

TIMONIUS PASOHENSIS (RUBIACEAE), A RARE NEW SPECIES FROM PASOH FOREST, MALAYSIA, AND ITS POPULATION CHARACTERISTICS IN THE 50-HA FOREST DYNAMICS PLOT

Hoo PK^{1,2}, Musalmah N³, Cheah YH³, Wong KM⁴ & Sugumaran M^{1,*}

¹Institute of Biological Sciences, University of Malaya, 50603 Kuala Lumpur, Malaysia

²Institute of Biodiversity and Environmental Conservation, Universiti Malaysia Sarawak, 94300 Kota Samarahan

³Forest Research Institute Malaysia, 52109 Kepong, Selangor Darul Ehsan, Malaysia

⁴Singapore Botanic Gardens, 1 Cluny Road, Singapore 259569, Republic of Singapore

*sugumaran.m@gmail.com

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The intensely rich flora of lowland tropical rain forests includes rare species that represent a significant portion of the overall diversity. In the Pasoh Forest Reserve, Malaysia, *Timonius* is represented by two sympatric species: *T. wallichianus*, and a new species described and illustrated here. The new species *T. pasohensis* is rare and so far known only from this reserve. The population characteristics of the new species and the commoner and more widespread *T. wallichianus* were compared in the 50-ha plot. The distribution of both species overlapped in several habitat types. The torus translation test indicated that *T. pasohensis* is positively associated with swamps and slopes, whereas *T. wallichianus* prefers alluvium. However, other factors such as competition, fecundity, susceptibility to droughts, and herbivory, may also be important in influencing the distribution of the two species. They have a similar population structure but are distinctly different in other aspects. From 1986 to 2015, the abundance of *T. pasohensis* has greatly declined to less than half its original population, and saplings and trees < 10 cm diameter at breast height appear to be the most affected. In contrast, the population size of *T. wallichianus* has remained relatively stable during the same period, possibly owing to the abundance of suitable habitat type and higher seed set.

Keywords: *Timonius wallichianus*, sympatric species, congeners, population structure, habitat preference

INTRODUCTION

Tropical rain forests are known for their intense biodiversity (Ashton 2014). Peninsular Malaysia and Borneo, both making up a core area of the Sundaland continental shelf region, have among the most diverse forests in the Indo-Malesian region in terms of plant species richness and endemism (Gentry 1992, Barthlott et al. 1996). Tropical forests are highly complex and exist in a range of geological contexts (Morley 2000) and physical environments (Ashton 2014), and species diversity is expectedly distributed unevenly across different forest types. In our understanding of the tropical forest system, lowland dipterocarp forests are floristically among the richest, and, on Sundaland, also the most widespread, once spanning across some 90% of the original land cover in Peninsular Malaysia (Gentry 1992, Saw 2010, Neo et al. 2021).

The rich lowland flora is in part contributed by the occurrence of a high number of rare species (species with low local abundance) in the tropics—a feature long recognised by many forest botanists (Ashton 1984, Wong 1998, Wong & Neo 2019). In the 50-ha forest plots at both Pasoh (Peninsular Malaysia) and Barro Colorado (Panama, where the first of such plots was begun), more than one-third of the species present have low population densities of one individual or less per hectare (Hubbell & Foster 1986, Manokaran & LaFrankie 1990, He et al. 1997). Rare species, despite persisting at low frequencies, contribute significantly to the biodiversity of a tropical forest on the whole. Indeed, rare and common species may express significantly different functional traits, suggesting that their roles in the ecosystem are complementary (Zhang et al. 2022). Rare species

also tend to have more unique combinations of traits, highlighting their importance in ecosystem functioning (Zhang et al. 2022).

Rare species in particular, are usually habitat specialists, though even in their preferred sites they are present in low densities or even sometimes entirely absent, suggesting that reproductive biology and fecundity may be the limiting factors (Hubbell & Foster 1986, Ashton 2014). It could be that rare species are often regulated by niche specialisation to microhabitats and regeneration conditions, as well as interspecific competition.

