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VILLAGE BAMBOOS REVISITED: COMPARING GENETIC DIVERSITY OF *BAMBUSA VULGARIS* 'STRIATA' AND *THYRSOCALAMUS LIANG* WITH *GIGANTOCHLOA SCORTECHINII* AS A FOREST BAMBOO

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The tropical woody bamboos are culturally and economically important in many Asian countries. The bamboos that have been grown or cultivated are regarded as village bamboos, contrary to the forest bamboos that grow in the wild. However, very little is known about the history of bamboo cultivation or domestication. The fact that the cultivated bamboos are usually vegetatively propagated and less fertile has led to the postulation that forest bamboos possess a greater genetic diversity than village bamboos. Using an Inter-Simple Sequence Repeats (ISSR) profiling approach, this study assessed the genetic diversity of the village bamboos, as represented by *Bambusa vulgaris* 'Striata' and ×*Thyrsocalamus liang*, as compared to that of the forest bamboos. The results showed an extremely low genetic diversity in *B. vulgaris* 'Striata' and ×*T. liang*. We suggest sterility of the village bamboos is one of the possible explanations for the intra-specific genetic diversity. On the other hand, high diversity in *Gigantochloa scortechinii*, a forest bamboo, is driven by its outcrossing nature. We discussed the implications of our results for genetic stock conservation in agriculture and the bamboo industries.

Keywords: Ancient Enduring Clones (AECs), genetic uniformity, hybridisation, ISSR profiles, introgression

INTRODUCTION

Bamboos have long been cultivated by the peoples of China, India, Japan and Southeast Asian countries because of their cultural and economic importance. Within the tropical woody bamboo tribe Bambuseae (Sungkaew et al. 2009), the useful species in Malaysia are mainly from the members of the subtribes Bambusineae and Melocanninae (Wong 1995). The useful bamboo species that are grown in the village neighbourhood were regarded as village bamboos by Holttum (1958), as opposed to the native bamboos that are found in the forests (forest bamboos). Similar concept was adopted by Lobovikov et al. (2007) in referring to the planted bamboos as private bamboos, as in privately owned by the farmers and the forest bamboos as public bamboos.

Selection of the useful bamboo clones could be associated with the natural hybridisation among bamboo species. Holttum (1958) surmised the existence of hybrid swarms among the closely related *Gigantochloa* taxa, based on the bewildering morphological variation among the wild *Gigantochloa* bamboos especially in the *G. latifolia-G. ligulata* complex in the northern Malay Peninsula. From the varieties produced in the hybrid swarms, the desired clones of *Gigantochloa* could have been selected, cultivated clonally, and eventually brought southward to Malaya and Java from the Lower Burma region where the genus appears most diverse. This could probably explain why some village bamboos are not seen growing in the wild.

Muller (1998, 2003) observed the phenotypic variations in the seedlings of his isolated clumps of *Gigantochloa ridleyi* and explained his observations with hybridisation and self-fertilisation in the F1 hybrids. He coined the term ancient enduring clones for the bamboo clones that existed only in cultivation in Indonesia and Malaysia. More examples of bamboo taxa showing characteristics of ancient enduring clones as elaborated by Wong (2004), include infertility, long vegetative phase, and poor seed set.

This study aimed to test the hypothesis that village bamboos had originated from a relatively uniform genetic stock, even though they could have been established in a wide geographic range for extended periods of time. Representatives of the village bamboos in this study were *Bambusa vulgaris* 'Striata' and ×*Thyrsocalamus liang*.

Bambusa comprises over a hundred of species, many of which are cultivated species with unknown origin or very limited wild populations (Xia et al. 2006) and *B. vulgaris* is one of them (Ohrnberger 1999). It comprises many varieties that have been widely cultivated across tropical Asia and introduced to Europe and the United States as early as the 1700s (Meredith 2002). In Malaysia, the popular cultivars of *B. vulgaris* are 'Striata' in green and yellow forms and 'Wamin' (Wong 1995). ×*Thyrsocalamus liang* or Phai Liang in Thai and Buluh Madu in Malay is a hybrid species from Thailand which has become a popular ornamental in Malaysia and Singapore in recent decades (Goh et al. 2018). A few varieties of it were cultivated in Thailand; some for ornamental purposes (Phai Liang Dam and Phai Liang Si Thong) while others for edible shoots (Phai Liang Thawai and Phai Liang Wan) (Ohrnberger 2017). The forest bamboo examined in this study was *Gigantochloa scortechinii*. It is a widely distributed wild species in Peninsular Malaysia and southern Thailand. It is found in lowlands and hills and naturally grows in abundance along the rivers and in the valleys (Wong 1995).

