



## Research Article

**Cite this article:** Yamada T, Oshige C, Nakabayashi M, Okuda T, Zaw Moe A, and Hlaing EE (2023). Spatial association of bamboos with trees in a commercial tree plantation forest in Myanmar. *Journal of Tropical Ecology*. 39(e31), 1–9. doi: <https://doi.org/10.1017/S0266467423000172>

Received: 5 January 2023

Revised: 10 April 2023

Accepted: 15 April 2023

**Keywords:**

*Bambusa polymorpha*; *Cephalostachyum pergracile*; *Dinochloa maclellandii*; habitat preference; point process analysis; spatial association; spatial relationship; topography

**Corresponding author:**

Toshihiro Yamada;

Email: [yamada07@hiroshima-u.ac.jp](mailto:yamada07@hiroshima-u.ac.jp)

Toshihiro Yamada<sup>1</sup>, Chihro Oshige<sup>2</sup>, Miyabi Nakabayashi<sup>1</sup>, Toshinori Okuda<sup>1</sup>, Aung Zaw Moe<sup>3</sup> and Ei Ei Hlaing<sup>3</sup>

<sup>1</sup>Graduate School of Integrated Sciences for Life, Hiroshima University, Higashi-Hiroshima, Japan; <sup>2</sup>Graduate School of Integrated Arts and Sciences, Hiroshima University, Higashi-Hiroshima, Japan and <sup>3</sup>Forest Department, Myanmar Forest Research Institute, Yezin, Nay Pyi Taw, Myanmar

**Abstract**

Bamboos are mainly distributed in subtropical to tropical areas. Bamboos provide numerous ecosystem services, while the expansion of bamboo gives negative impacts on forest ecosystems. Despite big impacts of bamboos on a forest ecosystem, ecological characteristics of bamboo remain poorly understood. The spatial distributional patterns of three bamboo species, *Cephalostachyum pergracile*, *Bambusa polymorpha*, and *Dinochloa maclellandii*, were studied in a commercial tree plantation of native deciduous tree species in the Bago Mountains, Myanmar. A point process analysis revealed a clumped distribution for each bamboo species. The distributional overlapping of the species was analysed for every pair of two species. The distribution of *C. pergracile* was little overlapped with those of *D. maclellandii* and *B. polymorpha*. *Cephalostachyum pergracile* was significantly more abundant on gently sloping ridges, whereas *D. maclellandii* was more abundant on a steeply sloping site. *Bambusa polymorpha* did not show these patterns with topography. The exclusive distribution of *C. pergracile* and *D. maclellandii* may be, at least partly, explained by the opposite topographic preferences of the species. *Cephalostachyum pergracile* tended to be found far from large trees that cast shade, although *B. polymorpha* tended to be found with large trees, suggesting that *B. polymorpha* may be more shade tolerant than *C. pergracile*. The difference in shade tolerance may contribute to the exclusive distribution of the species. The habitat preference information obtained in this study will contribute to sound bamboo management practices in Myanmar and enable bamboo population sizes to be increased through creation of favourable habitats in forests.

**Introduction**

Bamboos comprise a diverse group of approximately 1250 species and 75 genera (Scurlock *et al.* 2000, Yuen *et al.* 2017). Bamboos are distributed over approximately 31.5 million ha worldwide (FAO, 2010) and about 80% are indigenous to the Asia–Pacific region, mainly in subtropical to tropical areas (Lobovikov *et al.* 2012). Bamboos provide numerous ecosystem services, such as prevention of landslides and soil erosion, improvement of soil fertility, water conservation, carbon sequestration, and the provision of food and construction materials (Ben-zhi *et al.* 2005, Lobovikov *et al.* 2012, Scurlock *et al.* 2000, Yuen *et al.* 2017), although the expansion of bamboo gives negative impacts on forest trees, such as the erosion of tree biodiversity and the delay of tree regeneration (Larperkern *et al.* 2011). Despite the significant roles played by bamboos in a forest ecosystem, certain ecological characteristics of bamboo species, such as regeneration processes, flowering ecology, and habitat preference, remain poorly understood.

Bamboos are important components of forests in Myanmar. The area of forest occupied by bamboos is 27.85 million ha, representing 84% of the total forested area of 33.32 million ha in Myanmar (FAO, 2015). Bamboos are important resources for human communities in Myanmar, who utilise bamboos for housing materials, materials for daily necessities such as hats, mats and baskets, and food (ITTO, 2007, Rao *et al.* 1998). In addition to domestic consumption, bamboo products are sold at markets as an additional source of income.

The size of bamboo populations in Myanmar forests is mainly influenced by two anthropogenic factors. The first factor is disturbance caused by human activities. Bamboos dominate at early to intermediate stages of succession in forest (Lessard and Chouinard, 1980, Rao and Ramakrishnan, 1987). Therefore, if an old-growth forest is disturbed by human activities and is transformed into an early successional forest, bamboo populations will expand (Franklin *et al.* 2010, Gagnon and Platt, 2008, Gagnon *et al.* 2007, Guilherme *et al.* 2004, Söderström and Calderon, 1979, Zaczek *et al.* 2010). The second factor is excessive exploitation of bamboos by local residents, causing a reduction in bamboo population size. These two factors usually coincide in Myanmar forests, including at the present study site at Ottarathiri Township,

Naypyidaw Union Territory, Myanmar. Thus, fluctuation in bamboo population size is determined by the balance between these factors.

Changes in bamboo population size may have serious consequences for the forest environment and livelihood of local inhabitants. For example, bamboo expansion may negatively affect forest trees. It may result in lower tree-species diversity in a forest (Larpkern *et al.* 2011) and may delay forest regeneration after a disturbance event by suppressing seed germination and survival of tree seedlings (Budke *et al.* 2010, Griscom and Ashton, 2003, Larpkern *et al.* 2011, Montti *et al.* 2011, Nakashizuka, 1988). However, it may enable improved accessibility to bamboo resources for the local community. Conversely, decrease in the bamboo population size may negatively impact the livelihoods of local residents by limiting the availability of bamboo resources. Therefore, sustainable management of bamboo populations is of paramount importance in rural areas of Myanmar. For implementation of appropriate and sustainable management practices, ecological information on the habitat preferences of bamboos is vital because it will enable the creation of suitable sites in forests to enhance bamboo populations.

In forests, the spatial distribution of trees and bamboos is influenced by biotic and abiotic factors. When considering biotic factors, the spatial relationship of a tree species with other tree species often affects the spatial distribution of trees in a forest (Masaki *et al.* 1992, Yamada and Suzuki, 1997). For example, shade-intolerant short-stature trees are usually clumped in canopy gaps and avoid large trees because they cannot survive in dense shade. Consequently, such species may not distribute with large trees. In Myanmar forests, bamboos are sub-canopy or understorey species and are fast-growing, early successional species (Gadgil and Prasad, 1984, Lessard and Chouinard, 1980, Rao and Ramakrishnan, 1987, Söderström and Calderon, 1979). Hence, we hypothesise that bamboos are spatially separated from large trees to avoid the direct shade that is created by the large trees.

