



Local and geographical distributions for a tropical tree genus, *Scaphium* (Sterculiaceae) in the Far East

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Abstract

Tropical rain forests have an amazingly large number of closely related, sympatric species. How the sympatric species coexist is central to understanding the maintenance of high biodiversity in tropical rain forests. We compared local and geographical distributions among trees in *Scaphium* (Sterculiaceae), a tropical canopy tree genus. *Scaphium* is endemic to the Far Eastern tropics and comprises six species. *Scaphium scaphigerum* is distributed in drier regions than the other species' geographical distribution ranges. *Scaphium longiflorum* is distributed swamp forests, whereas the others were distributed in lowland and hill tropical rain forests on undulating land. *Scaphium borneense*, *S. longipetiolatum*, and *S. macropodum* co-occurred in a 52-ha plot in Lambir, Sarawak and clearly showed an allopathic pattern of distribution related to elevation in it. In the plot, the elevational difference was correlated with soil variation. Consequently, the difference in edaphic condition promoted the habitat segregation of the species. Thus these five *Scaphium* species have divergent habitats at various spatial scales and coexist because they reduce direct competition by habitat niche differentiation. Although the non-equilibrium hypothesis for the coexistence of *Scaphium* species cannot be rejected categorically due to the lack of enough information about *S. linearicarpum*, the equilibrium force may play the predominant role which permits their coexistence.

Introduction

Many ecologists have been intrigued by the maintenance mechanism of woody plant species diversity in tropical rain forests and various theoretical hypotheses have been proposed. These hypotheses developed in two different directions, equilibrium and non-equilibrium hypotheses. The former postulate the existence of equilibrium forces which maintain a particular species mixture in a community. In an equilibrium community, each species occupies a different niche which results from and reduces direct competition (Whittaker 1975), and thus species composition is more or less stable according to environmental pre-

dictability. The species-specific correlations between tree distribution and soil and/or topography in tropical rain forests have been reported by many scientists (Ashton 1969; 1988a; Lescure & Boulet 1985; Austin et al. 1972; Richards 1952; Rogstad 1990; Svenning 1999; etc.) are consistent with the existence of equilibrium force in tropical rain forests. On the contrary, the non-equilibrium hypothesis posits that equilibrium forces at work are weak. By this argument, species diversity is decreased through random local extinction in a stochastic dynamic system. However, species diversity can be maintained when the rates of local extinction are low and balanced by lo-

cal immigration and speciation. Therefore, the species composition of non-equilibrium communities is unstable and the order of abundance constantly changing. Hubbell & Foster (1986), who studied the distribution of trees in a 50-ha plot in Barro Colorado Island (BCI), showed that most of the common trees in this neotropical rain forest belonged to a large habitat generalist guild. They emphasized that it is impossible to explain species richness by niche differentiation, and treated non-equilibrium forces as the working mechanism of species richness. Duivenvoorden (1995) showed that most of Colombian tropical rain forest trees inhibiting in the well-drained upland habitat would be soil generalists, which limits the importance of habitat specialization for maintaining tree species richness.

Whether or not tropical rain forests are equilibrium communities and how strong are equilibrium forces in tropical rain forests are still obscure and controversial. Further studies are needed to determine the degree to which the equilibrium hypotheses contribute to the structure and species composition of tropical rain forests. The strongest way to assess the relative importance of equilibrium forces in a community is to thoroughly study niche differentiation among all species found in the focal community. However, such studies are often limited due to restricted time, manpower, and poor knowledge of tropical systematic. In such cases, choice of study species is a substantial problem. Rogstad (1989) as well as Itoh (1995a) recommended closely related sympatric species. One of the remarkable features of tropical woody biodiversity is the presence of a series of sympatric congeneric species in some genera (cf. Ashton 1982; Fedorov 1966; Whitmore 1984; Rogstad 1990; Kochummen et al. 1990; Itoh 1995a; Yamada et al. 1997). Such species are most likely to have relatively similar niches, because they share the same ecological and physiological heritage via their common ancestral lineage (Rogstad 1989). The maintenance mechanisms may therefore appear to be most critical for the coexistence of such species. Moreover, monophyletic groups are more informative for evolutionary processes of tropical trees because they differ at fewer gene loci and therefore in fewer life history characteristics.