We adopted the Inter-Simple Sequence Repeats (ISSR) marker for this study (Zietkiewicz et al. 1994). The ISSR profile is an array of DNA fragments between the microsatellites in the nuclear genome and it can be relatively easy to obtain with high reproducibility. This marker has been used in numerous crop genetic studies, including those for the bamboos in the past (Desai et al. 2015, Yeasmin et al. 2015, Amom et al. 2018), and is shown to be especially informative in the assessment at the population level (Tian et al. 2012, Yang et al. 2012, Nilkanta et al. 2017).

MATERIALS AND METHODS

Sampling design

Ten leaf specimens of ×*T. liang* and *B. vulgaris* 'Striata' each (i.e., JD1–JD 10 and JD11–JD 20, respectively) were collected across Peninsular Malaysia (Figure 1), assuming that they were acquired from different sources and planted at different times. Details of the sample reference numbers and collection localities were shown in Table 1. A total of 10 specimens of *G. scortechinii*, a native species in Peninsular Malaysia were included in this study (Figure 1, Table 1).

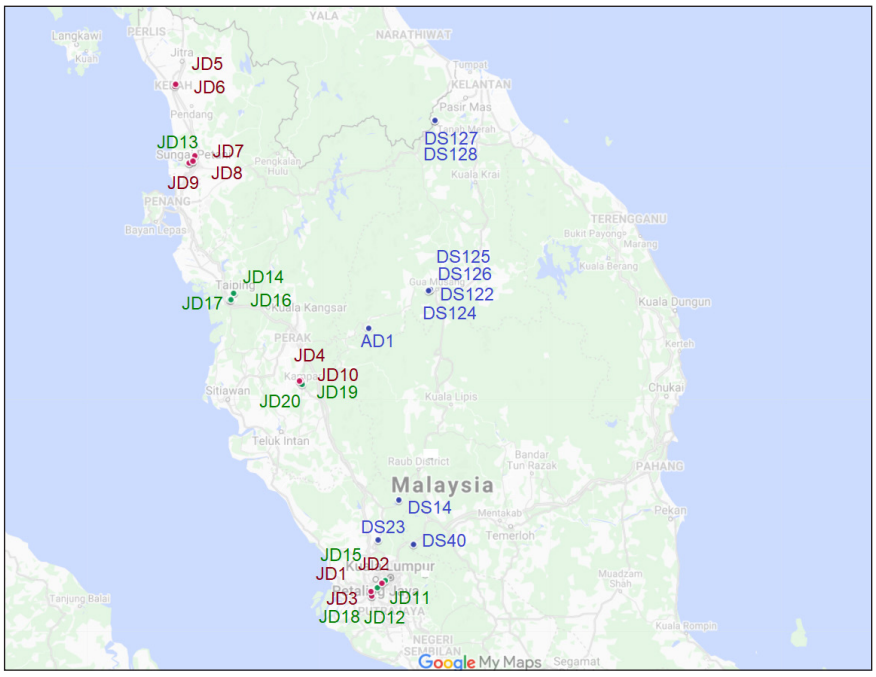

Figure 1 Sampling sites of *Bambusa vulgaris* 'Striata' (red), *Thyrsocalamus liang* (green), and *Gigantochloa scortechinii* (blue) in Peninsular Malaysia. The sampling localities are provided in Table 1

Table 1 Details of the specimens collected for this study. Specimen collection dates ranged from 24/12/2014 to 30/3/2019