Abiotic factors are also important determinants of the spatial structure of forests. The soil water and nutrient availabilities are distributed heterogeneously in a forest and are strongly associated with topography (Famiglietti *et al.* 1998). For example, ridge sites tend to be drier and more nutrient deficient than valley sites (Hirai *et al.* 1997, Ishizuka *et al.* 1998, Palmiotto, 1998, Tan *et al.* 2009, Tateno and Takeda, 2003, Yamada *et al.* 2006). Tree species often require a specific combination of resources, resulting in an association of trees with topography (Bazzaz, 1991, Sork *et al.* 1993, Whitmore, 1990). Habitat associations of trees in relation to topography have been repeatedly observed among tropical tree species (Davies *et al.* 1998, Debski *et al.* 2002, Harms *et al.* 2001, Hubbell and Foster, 1986, Marod *et al.* 2019, Marod *et al.* 2021, Sri-Ngernyuang *et al.* 2003, Svenning, 1999, Webb and Peart, 2000, Yamada *et al.* 2000, Yamada *et al.* 2010, Yamada *et al.* 2007, Yamada *et al.* 2006). Therefore, the distribution of bamboo may be highly influenced by topography (Hayashi and Yamada, 2008). However, no previous study has verified this influence in Myanmar and limited information is available on the relationship between bamboos distribution and topography (Tanaka *et al.* 2010).

The present study was conducted in a commercial tree plantation forest established in a mixed deciduous forest in Ottarathiri Township, Naypyitaw Union Territory, Myanmar. In total, three bamboo species (*Cephalostachyum pergracile* Munro, *Bambusa polymorpha* Munro, and *Dinochloa maccllellandii* (Munro) Kurz.) were present. We examined the spatial distribution of the three bamboo species with specific reference to the

distribution of large trees and topography. First, we assessed whether the bamboo species were not distributed with large trees. Next, we examined the relationship between the distribution of these bamboos and topography. If a bamboo species showed a preference for a specific topographic condition, the following two premises should be met: (1) bamboos are heterogeneously distributed in accordance with the heterogeneous distribution of topographic conditions in a forest and (2) bamboos are more concentrated at a site with a specific topographic condition. We therefore explored whether these premises were met for the three bamboo species. In addition, assuming that bamboo species prefer a site with specific topographic conditions, we assessed the suitable topography for each species. However, adopting this approach, we aimed to obtain information on the topographic site where a bamboo species appears more than the other topographic site (i.e., habitat requirements of the bamboo species) to enhance the management of bamboo populations in Myanmar forests.

## Method

### Study site

The study was conducted in a commercial tree plantation forest established in a mixed deciduous forest in the Bago Mountains, Ottarathiri Township, Naypyitaw Union Territory, Myanmar (ca. 200 m a.s.l.), in 2016. The study site is located in a tropical monsoon climatic zone with a distinct rainy season (from mid-May to mid-October) and a dry season (from mid-February to April). The average annual temperature is 24.5°C and average annual precipitation is 1421.1 mm with 97% falling in the rainy season (Moe Swe Forest Research Center, unpublished data; the average monthly temperature and precipitation are shown in Figure S1). The natural vegetation at the study site was dominated by broad-leaved deciduous trees, such as *Tectona grandis* L.f., *Pterocarpus macrocarpus* Kurz., *Markhamia stipulata* (Wall.) Seem., and *Xylia xylocarpa* (Roxb.) W.Theob. Three bamboo species, *C. pergracile*, *B. polymorpha*, and *D. maccllellandii*, were present in the forest. *Tectona grandis* can attain a diameter at breast height (DBH) of 60 cm in old-growth forests in the study site. The forest canopy height of old-growth forest was about 25 m. The forest canopy was not closed because some canopy trees had been cut by local residents. The local community obtains forest products from the forest for daily use, and scars from the logging of trees and cutting of bamboos were observed.

We established an 80 m × 110 m (0.88 ha) plot, which was divided into 88 quadrats, each 10 m × 10 m, within a commercial tree plantation (*T. grandis*, *X. xylocarpa*, *P. macrocarpus*, and *Millettia tetraptera* Kurz.) established in 1978 by the Myanmar Government. Planting intervals between trees were about 2.5 m. Prior to the establishment of the plantation, the site was cut and burned. Weeding was conducted several times until 2 years after the establishment of the plantation. Bamboos might have been able to survive these treatments because they are tolerant of fire and other disturbances (Kachina *et al.* 2017, Tanaka *et al.* 2010). No tree-planting activities have been conducted subsequently; therefore, all commercial trees were planted in 1978. In this forest, naturally regenerating trees, which emerged after the plantation establishment, were observed. Thus, all trees growing in the plot originated during or after the establishment of the plantation. The height of the forest was approximately 25 m. The largest tree had attained DBH of approximately 50 cm. The forest floor was burnt annually by local residents in the dry season to manage forest

understorey. Forest fire may delay forest tree regeneration while enhancing the production of bamboo shoots to eat and the growth of some useful understorey grasses for thatch.

A topographic survey of the plot was conducted to generate an elevational contour map. The height difference between the highest and lowest points in the plot was 15 m. By using the slope angle of quadrats, we classified the 88 quadrats classified as either steep slope (slope angle  $>20^\circ$ ) or gentle slope (including gentle ridge, slope angle  $\leq 20^\circ$ ). The plot did not include any valley bottoms. We identified 9 steep slope quadrats and 79 gentle slope quadrats (Figure S2).

### Study species

The three bamboo species studied were deciduous that shed leaves in dry seasons. McClure (1993) distinguished two distinct rhizome patterns among bamboo species, namely leptomorphic and pachymorphic rhizomes. A leptomorphic rhizome (a horizontally spreading rhizome) bears solitary culms that are evenly spaced between culms, resulting in a large clonal colony with scattered culms. Temperate bamboo species, such as *Phyllostachys heterocyclus* (Carrière) Mitford, *P. bambusoides* Siebold et Zucc., and *P. nigra* (Lodd. et Lindl.) Munro var. *henonis* (Mitford) Stapf ex Rendle, often develop leptomorphic rhizomes. In contrast, pachymorphic rhizomes lack leptomorphic rhizomes and show limited horizontal spread, resulting in dense aggregated clumps of culms (Figures S3a and S4). Many tropical bamboo species exhibit the latter rhizome pattern, including the three bamboo species in the present study. As a result, we could separate each clump spatially from another as an apparent genet.

At the study site, the tallest bamboo species, *C. pergracile*, seldom attained a height of 16 m (Figure S5). Culm diameters were always less than 7 cm. *Bambusa polymorpha* was the second-tallest species and was always shorter than 15 m in height (Figure S5). The maximum attainable culm diameter was 10 cm. *Dinochloa maclellandii* was the shortest bamboo species and never grew taller than 9 m (Figure S5). Culm diameters were always less than 7 cm. The sizes of bamboos in the study plot were identical to those found in old-growth forests around the study plot.