In this paper, we discuss evidence for habitat niche divergence in a small and homogeneous tree genus, *Scaphium* Schott and Endl. (Sterculiaceae). We use data of species-specific geographical distribution patterns in the Far East and local distribution patterns in a 52-ha plot set in Lambir Hills National Park, Malaysia, and with them review the importance of equilib-

rium and non-equilibrium forces on the coexistence of *Scaphium* species.

Materials and methods

Study species

Scaphium is a small genus of large, briefly deciduous trees comprising six species: *S. borneense* (Merr.) Kosterm., *S. linearicarpum* (Mast.) Pierre., *S. longiflorum* Ridley., *S. longipetiolatum* (Kosterm.) Kosterm., *S. macropodium* (Miq) Beumee ex Heyne, and, *S. scaphigerum* (G. Don) Guibourt et Planch. The genus is endemic to the Indo-Malaysia Subkingdom defined by Good (1974) and is distributed throughout Indochina, Malaya, Borneo, and Sumatra. The species' saplings are shade tolerant and are abundant under the closed canopies (Yamada & Suzuki 1997). The stature of *S. macropodium*, the most common and wide-spread species, is over 45 m in Borneo (Yamada & Suzuki 1996). The trees flower on bare twigs after leaf-fall (Kostermans 1953) and produce gyration or wind-dispersed fruits with a boat-shaped wing derived from a dehiscing follicle. The dispersal distance of the fruit seldom exceeds 50 m from the base of parent trees (Ridley 1930; Yamada & Suzuki 1997).

Geographical distribution pattern

We have mapped collection sites of *Scaphium* trees reviewed by Kostermans (1953, 1962, 1969) to clarify the geographical distribution patterns of *Scaphium* species. To add collection sites of *Scaphium* trees after reviewing Kostermans', we checked the specimens in Singapore Herbarium, Forestry Department herbaria in Kuching, Sarawak, and Bangkok, Thailand, and Forest Research Institute Malaysia herbarium in 1997.

Local distribution pattern

This study was performed in a mixed dipterocarp forest in Lambir Hills National Park (4°12' N, 114°00' E, ca. 60–450 m a.s.l.) in Sarawak, East Malaysia. The park is spread over an area of 6949 ha, and most of the area is covered by a mixed dipterocarp forest (Watson 1985). The mean annual precipitation at Miri, about 30 km north of the study site, from 1917 to 1957 is 3150 mm (Yamakura et al. 1995). The average monthly rainfall is above 150 mm in all cases. Details of the vegetation, geology, geomorphology, and soil of

the site are described elsewhere (Yamakura et al. 1995; Watson 1985; Itoh 1995).

A permanent plot of 52 ha (1040 m × 500 m) has been established within the forest. The plot is divided into 1300 subquadrats of 20 m × 20 m. The relative elevations of each corner of the subquadrats are measured (Yamakura et al. 1996). One point in the plot was estimated as 150 m in elevation a.s.l. and was used as the base from which the others were measured by level survey. The difference between the highest and lowest points in the plot was 168 m. The plot physiography is hilly and complex compared with the 50-ha plots in Pasoh, Malaysia (Manokaran & LaFrankie 1990) and on BCI, Panama (Hubbell & Foster 1986). Yamakura et al. (1996) observed that fragments of various habitats are mixed on a small scale in the plot and this is accompanied by habitat segregation between species and thus high diversity. The plot is underlain by shale and by sandstone, and therefore two soil types: finer textural soils (clay and clay loam soils) and coarser textured soils (sandy loam and sandy-clay loam soils). The distribution of finer textural and coarser textured soils roughly coincides with locations lower than and higher than ca. 160 m in elevation, respectively. Therefore elevational differences are parallel to differences in soil texture in the plot.

All trees equal to or larger than 1 cm Dbh (diameter at breast height) have been tagged with aluminium number plates, identified, measured by Dbh, and mapped between 1990 and 1993. Among the six *Scaphium* species, *S. borneense*, *S. longipetiololum*, and *S. macropodum* were found in the plot. In this paper, the data set of trees identified as genus *Scaphium* was used for the analysis. To correct identification errors in the first forest inventory, all *Scaphium* trees in the plot were checked in the field between February and March 1996. These *Scaphium* trees are easily identifiable at every stage of life history due to their unique leaf shape and crown form (Ashton 1988b; Yamada & Suzuki 1996).