Pasoh and the 50-ha plot are among the most well-studied tropical forest sites in the world (see Yao et al. 2023 for a recent bibliographic listing of publications). The floristic composition and stand structure of the 50-ha plot were first discussed in Kochummen et al. (1990) and Manokaran and LaFrankie (1990) respectively, followed by subsequent studies of forest dynamics (Manokaran et al. 1993, Condit et al. 1999). Yet, new species from the plot are still being discovered and described, possible through sustained taxonomic interest (Kochummen 1997, Omar & Latiff 2014). The Pasoh 50-ha plot is an ongoing collaborative project between Forest Research Institute Malaysia (FRIM), ForestGEO, Smithsonian Tropical Research Institute (STRI), and the National Institute for Environmental Studies (NIES).

Timonius (Rubiaceae) is a genus of about 300 species distributed from the Seychelles, Sri Lanka and the Andaman island group eastwards to Malesia, Taiwan, Papuasias, and tropical Australia (Chen & Wong 2023). It consists of shrubs, treelets or small trees to hemi-epiphytes; the last growth habit not found among the Malay Peninsula taxa. The diagnostic characters include axillary and opposite inflorescences, male and female flowers on separate individuals, typically four corolla lobes, an ovary containing from four to many locules with a single pendulous ovule in each locule, and pyrenes with separate walls. Together with *Guettarda* and *Guettardella* (each with one species: *Guettarda speciosa* L. and *Guettardella atropurpurea* (Craib) M.E.Jansen, respectively), they form the Guettardeae native to the Malay Peninsula.

We revisited the taxonomy of *Timonius* in the Malay Peninsula following the last treatment by Wong (1988). Of the 14 species enumerated in Wong (1988), four were undescribed owing to insufficient material, and were thus simply referred to as *Timonius* spp. A, B, C, and D. In our examination of herbarium material, a number of specimens from Pasoh Forest Reserve previously assigned as *Timonius* sp. A indeed turned out to be new. The new species is described here as *T. pasohensis* P.K.Hoo, named after the locality where it was first discovered. With the recent description of another two new species in the Malay Peninsula (Hoo et al. 2023), the total number of species recognised has reached 16.

We also compared the change in population structure of the new species and its sympatric congener, *Timonius wallichianus* Valetton, using census data from two years (1986, the year of first enumeration of the Pasoh plot, and 2015). Finally, we inferred whether the co-existence of sympatric *Timonius* species in the plot can be explained by the habitat specialisation hypothesis.

MATERIALS AND METHODS

Study site

Situated near the southern end of the Main Range in Negeri Sembilan state, Pasoh Forest Reserve represents one of the few remaining lowland dipterocarp forest patches in Peninsular Malaysia. Within the reserve, an area of 2450 ha characterised by low hills and alluvium with a 450 m elevation granite ridge rising along the eastern border was gazetted as a Research Forest (Figure 1). This study was conducted in a 50-ha permanent plot established within the Research Forest in 1985, where all trees with diameter at breast height (DBH) \geq 1 cm were enumerated, identified, and measured. Detailed protocols from plot establishment to stand enumeration and measurement were taken from Manokaran et al. (1990). The main objective of the 50-ha plot was to investigate tree species composition and its dynamics, enabling comparative study with similarly designed plots elsewhere (Ashton et al. 2003). The plot was recensused every five years and had just completed its eighth census in 2023.

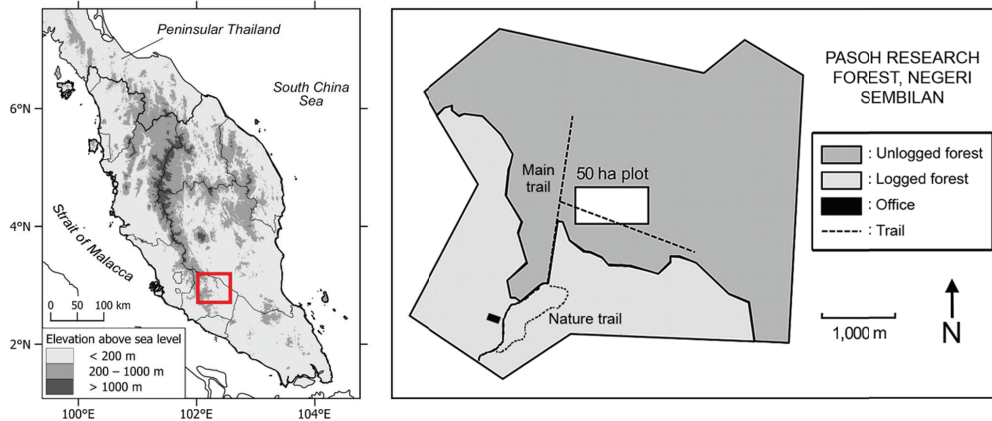


Figure 1 (Left) Location of Pasoh Research Forest indicated by the red border; (right) map of Pasoh Research Forest (adapted from Fujinuma & Harrison 2012)