The bamboo species are monocarpic and sexually reproduce only once in their life and die soon after sexual reproduction. Some conspecific clumps in a local area often bloom simultaneously (Janzen, 1976, Makita *et al.* 1993, Söderström and Calderon, 1979, Zheng *et al.* 2020), resulting in sporadic to mass flowering in the region (Janzen, 1976, Kharlyngdoh *et al.* 2021, Marod D *et al.* 1999, Takeda, 2019). The flowering interval of *B. polymorpha* is 60 years, whereas those of *C. pergracile* and *D. maclellandii* are still unknown (Zheng *et al.* 2020). The most recent flowering event for *C. pergracile* occurred in 1997 at the study site (Nyan Htun, Forest Research Institute Myanmar, personal communication). There is no record of the most recent sporadic flowering event for *B. polymorpha* and *D. maclellandii*, although it is known that *B. polymorpha* has not flowered after 1997 (Nyan Htun, Forest Research Institute Myanmar, personal communication).

*Cephalostachyum pergracile* is utilised by the local community for housing materials and materials for daily necessities, such as baskets and hats. *Bambusa polymorpha* shoots are edible and consumed for food, whereas *D. maclellandii* is not utilised for any purpose (ITTO, 2007, Kharlyngdoh *et al.* 2021, Rao *et al.* 1998).

### Field methods

We measured the heights of 27 trees, 20 *C. pergracile*, 10 *B. polymorpha*, and 10 *D. maclellandii* individuals to examine the allometric relationship between DBH and height (Figure S5). These samples ranged from the smallest to the largest individuals.

Typically, a bamboo seedling develops only a few, annual culms less than 2 cm in diameter in a clump. Subsequently, it eventually produces perennial culms more than 2 cm in diameter. We mapped bamboo clumps with a perennial culm greater than 2 cm in diameter and identified their species. The number of culms in a clump was also counted. We measured the perimeter of a polygon formed by culms in a clump at breast height (Figure S3b). By approximating the polygon to a circle with the same circumference, the perimeter of the polygon was converted into the diameter of the circle. We termed this diameter the 'clump diameter'.

Immature *Bambusa tulda* Roxb. plants in Thailand show little growth under suppression by other bamboos or trees but promptly produce rapid growth after removal of the suppression (Tanaka *et al.* 2010). Because we were interested in the suitable conditions for growth and regeneration of bamboos, we focused only on the distribution of large (mature) clumps. Therefore, we used only large bamboo clumps for analysis of spatial distributions. We assumed that clumps larger than 50 cm in clump diameter were large and mature for *C. pergracile* and *B. polymorpha*, and those clumps larger than 20 cm in diameter for *D. maclellandii* (Figure S6). These clumps usually had a culm that attained the maximum attainable height of the species.

In this study, trees were classified into two size classes, large and small, in relation to bamboo heights in the plot. Because the tallest bamboo in the plot was approximately 16 m (Figure S5), trees taller than 16 m were categorised as 'large'. In the forest, bamboos were never taller than the large trees. The other trees were categorised as 'small'. According to the relationship between DBH and height for trees (Figure S7), the 16 m height of trees approximately coincided with 20 cm DBH. Therefore, trees larger than 20 cm DBH were classified as 'large'. Within the plot, we mapped large trees (DBH  $> 20$  cm) and identified them to species.

### Spatial patterns and spatial relationship between bamboos

The spatial patterns of the bamboo species were analysed using Besag's  $L(t)$  function (Besag, 1977) and a square-root transformation of Ripley's  $K(t)$  function (Ripley, 1977). A value of  $L(t) = 0$  indicates that the spatial distribution of a given bamboo species is random. A value of  $L(t) > 0$  indicates a clumped (aggregated) distribution, and a value of  $L(t) < 0$  indicates a uniform distribution.

The spatial relationship between pairs of bamboo species was analysed using  $L_{12}(t)$ , a square-root transformation of the  $K_{12}(t)$  function (Lotwick and Silverman, 1982), which is a modification of Ripley's  $K(t)$  for bivariate data (Fortin and Dale, 2005). A value of  $L_{12}(t) = 0$  indicates that the spatial distributions of the two bamboo species are spatially independent of each other. A value of  $L_{12}(t) > 0$  indicates that the spatial distributions of the two bamboo species are attraction between them (a species tends to distribute with the counterpart species). Hereafter, this is referred to as a positive association between them. Lastly, a value of  $L_{12}(t) < 0$  indicates that the spatial distributions of the two bamboo species are repulsion between them (each species tends to exclusively distribute from the counterpart species). Hereafter, this is referred to as a negative association. The significance of both  $L(t)$  and  $L_{12}(t)$



was determined by Monte Carlo simulations (Besag, 1977, Besag and Diggle, 1977, Marriott, 1979, Yamasaki *et al.* 2013). For analysis of the spatial pattern of bamboos ( $L(t)$ ), the null hypothesis is complete spatial randomness, whereas the null hypothesis for the spatial relationship between two tree species ( $L_{12}(t)$ ) is spatial independence of their distributions. The 95% confidence envelopes for  $L(t)$  were obtained from 5000 permutations of random points of the same number of bamboos analysed, and those for  $L_{12}(t)$  were obtained by 5000 permutations of torus-translation shifts of the spatial distribution of one bamboo species (Diggle, 1983, Yamada *et al.* 2006, Yamasaki *et al.* 2013).

In addition, we analysed the spatial relationship between bamboos and large trees or stumps. We examined the spatial relationship of bamboos with large trees because large trees may cast shade on bamboos, making the site unfavourable for bamboo growth. Furthermore, bamboos are expected to be distributed exclusively from large trees. Similarly, bamboos may have a positive spatial relationship with stumps, because bamboo growth is likely to be enhanced by the removal of large trees.

### Association of bamboos with topography

The distributional association of bamboos with topography was analysed using Fisher's exact test for count data. This test revealed only whether a bamboo species is distributed significantly more abundantly on steep or gentle slopes. To determine if bamboos were distributed more abundantly on steep or gentle slopes, we calculated the adjusted density of each bamboo species for steep and gentle slopes by dividing the density of the bamboo species in the focal topography by the average density of the bamboo species across the entire plot (Yamada *et al.* 2007, Yamada *et al.* 2006). Adjusted density values  $>1$  suggest more abundantly than the average across the plot (a positive association between the species and topography), whereas values  $<1$  suggest that the species less abundantly than the average across the plot (a negative association between the species and topography).

### Results

The density of trees larger than 20 cm DBH was 111 trees  $\text{ha}^{-1}$ , and the total basal area was 8.79  $\text{m}^2 \text{ha}^{-1}$  in the plot (Table S1). Approximately, 62.5% of the trees in the plot were planted trees of *T. grandis*, *X. xylocarpa*, *P. macrocarpus*, and *M. tetraptera*. We recorded 150 tree stumps of more than 20 cm in diameter in the plot, and 90% of these stumps were of the commercially planted tree species. In total, 489, 76, and 62 clumps of *C. pergracile*, *B. polymorpha*, and *D. maclellandii*, respectively, were recorded in the plot (Table S2). Among these clumps, 219, 62, and 49 clumps were categorised as 'large' for *C. pergracile*, *B. polymorpha*, and *D. maclellandii*, respectively. The number of culms per clump increased with clump diameter for all species (Figure S8).