The spatial distribution patterns and their clump sizes of *Scaphium* trees were analyzed by Iwao's m^*/m index (Iwao 1972), or the mean crowding (m^*) divided by the mean density (m). A statistical difference between the observed distribution and the Poisson model of the random distribution was tested by the F test (Morisita 1959).

For the quantitative analysis of the habitats of *Scaphium* trees, we designated the habitat of each individual tree as the 20 m × 20 m subquadrat where

it was found. We then calculated the elevations of the subquadrat defined as the average elevation of the four corners.

Results

Geographical distribution pattern of Scaphium species

Figure 1 shows the distribution of *Scaphium* species in the Far East. *Scaphium scaphigerum* is distributed in the continental South-East-Asiatic region defined by Good (1974) where it experiences the typical dry season due to the influence of the monsoon, whereas the five other species are distributed in the rainfall-aseasonal ever-wet Malaysian region. The collection records of *S. longiflorum* are completely restricted to swamp forests (Kostermans 1953, 1962). The four other species were collected in lowland and hill mixed dipterocarp forests on undulating land (Kostermans 1953, 1962, 1969; Ashton 1988b), although center and range of distribution differed among the species. Therefore, of the six species, one is distributed in drier regions, one in swamp forests, and the others in mixed dipterocarp forests in undulating lands.

Population structure of Scaphium species in the 52-ha plot

Among the three *Scaphium* species occurring within the 52-ha plot, the abundance of *S. borneense* was the highest, with 1135 individuals. *Scaphium macropodum* and *S. longipetiolatum* had 122 and 63 trees, respectively. The maximum Dbh differed among the three species. The maximum size of Dbh of *S. borneense*, which was 40.8 cm, was substantially smaller than those of *S. longipetiolatum* and *S. macropodum*, which were 53.0 and 57.3 cm, respectively.

The values of the index of skewness of Dbh distribution were positive for each species, suggesting that some big trees occurred with many small trees, the classical L-shaped frequency distribution of the Dbh for shade tolerant species with plentiful regeneration.

Spatial patterns of Scaphium species in the 52-ha plot

Figure 2 shows the spatial distribution of *Scaphium* species in the plot. All the *Scaphium* species occurred along ridges but that was obscure for *S. longipetiolatum*. *Scaphium borneense* was distributed more widely