Taxonomic approach

The new *Timonius* species was diagnosed through morphological assessments of specimens from the following herbaria: KEP (Forest Research Institute Malaysia), KLU (University of Malaya) and SING (Singapore Botanic Gardens); acronyms follow Thiers (2023). A dedicated collection of specimens from the Pasoh 50-ha plot was also consulted at KEP. Additionally, fieldwork was carried out at the plot to obtain fresh material to assist the morphological study. A preliminary assessment of the species conservation status was provided according to IUCN Red List Categories and Criteria (IUCN 2012).

Data analyses

To evaluate the change in population structure and size of the *Timonius* species, demographic data collected for the 50-ha plot for two census years, i.e. 1986 and 2015, were used. Using the ‘tidyverse’ R package (Wickham et al. 2019), we plotted the number of individuals against diameter size classes for the two years.

Although relatively flat terrain characterises about half of the 50-ha plot with a low hill at the center rising to about 24 m above the lowest point, detailed soil survey has yielded four main groups of soil (Yamashita et al. 2003). As the soil groups correspond well with topographic features, four main habitat types are generally recognised, namely, swamp, alluvium, slope, and ridge (Adzmi et al. 2010). According to this identified habitat, a true habitat map

of 1000 m × 500 m plot was considered in basic units (subplots) of 20 m × 20 m, so that there were 1250 subplots and each subplot was assigned a habitat type.

Using the torus-translation test, a total of 4999 simulated habitat maps were generated by shifting the true habitat map across a two-dimensional torus by 20-m steps and applying 180° rotation, mirroring, and 180° rotation of the mirrored image to each step (Harms et al. 2001). To test for habitat association of the two *Timonius* species, we have overlaid each of the habitat maps (true and simulated) with the distribution data and calculated the relative density of each species in each of the four habitat types. If the observed relative density on a given habitat is greater than 97.5% or less than 2.5% of the simulated relative densities, then the species is considered positively or negatively associated with the habitat, respectively. The habitat association test was carried out for the years 1986 and 2015. The torus-translation test was performed via the ‘fgeo.analyse’ R package (v1.1.14). All analyses were carried out using the R Statistical Software (v4.3.2).

RESULTS AND DISCUSSION

The new species

Timonius pasohensis P.K.Hoo, sp. nov. (Figure 2)

Diagnosis: Resembling *Timonius denigricans* P.K.Hoo in having densely hairy twig and midrib on lower leaf surface, sparsely hairy lower leaf lamina, and pistillate inflorescences with a single flower, but differs in having 4–6 mm