The positions of *C. pergracile*, *B. polymorpha*, and *D. maclellandii* clumps in the plot are shown in Figure 1a–c. The  $L(t)$  values for all bamboo species were above the 95% confidence envelopes (Fig. 2a–c), indicating that each of the bamboo species showed a clumped distribution of clumps, which was significantly different from a random distribution.

The pair of *C. pergracile* and *D. maclellandii*, and that of *C. pergracile* and *B. polymorpha*, showed a significant negative spatial association. Hence, the species were exclusively distributed separately from each other in the plot (Figure 3). However, the pair

of *B. polymorpha* and *D. maclellandii* showed a statistically non-significant spatial relationship with each other.

*Cephalostachyum pergracile* and *D. maclellandii* were distributed significantly more abundantly on either gentle slopes or steep slopes (Table 1). However, the nature of the associations was opposite for these two species. *Cephalostachyum pergracile* was more abundant on gentle slopes. In contrast, *D. maclellandii* was most abundant on steep slopes and less common on gentle slopes. The adjusted density of *D. maclellandii* on steep slopes was more than 10 times higher than that on gentle slopes (Table 1), suggesting that this species was strongly associated with steep slopes. *Bambusa polymorpha* was not distributed significantly more abundantly on neither gentle slopes nor steep slopes. However, the adjusted density of *B. polymorpha* on gentle slopes was higher than that on steep slopes (Table 1).

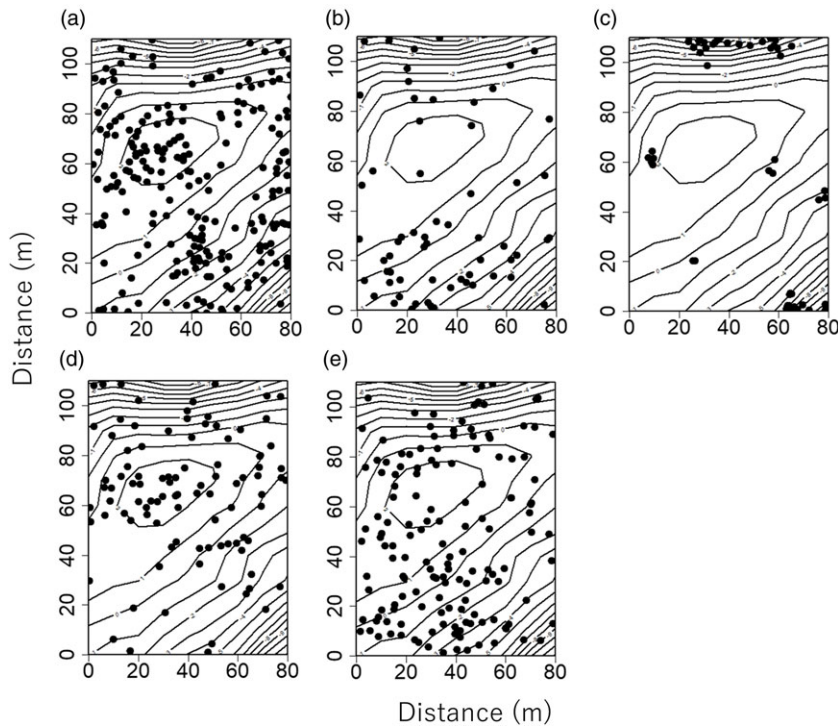
Large trees and stumps were not distributed significantly more abundantly on neither gentle slopes nor steep slopes (Table 1). Analysis of the spatial relationship between bamboos and large trees yielded the following results (Figure 4). *Bambusa polymorpha* showed a significant negative relationship with large trees, whereas the other two bamboo species did not show such a relationship. *Dinochloa maclellandii* showed a statistically non-significant spatial relationship with large trees, and *C. pergracile* had a significant positive spatial relationship with large trees.

*Bambusa polymorpha* showed a significant positive spatial relationship with stumps (Figure 4), implying that *B. polymorpha* growth might have been enhanced by the removal of large trees. However, the other two bamboo species differed in their spatial relationship with stumps. A statistically non-significant spatial relationship between *C. pergracile* and stumps was observed. *Dinochloa maclellandii* showed a significant negative spatial relationship with stumps, suggesting that the distribution of this bamboo species did not coincide with stumps.

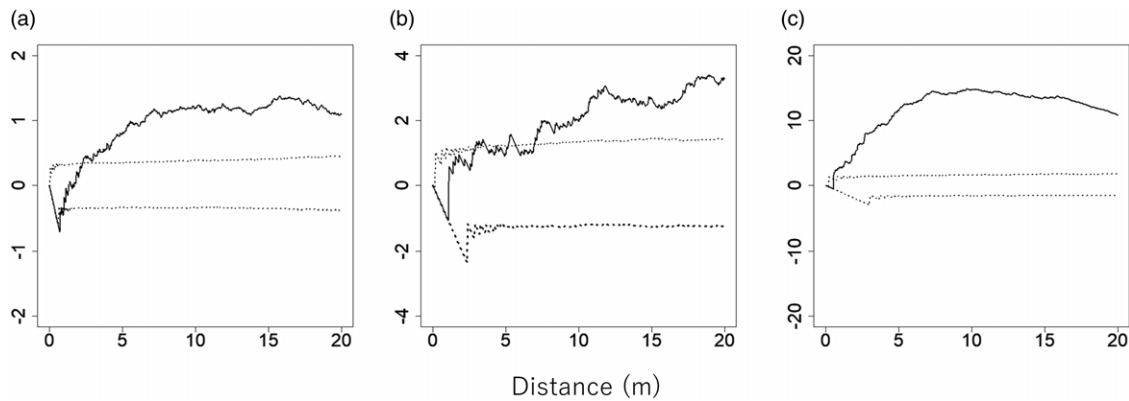
### Discussion

If bamboo distribution is associated with topography, the following two premises should be met: (1) bamboos are heterogeneously distributed in a forest in accordance with the heterogeneous distribution of topographic conditions and (2) bamboos are more abundant at a site with a specific topographic condition. In the present study, we examined whether these two premises were supported by the experimental data. The spatial analyses revealed a clumped distribution, which was significantly different from a random distribution for all three bamboo species examined. This suggests that all bamboo species heterogeneously distribute in a forest because they appeared more in one site while distributed less in the other sites. Therefore, the first premise was confirmed to be met for each species.

