A$			n	Range in area (ha)
	$c$	$z$	$r$	$c$	$z$	$r$		
1	-14.80	25.72	0.94 *	1.157	0.202	0.91 *	38	0.010–7.84
2	-21.73	19.79	0.95 *	0.995	0.191	0.94 *	18	0.023–4.40
3	-35.24	21.44	0.94 *	0.766	0.229	0.93 *	29	0.025–16.40
4	-12.93	14.32	0.95 *	0.807	0.215	0.94 *	18	0.010–2.10

1: central Miyazaki; 2: southern Tsushima; 3: southeastern Hyogo; 4: northern Kyoto.

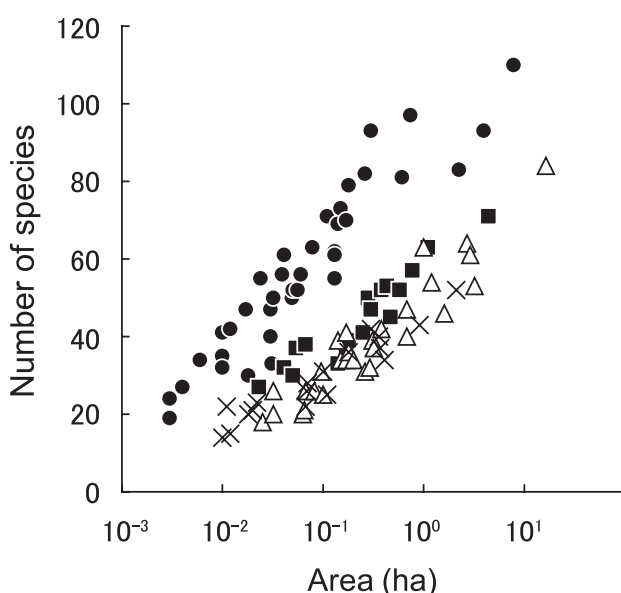
\*  $p < 0.001$



**Figure 1.** Relationships between the number of lucidophyllous elements and the forest area (log scale) in the small lucidophyllous forests in the four regions. The solid and broken lines show the species-log area and log species-log area regression curves, respectively.

the other three regions ( $p < 0.05$ ), but that no difference was apparent between central Miyazaki, southern Tsushima and southeastern Hyogo ( $p > 0.05$ ). With the log species-log area model, there was no significant difference among the four regions ( $p > 0.05$ ). These results indicate that the rate of change in the number of species per unit area is comparable among the four regions and that there are therefore no clear regional differences in the rate of change in the number of species per unit area. We believe that this tendency is applicable to other regions, not just the four regions examined in the present study, and that the  $z$  value of the log species-log area model is likely to be approximately 0.20 in most regions.

Figure 2 summarizes the species-area relationships for the four regions in the study. As shown in the figure, the number of species per unit area was the highest in central Miyazaki, followed by southern Tsushima, and then southeastern Hyogo and northern Kyoto, which both had approximately the same number. In order to statistically analyze regional differences in the number of species, ANCOVA was performed using log species as a dependent variable and log area as a covariate (real numbers of species were not used because parallelism of regression curves could not be assumed). The results showed that while there was no significant difference between southeastern



**Figure 2.** Comparison of the number of lucidophyllous elements in the small lucidophyllous forests among the four regions. Filled circles: central Miyazaki; filled squares: southern Tsushima; open triangles: southeastern Hyogo; and crosses: northern Kyoto.

Hyogo and northern Kyoto ( $p > 0.05$ ), there were significant differences for all other comparisons ( $p < 0.05$ ). It has been shown that the species richness of lucidophyllous elements at the regional level is strongly influenced by temperature, with warmer climates associated with an increased number of species (Hattori, 1985; Hattori et al., 2002). Also, Hattori et al. (2003b) studied primeval lucidophyllous forests in the Kyushu region and reported that the number of lucidophyllous elements per unit area (100 m<sup>2</sup>) is positively correlated with the mean temperature of the coldest month (MTCM). These findings suggest that the regional differences in the number of species in the present study may be related to differences in temperature among the different regions. We therefore investigated the relationship between the intercept of the log species-log area model ( $c$  value) and climatic variables by calculating the average MTCM of the surveyed forests for each study region using measurements obtained from the closest meteorological station (Meteorological Agency, 1958) with a temperature lapse rate of 0.6°C/100 m. The climatic variables were then treated as independent variables in simple regression analyses against the  $c$  value, which was treated as the dependent variable. The results showed a significant positive correlation between  $c$  and MTCM with a correlation coefficient of 0.99 ( $p < 0.05$ ). This relationship can be expressed by the following regression formula:

$$c = 0.546 + 0.092 \text{ MTCM}$$

Because the  $c$  value changes depending on the units used for area (m<sup>2</sup>, ha, etc.), the results derived for the regression analyses also change if different units are used. We therefore analyzed the relationship between  $c$  and MTCM using hectares (ha). The results confirmed that there was a significant positive correlation between  $c$  and MTCM with a correlation coefficient of 0.98 ( $p < 0.05$ ). This correlation can be expressed by the following regression formula:

$$c = 1.477 + 0.070 \text{ MTCM}$$

The above findings suggest that the observed differences in the number of species greatly reflect regional differences in temperature, and that the  $c$

value of the log species-log area model can be estimated based on MTCM.