Voucher code	District, state	Geographic coordinates
(a) ×*Thyrsocalamus liang*		
JD1	Shah Alam, Selangor	3°1.668' N, 101° 34.290' E
JD2	Petaling Jaya, Selangor	3°3.192' N, 101° 34.230' E
JD3	Petaling Jaya, Selangor	3°6.273' N, 101° 37.953' E
JD4	Kampar, Perak	4°20.145' N, 101° 8.462' E
JD5	Alor Setar, Kedah	6°6.675' N, 100° 22.445' E
JD6	Alor Setar, Kedah	6°7.585' N, 100° 22.935' E
JD7	Sg. Petani, Kedah	5°41.412' N, 100° 29.687' E
JD8	Sg. Petani, Kedah	5°38.945' N, 100° 27.910' E
JD9	Sg. Petani, Kedah	5°39.560' N, 100° 29.042' E
JD10	Kampar, Pereak	4°19.873' N, 101° 8.198' E
(b) *Bambusa vulgaris* 'Striata'		
JD11	Shah Alam, Selangor	3°1.668' N, 101°34.290' E
JD12	Petaling Jaya, Selangor	3°3.192' N, 101°34.230' E
JD13	Sg. Petani, Kedah	3°6.273' N, 101°37.953' E
JD14	Taiping, Perak	4°20.145' N, 101°8.462' E
JD15	Kuala Lumpur	6°6.675' N, 100°22.445' E
JD16	Taiping, Perak	6°7.585' N, 100°22.935' E
JD17	Taiping, Perak	5°41.412' N, 100°29.687' E
JD18	Kuala Lumpur	5°38.945' N, 100°27.910' E
JD19	Kampar, Perak	5°39.560' N, 100°29.042' E
JD20	Kampar, Perak	4°19.873' N, 101°8.198' E
(c) *Gigantochloa scortechinii*		
DS14	Kuala Kubu Bharu, Selangor	3°36.560' N, 101°44.450' E
DS23	Serendah, Selangor	3°21.994' N, 101°36.742' E
DS40	Janda Baik, Pahang	3°20.132' N, 101°49.692' E
DS122	Gua Musang, Kelantan	4°52.761' N, 101°55.085' E
DS124	Gua Musang, Kelantan	4°52.761' N, 101°55.085' E
DS125	Gua Musang, Kelantan	4°52.761' N, 101°55.085' E
DS126	Gua Musang, Kelantan	4°52.761' N, 101°55.085' E
DS127	Rantau Panjang, Kelantan	5°54.424' N, 101°57.503' E
DS128	Rantau Panjang, Kelantan	5°54.424' N, 101°57.503' E
AD1	Lojing, Kelantan	4°37.797' N, 101°28.395' E

DNA extraction and Inter-Simple Sequence Repeats (ISSR)-PCR

Total DNA was extracted from silica-dried young leaves using the CTAB method as described by Fulton et al. (1995). Two ISSR primers; ISSR-899 (Goh et al. 2010) and $(TG)_6AC$ (Suyama & Matsuki, 2015) were used for Polymerase Chain Reaction (PCR) amplification. The PCR reaction mixture of 25 µL contained ca. 100 ng DNA template, 1× GoTaq® Green Master Mix and 0.4 µM of the ISSR primer. The PCR was run at 94.0 °C for 1 min; 35 cycles of 30 seconds at 94.0 °C, 60 seconds at the annealing temperature, and 90 seconds at 72.0 °C; and a final extension of 10 min at 72.0 °C. The annealing temperatures used for ISSR-899 and $(TG)_6AC$ were 50 °C and 48 °C, respectively. The amplified PCR products were electrophoresed on a 2.0% agarose gel at 80 V for 50 min and stained with ViSafe Red Gel Stain for visualisation.

Band scoring and genetic diversity analysis

The DNA bands obtained were manually scored and arranged into a binary matrix. The presence of a band at any given locus was scored as "1", whereas the absence of a band was scored as "0". Only distinct bands that showed high intensity were considered reliable for scoring. The binary matrices of all samples for the $(TG)_6AC$ and ISSR-899 profiles were then combined into a single matrix and loaded to GenAlEx v. 6.503 (Peakall & Smouse 2012).

Principle Coordinate Analysis (PCoA) was performed based on the standardised covariance matrix converted from the tri-distance matrix of Nei's genetic distance, *D* (Nei et al. 1983). Genetic diversity of the binary data *h*, was measured based on $1 - (p^2 + q^2)$, where p represents the band frequencies and $q = 1 - p$ (Peakall & Smouse 2012). The unbiased genetic diversity *uh*, was measured by $Nh / (N - 1)$, where N represents sample size (Peakall & Smouse 2012).

RESULTS

Intra-specific genetic diversity

The Inter-Simple Sequence Repeats profiles for *T. liang* (JD1–JD10), *B. vulgaris* 'Striata' (JD11–JD20) and *G. scortechinii* (DS14–DS128, AD1) based on the $(TG)_6AC$ and ISSR-899 markers were shown in Figure 2. *G. scortechinii* had the highest proportion of the polymorphic sites (68.42%) and had shown the greatest diversity (h = 0.244 0.043). This was followed by ×*T. liang*, which showed 21.05% of polymorphic loci and genetic diversity of 0.088 ± 0.040. *B. vulgaris* 'Striata' does not have polymorphic loci within the species and has shown zero genetic diversity (Table 2).