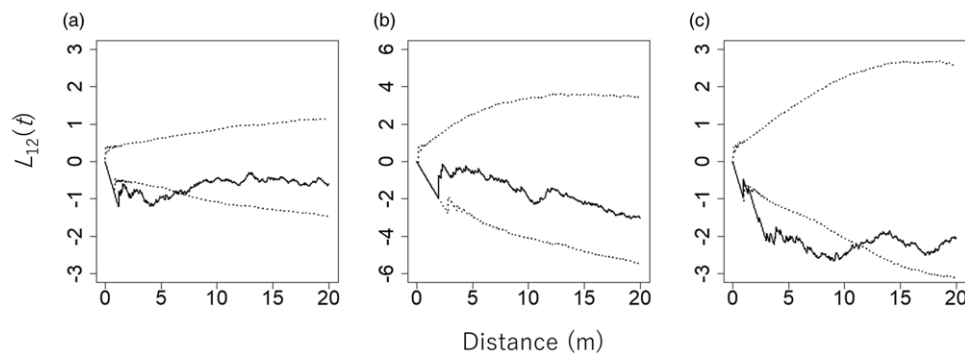
The second premise was met only for *C. pergracile* and *D. maclellandii*. The distribution of *C. pergracile* tended to be found more abundantly on gentle slopes (including gentle ridges) than on steep slopes. This spatial association pattern of *C. pergracile* is consistent with the findings of Tanaka *et al.* (2010), who reported that this species was distributed most frequently on a gentle ridge in a Thailand forest. Thus, the topographic habitat of *C. pergracile* should include gentle slopes and ridges. In contrast, *D. maclellandii* was strongly associated with steep slopes that *C. pergracile* avoided. Hence, steep slopes should be the topographic habitat for *D. maclellandii*. *Bambusa polymorpha* was evenly distributed irrespective of topography and thus may not exhibit a habitat preference in terms of topography.



**Figure 1.** Spatial distribution of *Cephalostachyum pergracile* (a;  $n = 219$ ), *Bambusa polymorpha* (b;  $n = 62$ ), and *Dinochloa maclellandii* (c;  $n = 49$ ) in an  $80 \times 110$  m plot in a commercial tree plantation forest on the Bago Mountains, Ottarathiri Township, Naypyitaw Union Territory, Myanmar. The contour interval is 1 m in elevation. Spatial distributions of large trees (DBH > 20 cm) (d) and stumps (e) are also shown.



**Figure 2.**  $L(t)$  values for *Cephalostachyum pergracile* (a;  $n = 219$ ), *Bambusa polymorpha* (b;  $n = 62$ ), and *Dinochloa maclellandii* (c;  $n = 49$ ) in an  $80 \times 110$  m plot in a commercial tree plantation forest on the Bago Mountains, Ottarathiri Township, Naypyitaw Union Territory, Myanmar (solid lines). A value of  $L(t) = 0$ ,  $L(t) > 0$ , and  $L(t) < 0$  indicates a random, clumped, and uniform distribution, respectively. The 95% confidence envelopes for  $L(t)$ , which were obtained by 5000 permutations of random points of the same number of bamboos, are indicated by dotted lines.



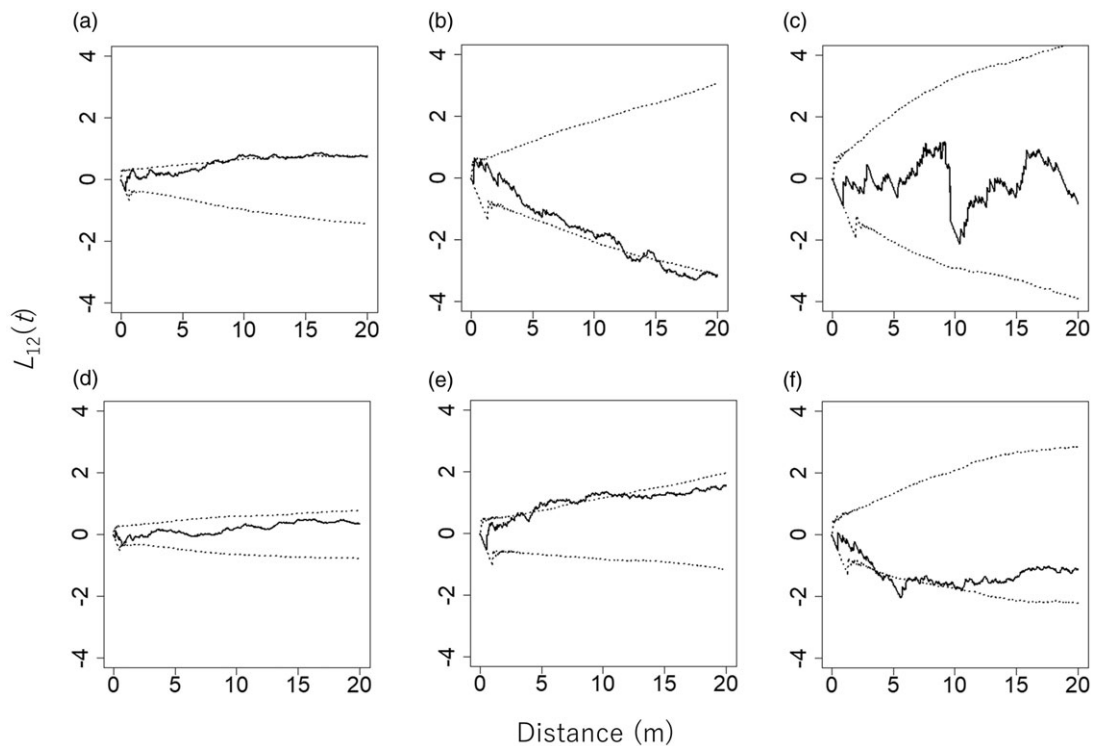
**Figure 3.**  $L_{12}(t)$  values between pairs of bamboo species in an  $80 \times 110$  m plot in a commercial tree plantation forest on the Bago Mountains, Ottarathiri Township, Naypyitaw Union Territory, Myanmar (solid lines). The pairs *Cephalostachyum pergracile* ( $n = 219$ ) and *Bambusa polymorpha* ( $n = 62$ ) (a), *B. polymorpha* and *Dinochloa maclellandii* ( $n = 49$ ) (b), and *D. maclellandii* and *C. pergracile* (c) are shown. A value of  $L_{12}(t) = 0$ ,  $L_{12}(t) > 0$ , and  $L_{12}(t) < 0$  indicates that the spatial distributions of the two bamboo species are spatially independent, positively associated (attraction), and negatively associated (repulsion), respectively. The 95% confidence envelopes for  $L_{12}(t)$ , which were obtained by 5000 permutations of torus-translation shifts of the spatial distribution of one bamboo species, are indicated by dotted lines.

**Table 1.** Association of three bamboo species, large trees and stumps with topography in an 80 m × 110 m plot in a commercial tree plantation forest on the Bago Mountains, Ottarathiri Township, Naypyitaw Union Territory, Myanmar.

Species	Gentle slope ( <i>n</i> = 77)		Steep slope ( <i>n</i> = 11)		Total no. of clumps or trees
	No. of clumps	Adjusted density <sup>†</sup>	No. of clumps	Adjusted density <sup>†</sup>	
<i>Cephalostachyum pergracile</i> *	211	1.07	8	0.36	219
<i>Bambusa polymorpha</i>	56	1.03	6	0.77	62
<i>Dinochloa maclellandii</i> ***	14	0.33	35	5.71	49
Large trees	89	1.03	7	0.71	96
Stumps	140	1.04	10	0.65	150

<sup>†</sup>Values of adjusted density >1.0 and <1.0 indicate that a species shows a positive and negative association with topography, respectively.