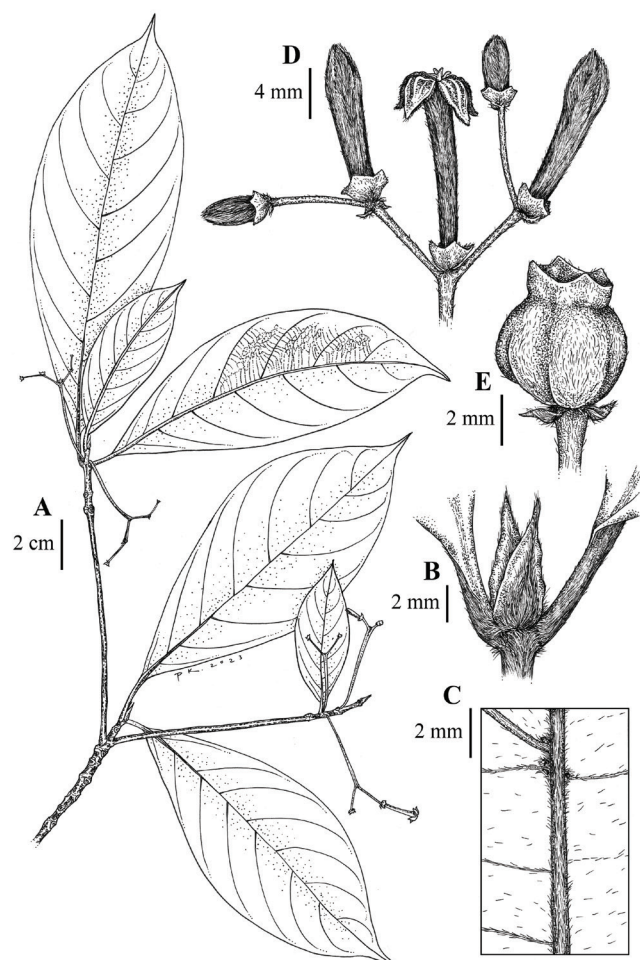


Figure 2 *Timonius pasohensis*; A) staminate flowering leafy branch, B) shoot apex with stipules, C) indumentum on lower leaf surface, D) staminate inflorescence, E) fruit; A, C, D from Hoo et al. *HPK* 56, B, E from Kochummen *FRI* 26615; drawn by Cheng PK; copyright Singapore Botanic Gardens

(vs 8–13 mm) diameter fruits, chartaceous (vs coriaceous) leaf lamina, and whitish grey (vs black) bark.

Type: Peninsular Malaysia, Negeri Sembilan, Pasoh Forest Reserve, 50-ha plot for Tree no. 25293, 14 May 1987, Kochummen *FRI* 26615 (holotype KEP [KEP203464]; isotypes KEP [KEP284752] – ♀ Fru).

Timonius sp. A in Wong, *Kew Bull.* 43(3) (1988) 509, *pro parte, quoad Klahn s.n., Tree no.* 14247.

Tree recorded as up to 5 m high. **Bark** whitish grey, smooth. **Young twigs** completely covered by appressed yellow hairs. **Stipules** triangular, imbricate, outer surface densely appressed yellow hairy becoming distinctly less so along margins. **Leaves: petioles** 2–15 mm long, 1–2 mm diameter, completely appressed yellow hairy;

blades drying discolorous (dark brown on upper surface, light brown on lower surface); elliptic to obovate, 6.5–23 cm × 3.5–8 cm, length:width ratio 1.5–3.2, base cuneate, apex cuspidate, margins plane; lamina chartaceous; secondary veins 6–9 pairs, fading towards leaf margin, tertiary veins on lower surface sub-parallel and trending almost perpendicular to the midrib, immersed in the lamina, faintly to clearly visible; lower lamina surface smooth, sparsely appressed silvery hairy to subglabrous, not silky to the touch, midrib and secondary veins drying brown (green when fresh), completely appressed silvery-yellow hairy; upper surface glabrous except for sparse appressed yellow hairs along veins in young leaves; domatia present in the axils of secondary veins. **Pistillate inflorescences** with a solitary flower; **hypanthium** densely appressed silvery hairy. **Staminate inflorescences** with 3–6 flowers,

branching dichasial, peduncles 1–4.5 cm long, 0.5–1 mm diameter, sparsely appressed silvery and yellow hairy, flowers other than the central one on distinctly developed side branches 8–13 mm long; bracts triangular, entire, 1–2 × 0.5–1 mm, sparsely appressed yellow hairy; **hypanthium** ca. 1 mm long, 1–1.5 mm diameter, inconspicuously lobed, completely appressed silvery hairy; **calyx** lobes 4, broadly triangular, less than 0.5 to 1 mm long, 0.5–1 mm wide, sparsely appressed silvery hairy; **corolla** tubes (10–)15 mm long, 2–2.5 mm diameter, completely appressed silvery hairy outside, lobes 4, ovate, 4–5 mm long, 1.5–2.5 mm wide, completely appressed yellow hairy outside. **Infructescences** with a solitary fruit, peduncles 2.5–5 cm long, ca. 0.5 mm diameter, sparsely appressed silvery and yellow hairy; bracts triangular, entire, 1–1.5 mm × 0.5–1 mm, densely appressed yellow hairy; **fruits** purplish when mature, globose, 4–6 mm long, 4–6 mm diameter, moderately to densely appressed silvery hairy, with 4 distinct lobes, internal matrix not seen; persistent calyx tube at fruit apex 1–1.5 mm long, sparsely appressed yellow hairy; persistent calyx lobes 4, broadly triangular, less than 0.5 mm long, ca. 1 mm wide, sparsely appressed yellow hairy, erect; **pyrenes** not seen.