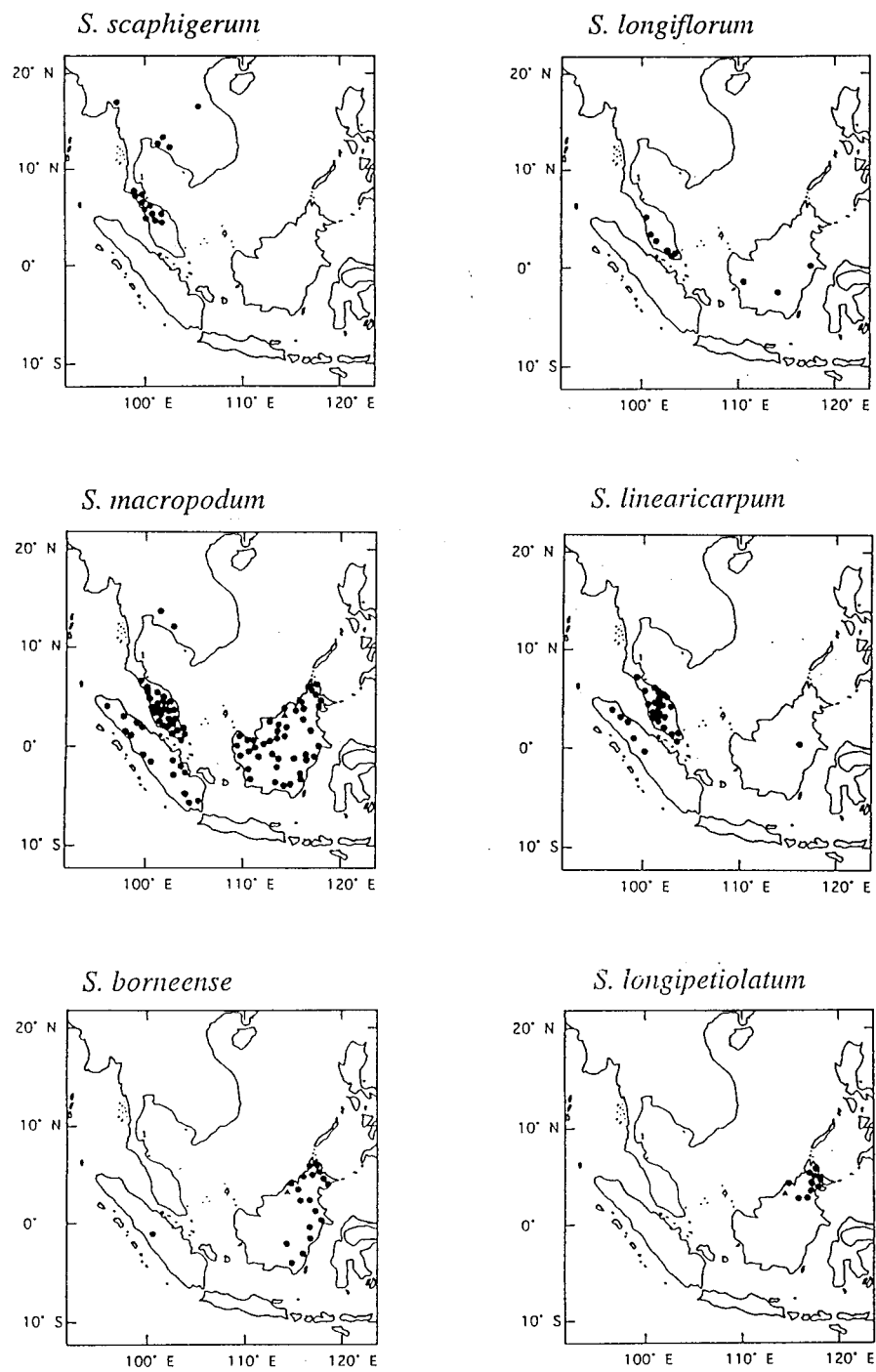


Figure 1. Geographical distributions of *Scaphium* species in the Far East. The symbol of blacktriangle indicates the position of a 52-ha plot in Lambir Hills National Park.

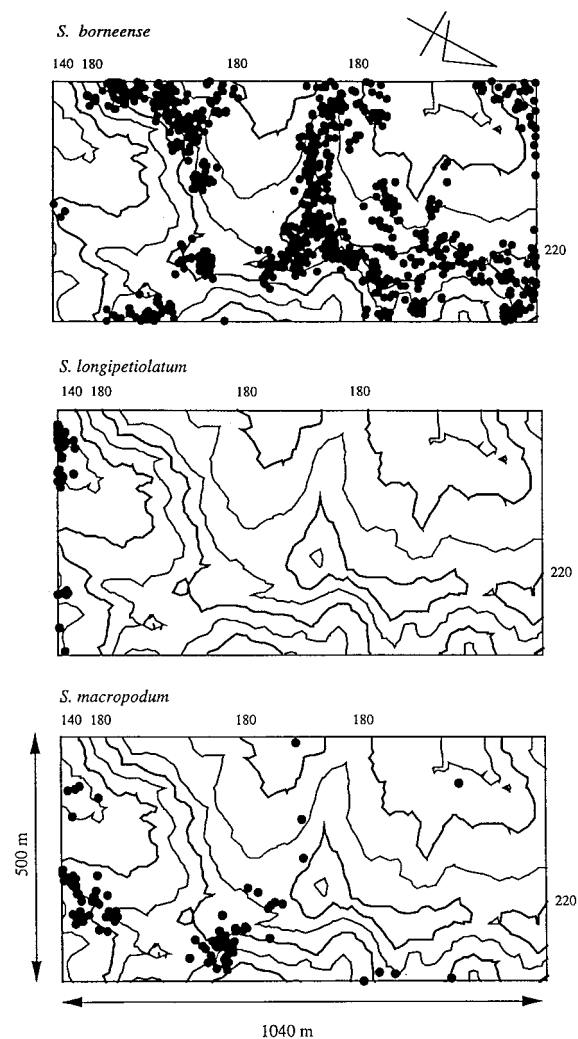


Figure 2. Spatial distributions of *Scaphium borneense*, *Scaphium longipetiolatum*, and *Scaphium macropodum* in the 52-ha plot.

than the others but was invariably restricted to sites higher than 140 m in a.s.l. *Scaphium macropodum* was mostly distributed in the eastern half of the plot. *Scaphium longipetiolatum* was completely restricted to the south-eastern edge of the plot. These distributions were statistically analyzed using Iwao's (1972) m^*/m index. All the species showed aggregated distributions which were significantly different from the Poisson model of Random distribution (F -test, $p < 0.01$). Larger clump sizes than ca. 4000 m^2 were found in each species.