Asterisks indicate the significance level from the analysis of the association of bamboo species and topography (count data, Fisher's exact test; \**P* < 0.05, \*\*\**P* < 0.001).



**Figure 4.**  $L_{12}(t)$  values between pairs of bamboo species and large trees (DBH > 20 cm, *n* = 96) in an 80 m × 110 m plot in a commercial tree plantation forest on the Bago Mountains, Ottarathiri Township, Naypyitaw Union Territory, Myanmar (solid lines). The pairs *Cephalostachyum pergracile* and large trees (a), *Bambusa polymorpha* and large trees (b), and *Dinochloa maclellandii* and large trees (c) are shown.  $L_{12}(t)$  values between pairs of bamboo species and stumps (DBH > 20 cm, *n* = 150) are also shown (solid lines). All stumps were the result of logging after establishment of the plantation in 1978. Shown are the pairs *Cephalostachyum pergracile* and stumps (d), *Bambusa polymorpha* and stumps (e), and *Dinochloa maclellandii* and stumps (f). The 95% confidence envelopes are indicated by dotted lines.

The influence of topography on bamboo distribution is unlikely to be direct. The topography within the plot may be correlated with edaphic variables, such as soil nutrient and soil water availabilities (Hirai *et al.* 1997, Ishizuka *et al.* 1998, Palmiotto, 1998, Tateno and Takeda, 2003, Yamada *et al.* 2006). A finer-resolution classification of habitats incorporating such edaphic characteristics in future analyses is highly likely to provide an improved understanding of the habitat association of bamboos.

*Cephalostachyum pergracile* showed an exclusive spatial relationship with *D. maclellandii*. This exclusive distribution may be, at least partly, explained by the opposite topographic preferences of the species. However, topography cannot explain the exclusive distributions observed between *C. pergracile* and *B. polymorpha*.

The bamboo species we studied were sub-canopy to understorey, fast-growing, early successional species. On this basis, we hypothesised that the species would be spatially separated from large trees to avoid the direct shade cast by the trees. Similarly, we predicted that bamboos would show a positive spatial relationship with stumps because bamboo growth is likely to be enhanced by removal of large trees. The present spatial analyses supported these hypothesised spatial relationships only for *B. polymorpha*. These results suggest that *B. polymorpha* is the most shade intolerant among the three bamboo species examined and is less likely to form a large (mature) clump when growing under the canopy of large trees. Release from suppression by large trees may be necessary for the regeneration of *B. polymorpha*.

In contrast, *C. pergracile* showed a positive spatial relationship with large trees, suggesting that this species tended to be found near large trees. This finding implies that *C. pergracile* is more shade tolerant than the other two bamboo species. Differences in shade tolerance between *B. polymorpha* and *C. pergracile* may explain the exclusive distribution of the two species. At the present study site, *B. polymorpha* may dominate in well-lit areas and *C. pergracile* may dominate in more densely shaded areas, resulting in their exclusive distribution. However, this interpretation fails to explain why *C. pergracile* did not invade well-lit areas.

The exclusive distribution of *B. polymorpha* and *C. pergracile* may not be solely caused by the abovementioned differences in shade tolerance. An additional possibility may be the timing of flowering. Both species flower sporadically (Devi *et al.* 2014, Marod *et al.* 2005, McClure, 1993, Suyama *et al.* 2010) and some clumps flower simultaneously within a region. *Bambusa polymorpha* flowers at 60-year intervals (Zheng *et al.* 2020), but the flowering interval for *C. pergracile* is unknown. Both bamboo species are monocarpic and the culms die soon after flowering. The flowering years differ between the species; the most recent flowering event for *C. pergracile* at the study site was recorded in 1997 and *B. polymorpha* did not bloom at that time.

Assuming that seedlings of *B. polymorpha* and *C. pergracile* must avoid shade from conspecific and heterospecific bamboos to grow into large (mature) plants, they will be unable to establish in a space already occupied by either species at the time of flowering. In other words, provided that the culms of a bamboo species have already occupied a space in a forest at the time of flowering of the other bamboo species, seedlings of the flowering species cannot enter the occupied sites and can only establish in unoccupied spaces. Ultimately, seedlings may be able to regenerate only in canopy gaps left by chance or in well-lit areas following the death of flowering culms. If this is true, it should create an exclusive spatial relationship between the two species. In this manner, occupation of spaces by a species may limit the spaces available for regeneration of the other species. This hypothesis should be tested in a future study by examining the distribution of seedlings and the process of seedling establishment at the next flowering event.

The information on habitat preferences obtained by this study will contribute to suitable bamboo management practices in Myanmar. *Bambusa polymorpha*, a shade-intolerant bamboo species, may regenerate only in a site where it can intercept sufficient light. A brightly lit understory environment is crucial to enhance the growth and regeneration of this species. The shade-tolerant *C. pergracile* may be more dependent on topography than the light environment. The topographic habitats preferred by *C. pergracile* are gentle slopes or ridges, whereas *D. maclellandii* regenerates on steep slopes. By providing or managing such habitats, it will be feasible to enhance populations of these two bamboo species in Myanmar forests.

Bamboos cover a wide area of the world (FAO, 2010). Especially in Asian mixed deciduous tropical forests, bamboos are commonly found and are among the important components (Marod *et al.* 2005, Kharlyngdoh *et al.* 2021). The bamboo species studied were widely distributed in Asia (Marod *et al.* 2005, Kachina *et al.* 2017, Kharlyngdoh *et al.* 2021). For example, *C. pergracile* was commonly found not only in Myanmar forests but also in wide areas from India to Thailand (Marod *et al.* 2005, Kharlyngdoh *et al.* 2021). Local residents in those areas exploited bamboo resources like people in Myanmar (Kharlyngdoh *et al.* 2021). The importance of the

information on bamboos' habitat preferences revealed by this study on the forest management will not be limited to Myanmar forests, and the findings will contribute to the forest management in the other mixed deciduous forests with the bamboos that widely spread over a huge area.

Local residents in our study site used forest fire to manage forest understory. The fire may delay the regeneration of forest trees, especially fire-intolerant species. Because bamboos can survive forest fire (Kachina *et al.* 2017), bamboos may obtain competitive advantage over tree species from annual forest fires. Consequently, forest fire may increase the dominance level of bamboos in mixed deciduous forests. Not only in our study site but also a lot of other mixed deciduous forests in Asia were managed by fire (Kachina *et al.* 2017). Since forest fire may give a big impact on species composition of a forest, for a sound practice of the forest management by fire, more studies to elucidate the roles of fire in the regeneration of bamboos and tree species in mixed deciduous forests are clearly necessary.

**Supplementary material.** The supplementary material for this article can be found at <https://doi.org/10.1017/S0266467423000172>

**Acknowledgements.** We thank M. Miura, K. Ueda, T. Horikane, and M. Kobayashi for helping with fieldwork. We thank Robert McKenzie, PhD, from Edanz (<https://jp.edanz.com/ac>), for editing a draft of this manuscript.

**Financial support.** This study was financially supported by the Environmental Research and Technology Development Fund (#4-1404 and #1-1903) and by the Japan Society for the Promotion of Sciences (grant no. 20K06827 from 2020 to 2022).