Etymology: The species is named after the Pasoh Forest Reserve, where tree inventory in the permanent 50-ha plot led to the discovery of this species.

Distribution and ecology: *Timonius pasohensis* is most likely endemic to Peninsular Malaysia and so far known only from the Pasoh Forest Reserve in Negeri Sembilan. It occurs in primary lowland dipterocarp forest at around 100 m elevation. No individual was found along the road leading to the office or the nature trail, suggesting that the species might be intolerant of habitat disturbance.

Preliminary conservation status: *Timonius pasohensis* is assessed as Vulnerable (VU D2). It is restricted to the Pasoh Forest Reserve where the ForestGEO 50-ha plot is located. Therefore, there is no evidence of decline in area of occupancy, extent of occurrence, area of habitat, and number of locations. However, owing to its apparent restriction to a single locality, it is

vulnerable to random catastrophic events such as forest fires and droughts which may quickly render the species Critically Endangered (CR) or Extinct (EX).

Notes: Its congener recorded from Pasoh, *T. wallichianus*, is a species of the southern parts of the Malay Peninsula, more common in regenerating forest or forest margins. It can be easily distinguished from *T. pasohensis* by having lower leaf surfaces completely covered in silvery hairs, up to 30 staminate flowers in an inflorescence, and 3–5 fruits per infructescence.

Although not known to occur in Pasoh, the more widespread *Timonius flavescens* can be distinguished from *T. pasohensis* in having shagreen (vs smooth) lower leaf surface, purplish (vs green) midrib and secondary veins when fresh, and staminate inflorescences with typically 5–11 (vs 3–6) flowers (Chen & Wong 2023).

Additional specimens examined:

PENINSULAR MALAYSIA: Negeri Sembilan, Jelebu District, Pasoh Forest Reserve, 50-ha plot, 2.983° N, 102.306° E, 117 m, 27 April 2022, Hoo, Cheah & Md. Saiful Azhar HPK 57 (KEP, SING—♀ Fru), 50-ha plot, 2.982° N, 102.307° E, 120 m, 27 April 2022, Hoo, Cheah & Md. Saiful Azhar HPK 56 (KEP, KLU, SING—♂ Fl), 50-ha plot, 1987, Klahn s.n., Tree no. 14247 (KEP—♂ Fl), 50-ha plot, sin. dat., Wong 4570* (KEP—♂ Fl), Wong 4647* (KEP—♂ Fl), Wong 4648* (KEP—♂ Fl).

*These are from a dedicated collection of Pasoh specimens housed in the KEP herbarium.

Population characteristics of *T. pasohensis* and *T. wallichianus* in Pasoh

Spatial distribution

There is an overlap in distribution between the two species. In fact, both are represented in all habitat types although at varying degrees (Figure 3). *Timonius pasohensis* has a rather scattered distribution in the alluvium, swamp, and slope habitat types, whereas *T. wallichianus* is well-represented in the same habitat types but appears to be concentrated in the alluvial site (Table 1).