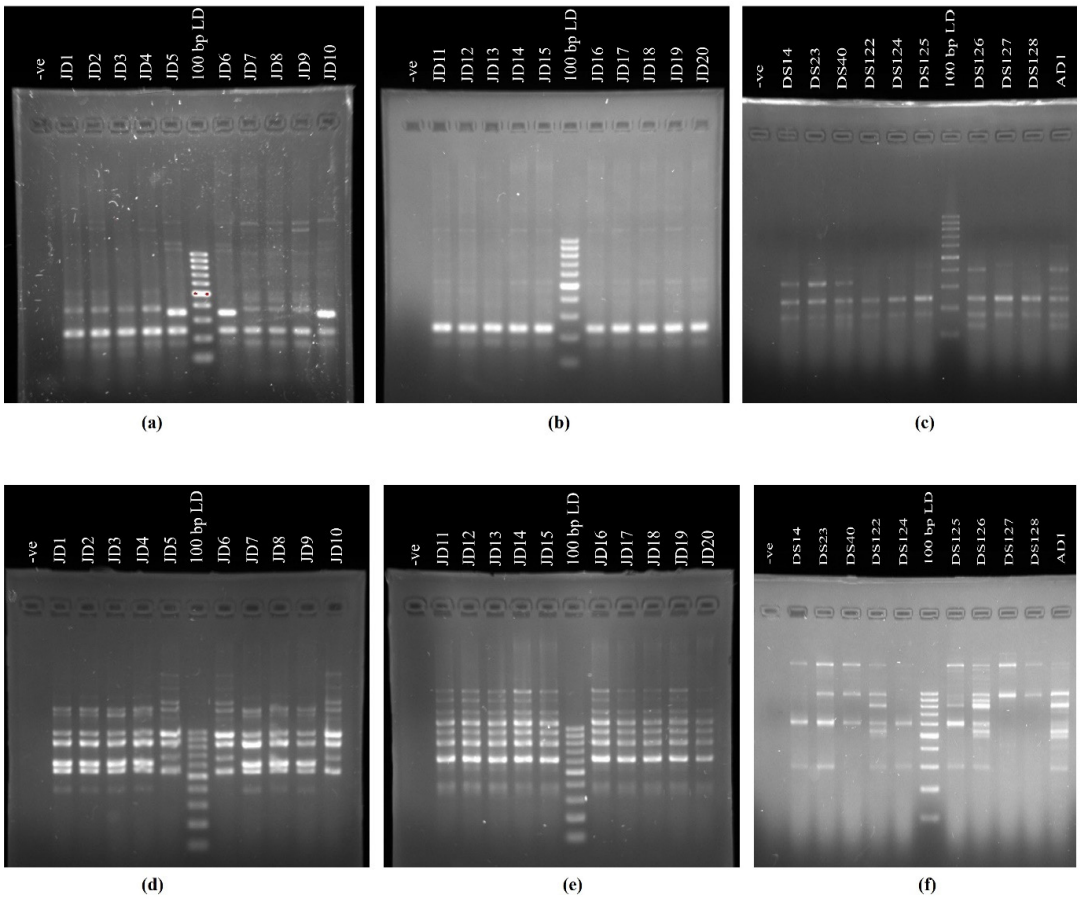

Figure 2 ISSR profiles for (a) *Thyrsocalamus liang* (JD1 – JD10), (b) *Bambusa vulgaris* 'Striata' (JD11 – JD20) and (c) *Gigantochloa scortechinii* (DS14 – DS128, AD1), based on $(TG)_6AC$ marker. The ISSR profiles for (d) *Thyrsocalamus liang*, (e) *Bambusa vulgaris* 'Striata' and (f) *Gigantochloa scortechinii* based on the ISSR-899 marker

Principle coordinate analysis (PCoA) based on Nei's genetic distance

G. scortechinii (circled in blue) appeared to be highly diverse as the plots DS14–DS128, AD1 did not overlap with one another (Figure 3). *B. vulgaris* 'Striata' (circled in green) appeared to be highly uniform as the plots JD11–JD20 were all overlapping. Plots of ×*T. liang* (circled in red), were distributed at two coordinates: one for JD1, JD2, JD3, JD4, JD7, JD8 and JD9 while the other for JD5, JD6 and JD10.