**Competing interests.** The authors declare none.

## References

- Bazzaz FA (1991) Habitat selection in plants. *American Naturalist* **137**, 116–130.
- Ben-zhi Z, *et al.* (2005) Ecological functions of bamboo forest: research and application. *Journal of Forestry Research* **16**, 143–147.
- Besag J (1977) Contribution to the discussion on Dr Ripley's paper. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)* **39**, 193–195.
- Besag J and Diggle PJ (1977) Simple Monte Carlo tests for spatial pattern. *Applied Statistical Science* **26**, 327–333.
- Budke JC, Alberti MS, Zanardi C, Baratto C and Zanin EM (2010) Bamboo dieback and tree regeneration responses in a subtropical forest of South America. *Forest Ecology and Management* **260**, 1345–1349.
- Davies SJ, Palmiotto PA, Ashton PS, Lee HS and Lafrankie JV (1998) Comparative ecology of 11 sympatric species of *Macaranga* in Borneo: tree distribution in relation to horizontal and vertical resource heterogeneity. *Journal of Ecology* **86**, 662–673.
- Debski I, Burslem DFRP, Palmiotto PA, Lafrankie JV, Lee HS and Manokaran N (2002) Habitat preferences of *Aporosa* in two Malaysian forests: Implications for abundance and coexistence. *Ecology* **83**, 2005–2018.
- Devi KT, SHARMA H, Singh P and Bhattacharyya D (2014) Flowering of *Schizostachyum pergracile* (Munro) R. B. Majumdar in Manipur. *Indian Forester* **140**, 633–635.
- Diggle PJ (1983) *Statistical Analysis of Spatial Point Patterns*. London: Academic Press.
- Famiglietti JS, Rudnicki JW and Rodell M (1998) Variability in surface moisture content along a hillslope transect: Rattlesnake Hill, Texas. *Journal of Hydrology* **210**, 259–281.
- FAO (2010) *Global Forest Resources Assessment 2010*. Rome: FAO.
- FAO (2015) *Global Forest Resources Assessment 2015*. Rome: FAO.
- Fortin M-J and Dale MRT (2005) *Spatial Analysis. A Guide for Ecologists*. Cambridge: Cambridge University Press.