### Species-area relationship for large areas of forest

In order to ascertain whether the species-log area or log species-log area model is better suited to representing the species-area relationship for large areas of forest, a simple regression analysis was conducted by combining the data for the small lucidophyllous forests within a region and the data for the large lucidophyllous forests within the same region for each of two regions: central Miyazaki and southern Tsushima (Table 2). As in the case of small lucidophyllous forests, the correlation coefficient for the two regions was very high using either model. However, in comparisons of the regression curves between the two models (Figure 3), the log species-log area model matched the

regression curve for the large lucidophyllous forests better than the species-log area model in both regions. These findings are consistent with those of Peterken and Game (1984) and Dzwonko and Loster (1989). We therefore concluded that the log species-log area model is better suited than the species-log area model for representing the species-area relationship for large areas of forest in central Miyazaki and southern Tsushima. Furthermore, it appears that this applies to fragmented lucidophyllous forests in other regions.

### Area necessary for maintaining species richness

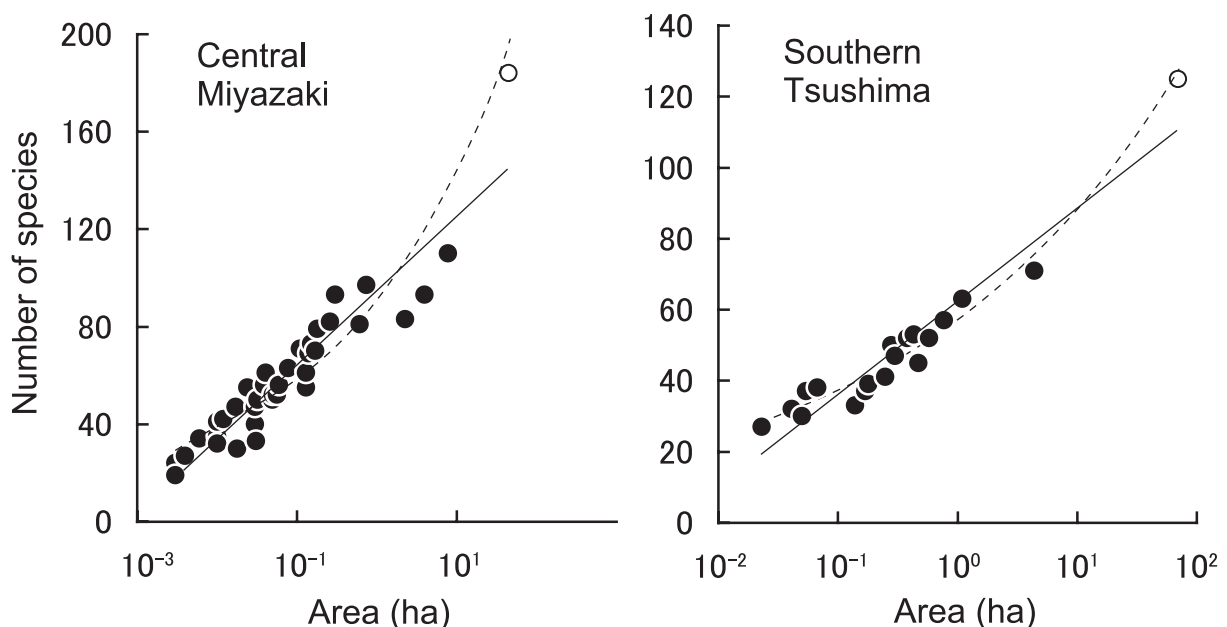
The present results indicate that it is necessary to secure as much area as possible when preserving or attempting to restore species richness in lucidophyllous forests. This raises the following question: How much area is necessary for

**Table 2.** Results of simple regression analyses on the relationship between the number of lucidophyllous elements ( $S$ ) and the forest area ( $A$ ; m<sup>2</sup>) for large areas of forest in the two regions.

Region	$S = c + z \log A$			$\log S = c + z \log A$			n	Range in area (ha)
	$c$	$z$	$r$	$c$	$z$	$r$		
1	-26.86	30.40	0.94 *	1.166	0.199	0.93 *	39	0.010–45.0
2	-42.50	26.21	0.96 *	1.004	0.188	0.97 *	19	0.023–70.0

1: central Miyazaki; 2: southern Tsushima.