Scaphium species was segregated along an elevational gradient. Figure 3 shows the relative frequency of *Scaphium* trees along the elevation in the plot. The elevation ranged between 101 m and 269 m a.s.l.

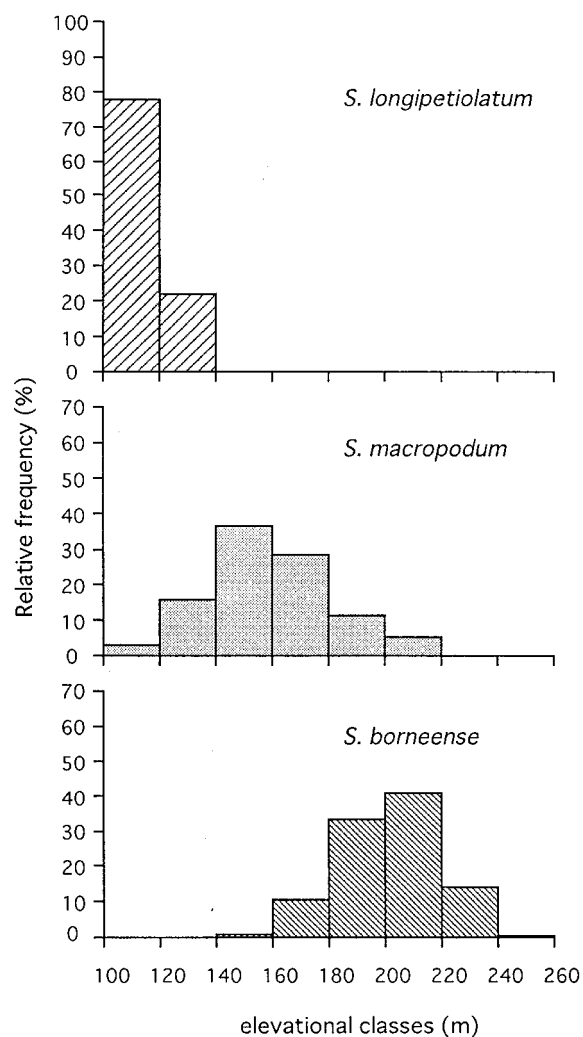


Figure 3. Relative frequencies of *Scaphium* species along the gradient of elevation in the plot.

Scaphium borneense occurred in higher sites in the plot and the mean elevation was 201 m. On the contrary, *S. longipetiolatum* occurred in the lower sites and the mean elevation was 118 m. The distributions of the two species did not overlap each other at all. *Scaphium macropodum* occurred over a wider elevational range. It overlapped with the other two species; its mean elevation was 159 m. The difference in these mean values was significant (ANOVA $p < 0.001$), and significant differences were found in all pairs of species (Tukey's HSD test for pairwise comparisons, $p < 0.001$). Soil textural maps have been prepared by P. Palmiotto (unpublished). Soil texture and elevation were highly correlated ($p < 0.001$). Correlation of soil textural classes by 20 m \times 20 m subquadrats in-

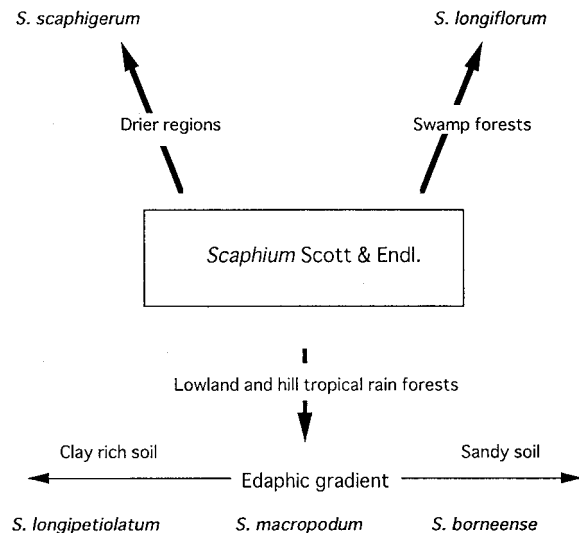


Figure 4. Schematic diagrams of the habitat niche differentiation of the *Scaphium* species.

indicates that *S. borneense* is distributed at the sandiest end of the plot, while *S. longipetiolatum* are on soils with the highest clay content. *Scaphium macropodum* are on soils of intermediate texture.