- Franklin DC, Prior LD, Hogarth NJ and McMahon CR (2010) Bamboo, fire and flood: consequences of disturbance for the vegetative growth of a clumping, clonal plant. *Plant Ecology* **208**, 319–332.
- Gadgil M and Prasad SN (1984) Ecological determinants of life-history evolution of 2 Indian bamboo species. *Biotropica* **16**, 161–172.
- Gagnon PR and Platt WJ (2008) Multiple disturbances accelerate clonal growth in a potentially monodominant bamboo. *Ecology* **89**, 612–618.
- Gagnon PR, Platt WJ and Moser EB (2007) Response of a native bamboo [*Arundinaria gigantea* (Walt.) Muhl.] in a wind-disturbed forest. *Forest Ecology and Management* **241**, 288–294.
- Griscom BW and Ashton PMS (2003) Bamboo control of forest succession: *Guadua sarcocarpa* in Southeastern Peru. *Forest Ecology and Management* **175**, 445–454.
- Guilherme FAG, Oliveira AT, Appolinario V and Bearzoti E (2004) Effects of flooding regime and woody bamboos on tree community dynamics in a section of tropical semideciduous forest in South-Eastern Brazil. *Plant Ecology* **174**, 19–36.
- Harms KE, Condit R, Hubbell SP and Foster RB (2001) Habitat associations of trees and shrubs in a 50-ha neotropical forest plot. *Journal of Ecology* **89**, 947–959.
- Hayashi K and Yamada T (2008) Is bamboo stand expansion independent of topographic conditions? *Japanese Journal of Conservation Ecology* **13**, 55–64.
- Hirai H, Matsumura H, Hirotani H, Sakurai K, Ogino K and Lee HS (1997) Soils and the distribution of *Dryobalanops aromatica* and *D. lanceolata* in Mixed Dipterocarp forest. – a case study at Lambir Hills National Park, Sarawak, Malaysia. *Tropics* **7**, 21–33.
- Hubbell SP and Foster RB (1986) *Biology, chance, and history and the structure of tropical rain forest tree communities*. In Diamond J and Case TJ (eds), *Community Ecology*. New York, US: Harper & Row, pp. 314–329.
- Ishizuka S, Tanaka S, Sakurai K, Hirai H, Hirotani H, Ogino K, Lee HS and Kendawang JJ (1998) Characterization and distribution of soils at Lambir Hills National Park in Sarawak, Malaysia, with special reference to soil hardness and soil textures. *Tropics* **8**, 31–44.
- ITTO (2007) *Handbook on Bamboo Properties in Myanmar*. Yezin, Myanmar: Ministry of Forestry, Myanmar and ITTO.
- Janzen DH (1976) Why bamboos wait so long to flower? *Annual Review of Ecology and Systematics* **7**, 347–391.
- Kachina P, Kurokawa H, Oguro M, Nakashizuka T, Tanaka H, Thinkampheang S, Sungkaew S, Panuthai S and Marod D (2017) Effect of forest fire on the regeneration of a bamboo species (*Cephalostachyum pergracile* Munro) at a mixed deciduous forest in Mae Klong Watershed Research Station, Thailand. *Tropics* **26**, 37–48.
- Kharlyngdoh E, Sahoo D and Shukla JK (2021) *Sporadic flowering of Cephalostachyum pergracile* Munro and its biological, ecological and social impacts in a mixed bamboo forest in Tengnoupal district, Manipur, Northeast India. In Devi RS, Kumar S, Hamdy RS and Khalkho AS (eds), *Medico Bio-Wealth of India*. MHRD, Govt. of India, Cuttack: Ambika Prasad Research Foundation Publisher, pp. 42–53.
- Larpkern P, Moe SR and Totland O (2011) Bamboo dominance reduces tree regeneration in a disturbed tropical forest. *Oecologia* **165**, 161–168.
- Lessard G and Chouinard A (1980) *Bamboo Research in Asia: Proceedings of a Workshop Held in Singapore*. Vienna: International Union of Forestry Research Organizations.
- Lobovikov M, Schoene D and Lou Y (2012) Bamboo in climate change and rural livelihoods. *Mitigation and Adaptation Strategies for Global Change* **17**, 261–276.
- Lotwick HW and Silverman BW (1982) Methods for analyzing spatial processes of several types of points. *Journal of the Royal Statistical Society Series B-Methodological* **44**, 406–413.
- Makita A, Konno Y, Fujita N, Takada K and Hamabata E (1993) Recovery of a Sasa-Tsuboiana population after mass flowering and death. *Ecological Research* **8**, 215–224.
- Marod D, Hermhuk S, Sungkaew S, Thinkampheang S, Kamyu T and Nuipakdee W (2019) Species composition and spatial distribution of dominant trees in the forest ecotone of a mountain ecosystem, Northern Thailand. *Environment and Natural Resources Journal* **17**, 40–49. <https://doi.org/10.32526/enrj.17.3.2019.21>.
- Marod D, Kutintara U, Yarwudhi C, Tanaka H and Nakashizuka T (1999) Structural dynamics of the natural mixed deciduous forest, Kanchanaburi, western Thailand. *Journal of Vegetation Science* **86**, 1414–1436.
- Marod D, Neumrat V, Panuthai S, Hiroshi T and Sahunalu P (2005) The forest regeneration after Gregarious flowering of Bamboo (*Cephalostachyum pergracile*) at Mae Klong Watershed Research Station, Kanchanaburi. *Kasetsart Journal – Natural Science* **39**, 588–593.
- Marod D, Phumphueng W and Wachrinrat C (2021) Effect of environmental gradients on tree distribution in lowland dry evergreen forest, northeastern Thailand. *Agriculture and Natural Resources* **55**, 795–805.
- Marriott FHC (1979) Barnard's Monte Carlo tests: how many simulations? *Applied Statistical Science* **28**, 75–77.
- Masaki T, Suzuki W, Niiyama K, Iida S, Tanaka H and Nakashizuka T (1992) Community structure of a species-rich temperate forest, Ogawa forest reserve, Central Japan. *Vegetatio* **98**, 97–111.
- McClure FA (1993) *The Bamboos*. Harvard: Harvard University Press.
- Montti L, Campanello PI, Gatti MG, Blundo C, Austin AT, Sala OE and Goldstein G (2011) Understorey bamboo flowering provides a very narrow light window of opportunity for canopy-tree recruitment in a neotropical forest of Misiones, Argentina. *Forest Ecology and Management* **262**, 1360–1369.
- Nakashizuka T (1988) Regeneration of beech (*Fagus crenata*) after the simultaneous death of undergrowing dwarf bamboo (*Sasa kurilensis*). *Ecological Research* **3**, 21–35.
- Palmiotto PA (1998) *The Role of Specialization in Nutrient-Use Efficiency As a Mechanism Driving Species Diversity in a Tropical Rain Forest*, Ph.D. Thesis. New Haven, CT, US: Yale University.
- Rao AN, Rao VR and Williams JT (1998) *Priority Species of Bamboo and Rattan*. Serdang, Malaysia: IPGRI and INBAR.
- Rao KS and Ramakrishnan PS (1987) Comparative-analysis of the population-dynamics of 2 Bamboo species, *Dendrocalamus-Hamiltonii* and *Neohouzeua-Dulloa*, in a successional environment. *Forest Ecology and Management* **21**, 177–189.
- Ripley BD (1977) Modeling spatial patterns. *Journal of the Royal Statistical Society Series B-Methodological* **39**, 172–212.
- Scurlock JMO, Dayton DC and Hames B (2000) Bamboo: an overlooked biomass resource? *Biomass and Bioenergy* **19**, 229–244.
- Söderström T and Calderon CE (1979) A commentary on the bamboos (Poaceae: Bambusoideae). *Biotropica* **11**, 161–172.
- Sork VL, Bramble J and Sexton O (1993) Ecology of mast-fruiting in 3 species of North-American Deciduous Oaks. *Ecology* **74**, 528–541.
- Sri-Ngernnyuang K, Kanzaki M, Mizuno T, Noguchi H, Teejuntuk S, Sungpalee C, Hara M, Yamakura T, Sahunalu P, Dhanmanonda P and Bunyavejchewin S (2003) Habitat differentiation of Lauraceae species in a tropical lower montane forest in northern Thailand. *Ecological Research* **18**, 1–14.
- Suyama Y, Suzuki J and Makita A (2010) For the comprehension of gregarious flowering in bamboos. *Japanese Journal of Ecology* **60**, 97–106.
- Svenning JC (1999) Microhabitat specialization in a species-rich palm community in Amazonian Ecuador. *Journal of Ecology* **87**, 55–65.
- Takeda S (2019) Labour mitigation and sustainable rural development in Myanmar. *Research for Tropical Agriculture* **12**, 103–104.
- Tan S, Yamakura T, Tani M, Palmiotto PA, Mamit JD, Pin CS, Davies S, Ashton PMS and Baillie I (2009) Review of soils on the 52 ha long term ecological research plot in mixed Dipterocarp forest at Lambir, Sarawak, Malaysian Borneo. *Tropics* **18**, 61–86.
- Tanaka H, Marod D, Ishida A, Takahashi M, Saitoh T and Nakashizuka T (2010) Regeneration of co-occurring tropical bamboos after the simultaneous flowering and death: a bamboo species formed sapling bank under the shade of the other species. *Japanese Journal of Ecology* **60**, 63–72.
- Tateno R and Takeda H (2003) Forest structure and tree species distribution in relation to topography-mediated heterogeneity of soil nitrogen and light at the forest floor. *Ecological Research* **18**, 559–571.
- Webb CO and Peart DR (2000) Habitat associations of trees and seedlings in a Bornean rain forest. *Journal of Ecology* **88**, 464–478.
- Whitmore TC (1990) *An Introduction to Tropical Rain Forests*. Oxford: Clarendon Press.



- Yamada T, Itoh A, Kanzaki M, Yamakura T, Suzuki E and Ashton PS** (2000) Local and geographical distributions for a tropical tree genus, *Scaphium* (Sterculiaceae) in the Far East. *Plant Ecology* **148**, 23–30.
- Yamada T, Noor NSM and Okuda T** (2010) Habitat association of trees in a 50-ha Malaysian rain forest plot. *Tropics* **19**, 1–8.
- Yamada T, Oka PN and Suzuki E** (2007) Habitat differences between two congeneric canopy trees, *Pterospermum javanicum* and *P. diversifolium* (Sterculiaceae) in an Indonesian floodplain forest. *Tropics* **16**, 165–169.
- Yamada T and Suzuki E** (1997) Changes in spatial distribution during the life history of a tropical tree, *Scaphium macropodum* (Sterculiaceae) in Borneo. *Journal of Plant Research* **110**, 179–186.
- Yamada T, Tomita A, Itoh A, Yamakura T, Ohkubo T, Kanzaki M, Tan S and Ashton PS** (2006) Habitat associations of Sterculiaceae trees in a Bornean rain forest plot. *Journal of Vegetation Science* **17**, 559–566.
- Yamasaki N, Yamada T and Okuda T** (2013) Coexistence of two congeneric tree species of Lauraceae in a secondary warm-temperate forest on Miyajima Island, south-western Japan. *Plant Species Biology* **28**, 41–50.
- Yuen JQ, Fung T and Ziegler AD** (2017) Carbon stocks in bamboo ecosystems worldwide: estimates and uncertainties. *Forest Ecology and Management* **393**, 113–138.
- Zaczek JJ, Baer SG and Dalzotto DJ** (2010) Fire and fertilization effects on the growth and spread of rhizome-transplanted giant cane (*Arundinaria gigantea*). *Restoration Ecology* **18**, 462–468.
- Zheng X, Lin SY, Fu HJ, Wan YW and Ding YL** (2020) The bamboo flowering cycle sheds light on flowering diversity. *Frontiers in Plant Science* **11**, Article 381.