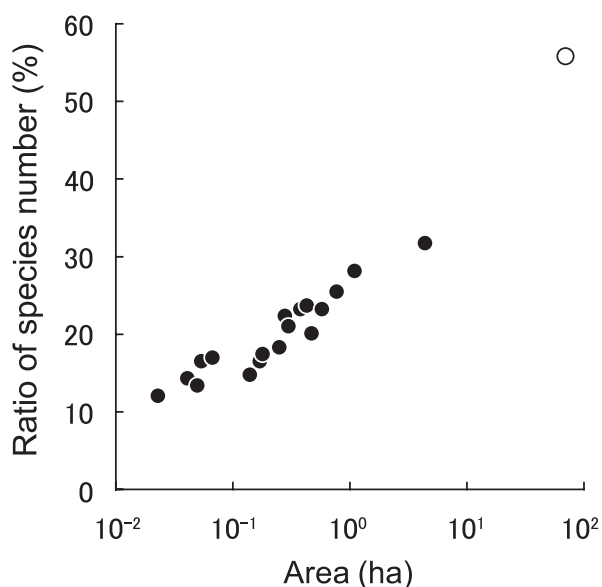
\*  $p < 0.001$



**Figure 3.** Relationships between the number of lucidophyllous elements and the forest area (log scale) for large areas of forest in the two regions. The solid and broken lines show the species-log area and log species-log area regression curves, respectively. Open circles: large lucidophyllous forest; filled circles: small lucidophyllous forest.

maintaining the flora of lucidophyllous elements in areas with similar environmental conditions (regional lucidophyllous flora)? In order to answer this question, we estimated the area necessary for maintaining lucidophyllous flora on Tsushima Island. We selected Tsushima Island for this investigation for these reasons: 1) compared to the other regions, the level of destruction of lucidophyllous forests was lower, and as a result, the number of extinct lucidophyllous elements could be expected to be lower; 2) lucidophyllous flora have been closely investigated on the island; and, 3) because Tsushima is an island, it is a well-defined spatial entity.

First, in order to clarify the lucidophyllous flora on Tsushima Island, a list of lucidophyllous elements was compiled based on the results of the present study for small and large lucidophyllous forests and several previous studies (Toyama and Matsubayashi, 1976; Toyama, 1980). A total of 224 species were identified on Tsushima Island. The ratio of the number of species in the small and large lucidophyllous forests to the total species count was calculated for each forest, and then the relationship between that ratio and the forest area was investigated (Figure 4). As shown in the figure, small lucidophyllous forests smaller than 1 ha were typically characterized as harboring fewer than 30%



**Figure 4.** Relationship between the ratio of species number (the number of lucidophyllous elements in the small and large lucidophyllous forests in southern Tsushima to the total number of lucidophyllous elements on Tsushima Island) and the forest area (log scale). Open circles: large lucidophyllous forest; filled circles: small lucidophyllous forest.

of the total species counted. Similarly, the large lucidophyllous forest only harbored approximately 56% of the total species counted. In other words, even forests as large as 70 ha are too small to maintain the full complement of lucidophyllous flora on Tsushima Island. By assuming that the above-mentioned total species count represents almost all the lucidophyllous flora on Tsushima Island, the area required to maintain 70, 80, 90 and 100% of the lucidophyllous flora was estimated using the regression formula derived for the species-area relationship (hereinafter referred to as A70, A80, A90 and A100, respectively). In this instance, the log species-log area model was used because, as mentioned previously, this model is better suited to approximate the species-area relationship for large areas of forest.

Using the regression formula shown in Table 1 ( $\log S = 0.995 + 0.191 \log A$ ), we found that the areas necessary to maintain 70, 80, 90 and 100% of the total species counted were approximately 200, 400, 700 and 1200 ha, respectively. In the case of using the regression formula shown in Table 2 ( $\log S = 1.004 + 0.188 \log A$ ), the areas necessary to maintain 70, 80, 90 and 100% of the total species counted were approximately 200, 400, 800 and 1400 ha, respectively. These results imply that approximately 200 ha are required to maintain 70% of the lucidophyllous flora, approximately 400 ha for 80% of the lucidophyllous flora, approximately 700 to 800 ha for 90% of the lucidophyllous flora, and approximately 1200 to 1400 ha for maintaining 100% of the lucidophyllous flora.

In the present study, we found that the slope of the regression formula for the species-area relationship was similar among the four regions and that the number of lucidophyllous elements in the fragmented lucidophyllous forests was strongly influenced by temperature, not just forest area. Several previous studies have shown that the temperature has a substantial influence on the species richness of regional lucidophyllous flora (Hattori, 1985; Hattori et al., 2002). These findings suggest that there are no marked regional differences in the extent of the area necessary for maintaining regional lucidophyllous flora, and that the aforementioned values for A70, A80, A90 and A100 can be commonly used as target values for the preservation and restoration of species-rich lucidophyllous forests.

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