DISCUSSION

Bambusa vulgaris 'Striata'

As a commonly cultivated bamboo species, *B. vulgaris* 'Striata' are usually propagated by division. Despite irregular flowering episodes that had been reported for this species, the seed set was never encountered. Sterility in *B. vulgaris* 'Striata', as suggested in the previous studies, was attributed to infrequent flowering, physical barriers in sexual reproduction and meiotic irregularities (John & Nadgauda 1997, Koshy & Pushpangadan 1997, Koshy & Jee 2001). This was reflected in our results that *B. vulgaris* 'Striata', even though derived from various sources and nurseries, had extremely low genetic diversity. All individuals used in this study possibly originated from extremely limited mother plants.

The Inter-Simple Sequence Repeats profiling method is expected to be useful in assessing the genetic stocks of the other economically important ancient enduring clone bamboo of unknown origin, such as *Dendrocalamus asper* which is well-known for its edible shoots. Such

Table 2 Mean diversity indices for *Bambusa vulgaris* 'Striata', ×*Thyrsocalamus liang* and *Gigantochloa scortechinii*.

Taxa	*N*	% of polymorphic sites	*Na* (SE)	*Ne* (SE)	*I* (SE)	*h* (SE)	*uh* (SE)
B. vulgaris 'Striata'	10	0	0.316 (0.110)	1.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)
×*T. liang*	10	21.05	0.632 (0.191)	1.152 (0.070)	0.129 (0.059)	0.088 (0.040)	0.098 (0.045)
G. scortechinii	10	68.42	1.421 (0.207)	1.399 (0.075)	0.368 (0.062)	0.244 (0.043)	0.271 (0.048)

Annotations: Sample size (*N*), Number of different alleles (*Na*), Number of effective alleles (*Ne*), Shannon's information index (*I*), Diversity (*h*), Unbiased diversity (*uh*), Standard error (SE)

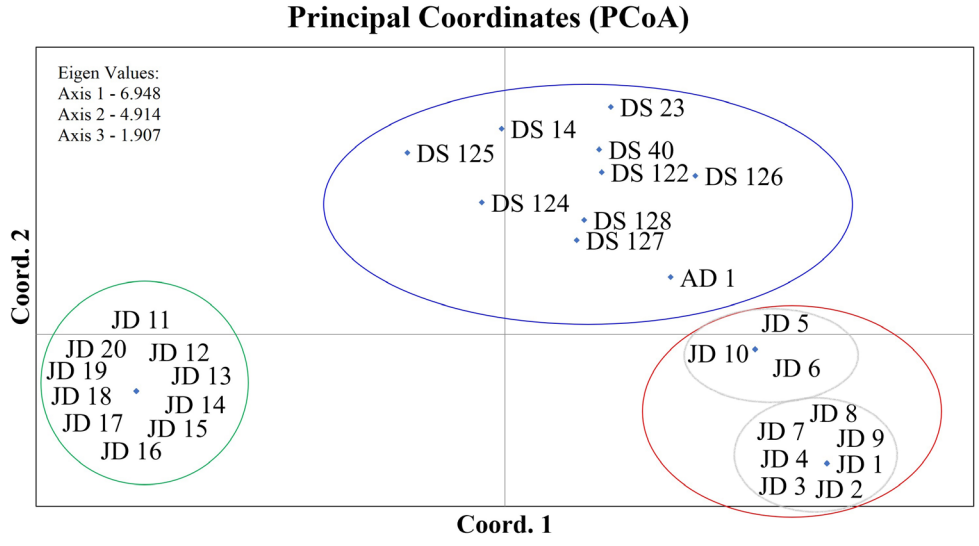

Figure 3 Arbitrary genetic distance among the specimens based on the top three axes as depicted in PCoA

information benefits the bamboo breeders in making trait selection and reducing the cost for maintaining the undesired bamboo clones. Diversifying the genetic stocks could reduce the risk of economic loss due to the large-scale death following by mass gregarious flowering, as experienced by farmers in Thailand in 1994–1995, as they raised *D. asper* from an extremely narrow genetic base (Thammincha et al. 1995).

×*Thyrsocalamus liang*

Among the ×*T. liang* individuals collected for this study, two types of Inter-Simple Sequence Repeats profiles were observed. For both $(TG)_6AC$ and ISSR-899 markers, the genetic profiles for JD1, JD2, JD3, JD4, JD7, JD8 and JD9 were identical and consistently different from the profiles of JD5, JD6 and JD10 (Figure 2(a) & 2(d)). These two groups of individuals fell on two coordinates in the principle coordinate analysis profile (Figure 3) which corresponded to the two distinct Inter-Simple Sequence Repeats banding profiles as observed in the Inter-Simple Sequence Repeats profiles.