Discussion

Our results clearly show the existence of habitat segregation within the closely related, monophyletic genus *Scaphium*. This is summarized in Figure 4. *Scaphium* species occupied divergent habitats at geographical as well as at local spatial scales. All six species co-occurred in the Indo-Malaysian Subkingdom, though each species had its own biogeographical range (Figure 1). Out of the six species, *S. scaphigerum* and *S. longiflorum* are species adapted to a drier climate and swamp forests, respectively, while the others occurred in rain forests on undulating lands. Consequently, *S. scaphigerum* and *S. longiflorum* avoid direct competition with any other congeners.

Of the four *Scaphium* species distributed in tropical rain forests on undulating land, we analyzed the habitat segregation of three species, *S. borneense*, *S. longipetiolatum*, and *S. macropodum* in the 52-ha plot. Frequency distributions of Dbh followed the L-shaped distribution in all cases, suggesting that they all belong to the guild of non-pioneer species (Swaine and Whitmore 1988), and had near-equilibrium population structures. We cannot therefore explain the apparent coexistence of these species by the differentiation of

regeneration niche in relation to light environments and successional stages. The observed maximum Dbh of *S. borneense*, which was the most abundant species of the three *Scaphium* species in the plot, was the smallest among the three. However, we can not determine whether the several centimeters difference in Dbh around 50 cm is enough for niche divergence at maturity in relation to forest stratification, as has been suggested by many scientists (Richards 1952; Rogstad 1990; Kohyama 1993); but it appears unlikely.

The *Scaphium* species clearly had an allopatric pattern of distribution along the elevational gradient in the plot (Figure 3). The larger clump sizes than ca. 4000 m² found in all species may reflect the suitable habitats in relation to elevation. We can thus conclude that the *Scaphium* species segregate habitat along the elevational gradient in the forest in Lambir Hills National Park. Their habitat ranges overlap and they may compete, but the center of the range of each species is distinct. However, the influence of elevation on tree distribution is unlikely to be direct. The elevational difference was less than 150 m. Ashton (1988b) recorded that the *Scaphium* species are distributed over wide elevational ranges below ca. 900 m in elevation in the Lambir area. Elevation within the 52-ha plot is correlated with other topographic variables such as slope direction, slope inclination, and relief which are usually combined with other factors such as soil condition, solar radiation, and others (Yamakura et al. 1995). The sites lower and higher than ca. 160 m in elevation are mainly covered by clay-rich and sandy soils, respectively. It is very likely that the differences in edaphic conditions may be responsible for the elevational segregation of the three *Scaphium* species. An 8 ha plot has been set on a ridge and slope only 1 km south-east of the 52-ha plot. This plot is covered by a clay-rich soil and contains only *S. longipetiolatum* (Ohkubo, unpublished data). We can thus conclude that the habitat segregation related to edaphic condition play a vital role in the coexistence of the three species.

Nevertheless, there is much habitat in the plot unoccupied by either species, yet apparently suitable for one or other of them. This seems to be due to restrictions imposed by periodic local bottlenecks in regeneration as proposed by lottery models (Chesson and Warner 1981). We therefore recognize this as potential evidence of a stochastic non-equilibrium factor in their distribution. Furthermore, it is unknown whether *S. linearicarpum* has allopatric patterns of distribution with other *Scaphium* species. We can not

therefore yet completely deny the importance of non-equilibrium force for the coexistence of the *Scaphium* species.

The distributional range of *S. macropodum* overlapped with those of other two species in terms of elevation (Figure 3), while there is no actual overlap on distribution map (Figure 2). This suggests that there are factors which lead to the actual allopatric pattern of distribution other than elevation. The pattern as well as cause underlying the spatial pattern need to be examined further.

The results contribute a further example of habitat niche divergence associated with coexistence of sympatric species. However, this study once again dwells on only one genus among the many comprising tropical rain forests. Integration of knowledge concerning niche divergence in many other genera is needed for comprehensive understanding of its significance for coexistence and for the maintenance of species diversity in tropical rain forests. Nevertheless surprisingly few have so far been made (Rogstad 1990; M. Ashton et al. 1995; Itoh 1995b). Now that plots large enough for demographic analysis of the majority of species they contain are available, we hope that many more studies on how closely related species coexist will emerge.

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