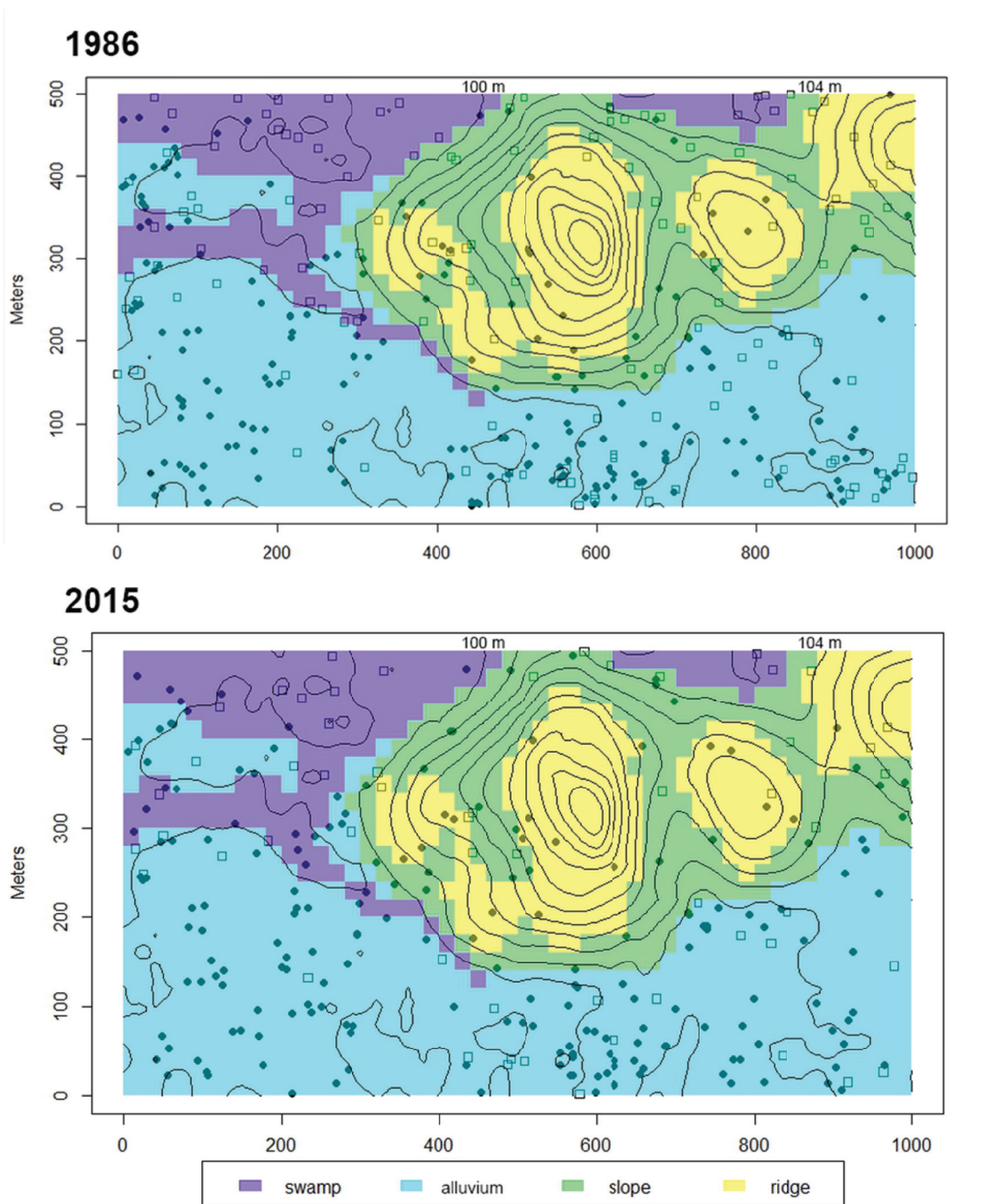


Figure 3 Spatial distribution of *Timonius pasohensis* (□) and *T. wallichianus* (●) overlaid with topographic and general habitat map in the Pasoh 50-ha plot in the 1986 and 2015 censuses; the contour interval is 2 m

Table 1 Number of *Timonius* individuals in four habitat types for the years 1986 and 2015

Habitat	Proportion of habitat (%)	1986		2015	
		<i>T. pasohensis</i>	<i>T. wallichianus</i>	<i>T. pasohensis</i>	<i>T. wallichianus</i>
Swamp	13.5	28	12	13	18
Alluvium	49.2	59	155	32	149
Slope	20.8	36	26	12	29
Ridge	16.5	14	18	6	18

Habitat association

Using the torus-translation method, both *Timonius* species displayed statistically significant positive or negative associations to swamp, alluvium, or slope habitat types only with the 1986 data, whereas for 2015, the species were only neutrally associated with the habitats (Table 2). As sample size is important in testing for statistical significance and the habitat association test involves identifying which habitats are disproportionately over- or under-represented by a certain species relative to all other species (Harms et al. 2001), our observation for the year 2015 could be due to the low sample size of *T. pasohensis* in that year (63 individuals, only slightly higher than the recommended sample size of 50 for the habitat association test). Thus, we only interpreted results obtained from the 1986 census data.