The popular ornamental, ×*T. liang* was introduced to Malaysia from Thailand in recent decades (Goh et al. 2018). In Thailand, it is called Phai Liang and known to have several varieties such as Phai Liang Wan, Phai Liang Dam, Phai Liang Si Thong and Phai Liang Thawai, some of which are meant for ornamentals and some for edible culm shoots. The two distinct ISSR-profile types observed for ×*T. liang* were likely indicating two of the varieties sampled for this study. The varieties of ×*T. liang* could have been obtained through selection based on the desired traits from the hybrid swarms formed between the parental species, *Dendrocalamus membranaceus* and *Thyrsostachys siamensis* (Goh et al. 2018). Maintaining the selected clones using vegetative propagation was likely to have contributed to the genetic uniformity within each variety. The Inter-Simple Sequence Repeats profiling method described in this work could serve as a promising tool for identification of the Phai Liang varieties.

Gigantochloa scortechinii

Relatively high genetic diversity in *G. scortechinii* (0.244 0.043) corroborated the previous studies on the natural populations of *Dendrocalamus giganteus* (Tian et al. 2012), *D. membranaceus* (Yang et al. 2012), and *Melocanna baccifera* (Nilkanta et al. 2015). Based on the Inter-Simple Sequence Repeats profiles, they were found to have high total genetic diversity and low population differentiation, attributed to their flowering behaviours such as outcrossing and self-incompatibility (Tian et al. 2012, Nilkanta et al. 2015). The same explanation was likely applicable to *G. scortechinii*. In *G. scortechinii,* self-incompatibility was evident by seeding failure in a solitary flowering clump (Wong 1995). Relatively more frequent outcrossing in this species could have resulted in the high population genetic diversity. Furthermore, diffused sporadic flowering in *G. scortechinii* (Wong 1995) was advantageous in terms of genetic diversification because it allowed flowering and hence pollination and seeding, for more than once in its lifetime (i.e., polycarpic)

Known locally as Buluh Semantan, *G. scortechinii* has been one of the most useful bamboo species in the construction industry (Mohamed 1999). Currently, its culm materials are sourced from the wild forest populations as this species is widely available. Its physicochemical and mechanical properties have been well studied in terms of the effects of culm age gradation (Mohmod et al. 1994), chemical treatment (Salih et al. 2020) as well as in comparison to the other species (Zakikhani et al. 2017). Considering its genetic variability, we suggest a careful investigation on the physicochemical and mechanical properties in relation to its population genetics will also be useful for the industry to select their harvesting sites.

CONCLUSIONS

The present study demonstrated the contrasting patterns of intra-specific genetic diversity between the cultivated (village) and wild (forest) bamboos. The cultivated bamboo species, as represented by *B. vulgaris* 'Striata' and ×*T. liang*, exhibited much lower genetic diversity as compared to that of the native bamboos, as represented by *G. scortechinii* in Peninsular Malaysia. Our results corroborated the perceptions that the cultivated bamboos were obtained from and maintained in a narrow genetic base. In Holttum's concept of village bamboo, hybridisation and introgression could have contributed to a range of variants, and some desired clones could have been selected and maintained by the villagers. These hybrids

or introgressed clones might not be fertile and hence persisted as ancient enduring clones only by vegetative means. On the other hand, outcross predominates reproduction of *G. scortechinii* in the wild.

Our study suggested that similar to *B. vulgaris* 'Striata' and ×*T. liang*, the other bamboo taxa which were only known in cultivations as the ancient enduring clones will show extremely low genetic diversity if they originate from very few episodes of selections. We acknowledged the limitations of the current study that was based on a relatively small number of samples and DNA markers and therefore does not capture the full spectrum of genetic diversity for any of them. More in-depth population studies on the ancient enduring clones will provide more insights, not only into the domestication and migration history of these village bamboos but also into the genetic stocks available for commercial cultivation. As highlighted by Wong (2004), the agenda for conserving the useful bamboos should include genetic identification of the distinct clonal materials for important traits such as longevity. The Inter-Simple Sequence Repeats marker would be a good choice to serve this purpose in terms of cost- and time- effectiveness.

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