Despite appearing to have overlapping distribution in the plot, it appears that both *T. pasohensis* and *T. wallichianus* have individual (and possibly distinct) habitat associations. The torus-translation test showed that *T. pasohensis* was positively associated with swamp and slope habitat types, whereas *T. wallichianus* was positively associated with alluvium. In interpreting our results, we acknowledge that swamps and slopes represent contrasting habitats with distinct soil moisture regimes; swamps are seasonally water-logged, whereas slopes are drier and well-drained. Thus, the fact that *T. pasohensis* has a broad tolerance of soil moisture level as shown by our test result does not explain its peculiar negative association with the alluvial site which is moderately drained and generally with greater water availability than slopes (Adzmi et al. 2010). One possible hypothesis is that there is likely intense

competition in the alluvial site where stem density is generally higher than other habitat types (Davies et al. 2003). Therefore, under such a scenario, species with higher competitive advantages including higher seed set (in this case, *T. wallichianus*) may be better represented in the alluvial site.

We also acknowledge that the interpretation of habitat associations of *T. pasohensis* could be limited by the variables used in the statistical test. We investigated species–habitat association based on only four broad habitat types which may be insufficient in explaining the co-existence for every species within the plot. As such, perhaps a finer-scale definition of habitat should be considered, if habitat (or micro-habitat) is an important contributor in explaining species distribution. On another note, we are also aware of the possibility that other factors, such as light conditions and herbivory (which may vary in each habitat type), could also be important. Some of the *T. pasohensis* specimens showed signs of herbivory, although the significance of this remains to be investigated further. Using the same statistical method on Sterculiaceae (then separate from but now included in the Malvaceae), Yamada et al. (2006) observed that for four species, small trees were less strongly associated with habitat than larger trees, but for another four species, the opposite pattern was detected. This points to the complexity of the tropical forest system in sustaining high species diversity, and that multiple niche dimensions probably interplay in the rain forest (Pianka 1976, He et al. 1997). Therefore, apart from habitat specialisation, it is possible that both *Timonius* species also occupy different ecological niches, which will require more detailed investigation. Our experience with the statistical test, thus, recommends against an over-simplistic interpretation of the test results.

Table 2 Habitat associations of *Timonius pasohensis* and *T. wallichianus* in the four habitat types for the years 1986 and 2015 using the torus-translation test at a significance level of 5%

Habitat	1986		2015	
	<i>T. pasohensis</i>	<i>T. wallichianus</i>	<i>T. pasohensis</i>	<i>T. wallichianus</i>
Swamp	+	–	N	N
Alluvium	–	+	N	N
Slope	+	–	N	N
Ridge	N	N	N	N

+, – and N denote positive, negative and neutral associations respectively

Change in population structure and size

The diameter distribution of *T. pasohensis* and *T. wallichianus* in the 50-ha plot for two years (1986 and 2015), with an approximately 30-year difference is shown in Table 3. The overall trend of the abundance-diameter distribution is consistent. The highest number of individuals was recorded in the lowest DBH class of 1–4.9 cm, which decreased exponentially with increasing size class, resulting in a reverse J-shaped curve.

The total number of *T. pasohensis* individuals dropped from 137 to 63 over the study period, a decline of 54% in population size. This is consistent with previous analyses of forest dynamics in the present study site, where Condit et al. (1999) reported that stand density for all trees ≥ 1 cm in DBH has continuously diminished from 1986 to 1990 to 1995. However, they noted that at DBH of 10 cm and above, the stand density has in fact increased, indicating that the decline is entirely contributed by trees in the 1–9.9 cm DBH size class. In our study, we can see a similar pattern where the dwindling of the population size was evidently more acute in trees 1–4.9 cm and 5–9.9 cm in DBH, which accounted for 66 and 30% of the total 74 individuals lost respectively. In contrast, the number of individuals in the largest size class (≥ 15 cm in DBH) remained constant at two. Despite the distinct reduction in population size by 2015, the percentage of individuals represented in each size class was similar for both years.

Most of the changes in the population size of *T. pasohensis* across the study period is reflected in trees of 1–9.9 cm in DBH. In other words, the population dynamics (e.g. mortality and recruitment rate) was relatively unstable in that diameter range. The rather high number of individuals in the lower size classes in 1986 may have represented an early phase of recruitment

before mortality sets in for a portion of that population through competition and other influences including herbivory, for example. An alternative scenario would be that the 1986 population represents near-equilibrium conditions, with the numbers dwindling before 2015 due to catastrophic events such as droughts. This, however, would only be evident with closer studies, not available in our case.

Two other factors might be considered regarding the diminishment of the *T. pasohensis* population in the study area. First, severe drought episodes in Pasoh between March 1995 and December 2010 may have caused serious hydrological imbalance (Corlett 2016, Musalmah 2022). Tree species associated with wetter habitats (such as *T. pasohensis*) are more vulnerable to the impacts of drought, leading to high mortality rates (Itoh et al. 2012). Understandably, younger trees would have a shallower root system and are therefore more susceptible to drying of the soil surface during drought events.

Secondly, wild boars are known to build nests by using understorey trees with DBH < 2 cm including saplings, which are snapped or uprooted, causing high mortality in woody vegetation around the nests (Ickes 2001). Development of rubber and oil palm plantations in the surrounding areas (Manokaran et al. 2004) meant that the available nesting grounds for the wild boars have reduced, contributing to an increase in frequency of nests in the remaining forest area including the 50-ha plot (Ickes & Thomas 2003). Besides, the local extinction of natural predators and the adaptability of wild boars to the oil palm plantations around the reserve have also contributed to the exceptionally high density of wild boars within the reserve, further exacerbating the damage caused by their nesting behaviour to saplings (Ickes & Thomas 2003).

Table 3 Abundance–diameter distribution of *Timonius pasohensis* and *T. wallichianus* in 1986 and 2015

DBH class (cm)	<i>T. pasohensis</i>		<i>T. wallichianus</i>	
	1986	2015	1986	2015
1–4.9	89	40	150	128
5–9.9	38	16	37	45
10–14.9	8	5	14	23
≥ 15	2	2	10	18
Total	137	63	211	214

Interestingly, *T. wallichianus*, which is significantly more common than the new species, has a stable population size between the years 1986 and 2015 (Table 3). This stark contrast in the population characteristics of the two sympatric congeners underlines the possible importance of their ecological, biological, and phylogenetic differences. One of the factors contributing to higher population size and stability of *T. wallichianus* is likely related to the fact that about 50% of the plot is alluvium, to which it is well adapted. In addition, one important factor may be that the seedling success of *T. wallichianus* (which may be translated to plant fitness) is much higher due to a higher seed set in *T. wallichianus* (each infructescence typically produces up to five fruits, which is five times more than that in *T. pasohensis*). Consequently, even if their fruiting frequencies are similar, *T. pasohensis* is significantly rarer and may display the typical characteristics of a rare species, such as lack of competitive advantages and higher per capita death rate than common species (He et al. 1997). It should be noted that although both species are part of a clade representing *Timonius* subgenus *Helospora* (Jack) Junhao Chen & K.M.Wong, they are nested in different subclades which are rather distantly related to one another (Hoo 2023).

CONCLUSION

As most species in the forest are naturally rare, large ecology plots have the advantage of uncovering rare species—species that would have otherwise escaped enumeration in much smaller-sized plots. Our newly described *T. pasohensis* highlights the importance of permanent plot survey in advancing our understanding of tropical tree diversity.

The present study has considered some population characteristics (including habitat association and changes in population structure and size) of two sympatric congeners, *T. pasohensis* and *T. wallichianus* in the Pasoh 50-ha plot. In general, we may not have found clearly distinct habitat associations for both species, which, in fact, have overlapping distribution in the plot. This could be because we have, like others, used the few broadly categorised habitat types for the plot, and did not investigate further parameters that may also impact on habitat quality and niche differentiation.

The drastic decline in the population of *T. pasohensis* at the lower diameter size class (1–9.9 cm DBH) should be investigated and monitored, especially in relation to the overall fitness of the population. In contrast, *T. wallichianus*, which is a species common in the Malay Peninsula and also distributed in south-west Borneo including the islands in between, has remained abundant in the plot, with a clearly more generalist adaptation. Owing to the overwhelming differences in these (and perhaps other) population characteristics, other potentially contributing factors might repay further study.

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