

THE DISTRIBUTION AND ECOLOGY OF *CECROPIA* SPECIES (URTICACEAE) IN SINGAPORE

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INTRODUCTION

The Neotropical genus *Cecropia* is the largest genus of the family Cecropiaceae, with 61 species known (Berg & Rosselli, 2005). However, recent studies have placed them in the family Urticaceae (APG, 2003). *Cecropia* species are generally small- to medium-sized (5–20 m tall), few-branched trees with a candelabrum-like branching system (Fig. 1) with large palmate and peltate leaves (Fig. 2) that are almost circular in circumference, and excentrically attached to the petiole. The venation is radiate and usually radially incised (Fig. 3), running down to the petiole.

The genus represents an important group of pioneer trees in arid and less humid regions, although some species do grow in montane forest (Berg & Rosselli, 2005). Most species of *Cecropia* are lowland species occurring from sea-level to 1,300 m altitude, while submontane species occupy an altitudinal range from 1,300–2,000 m, and montane species are found in cloud forest from 2,000–2,600 m. Many species have a narrow altitudinal and ecological amplitude, with certain species specializing in certain habitats, such as seasonally inundated habitats, rocky slopes, swamps, natural or man-made clearings and so on. All *Cecropia* species produce adventitious roots, which later become prop roots (Fig. 4), and are commonly manifested in larger individuals growing near rivers or marshy areas.



Fig. 1. *Cecropia pachystachya* at Lorong Asrama, near the Mandai Road area. (Photograph by: Alvin Francis Lok Siew Loon).



Fig. 2. *Cecropia pachystachya* sapling, showing large, almost circular palmate and peltate leaves. (Photograph by: Alvin Francis Lok Siew Loon).



Fig. 3. Main veins radiating from the petiole-lamina insertion of *Cecropia pachystachya*. (Photograph by: Alvin Francis Lok Siew Loon).



Fig. 4. *Cecropia pachystachya* with prop roots, growing near soft substrate beside a stream in the Mandai area, Singapore. (Photograph by: Alvin Francis Lok Siew Loon).

Cecropia species very often display myrmecophytism as a means of biotic defense, although not all congeners possess this association (Longino, 1989, 2005; Berg & Rosselli, 2005; Davidson, 2005). The myrmecophytism may also vary between species, and within species, over geographical locations (Longino, 1989; Berg & Rosselli, 2005). This biotic defense not only pertains to defence against herbivory by animals such as sloths, but also against encroaching vines, where the ants “trim back” vines to prevent them from reaching the host tree (Longino, 2005). *Cecropia* species are very well-adapted to myrmecophytism (Berg & Rosselli, 2005; Davidson, 2005). The genus has hollow stems, which widen at fixed developmental stages that correlate temporally with the onset of food body (Müllerian body) production (Berg & Rosselli, 2005). The plant also has prostomata (weakened sites) (Fig. 5) in the stem walls beneath intermodal septa, which are sites devoid of fibrovascular bundles, collenchyma, and lignified parenchyma. The colonizing ants recognise these sites and excavate these points to reach the hollow region of the stem, avoiding the rupturing of any stem transport tissue, which may otherwise result in the flooding of the hollow chamber with mucilage.

In addition to providing housing to their insect protectors, *Cecropia* species have also evolved to supply two types of food rewards in the form of trichomes (Longino, 1989; Berg & Rosselli, 2005; Davidson, 2005). The first type of food reward is the Müllerian body, which is rich in lipids and also contain proteins and glycogen. The Müllerian bodies are usually produced by species with an obligate ant (*Azteca* species) association (Berg & Rosselli, 2005). These trichomes usually occur in one or two patches of dense indumentum (called trichilia) found abaxially at the broadened base of the petiole of the adult leaf. These trichilia consist of three types of trichomes (Fig. 5) — unicellular whitish (to brownish) stiff hairs of various lengths, pluricellular trichomes, and Müllerian bodies. The Müllerian bodies in the trichilia are initially hidden within the dense brown pluricellular hairs to prevent harvesting by animals other than the *Azteca* ants inhabiting the tree. When matured, the Müllerian bodies detach from their bases and are pushed to the surface of the trichilia, where they are more accessible to their ant inhabitants. These trichilia are often closely guarded by *Azteca* worker ants that wait for the maturation of these Müllerian bodies. The second type of food reward is pearl bodies that contain glycogen plastids and lipids. The pearl bodies are found on the abaxial leaf lamina surfaces, and are usually produced by *Cecropia* species for unspecialized and opportunistic ant species.



Fig. 5. A single patch of dense indumentum (trichilia) at the base of the petiole of *Cecropia pachystachya*, consisting of short, stiff, brown, pluricellular hairs, long, whitish unicellular hairs, and numerous Müllerian bodies. Prostomata (singular, prostoma), or weakened sites in the stem walls beneath internodal septa, are also observed. (Photograph by: Alvin Francis Lok Siew Loon).

Cecropia trees, as mentioned above, are seldom smothered by vines, even though they are very often found in places rich with them. The *Cecropia* trees have developed a few ways to deal with encroaching vines. Firstly, in species with *Azteca* ant associations, the ants help to trim back approaching vines (Putz, 1982; Berg & Rosselli, 2005; Davidson, 2005). Secondly, *Cecropia* trees are apparently able to restrict the growth of vines upwards along the trunk by branching lower down the trunk length at a 45° angle. This apparently induces the vines to grow towards these lower branches, and not proceed further up the tree. Thirdly, *Cecropia* trees shed their leaves at a rather fast rate, to prevent vines from climbing up them and smothering their braches.

Cecropia species are also dioecious, with staminate (Fig. 6) and pistillate (Fig. 7) flowers on separate trees. *Cecropia* species are generally wind-pollinated and have pendulous spikes that can sway in the wind so shedding their pollen, or by the special adaptation of the detachment of anthers and their secondary attachment, allowing the shedding of pollen by motion of the anthers (Berg & Rosselli, 2005). The pollen in *Cecropia* species is dry and thus easily released by movement. Although the principle pollination of this genus is by wind, insects such as flies and small beetles have also been observed to transport pollen.

Full-grown trees of *Cecropia* can produce up to a million seeds, and this regular presence of fruits allows this genus to play a major role in the ecosystem. It is often the keystone food supply for frugivorous animals, such as birds, fruit bats, monkeys, opossums, and even fish (Berg & Rosselli, 2005). In the Neotropics, toucans and other birds help disperse the seeds of species with short infructescences, while bats are associated with species with long peduncles and spikes. Species growing near rivers on the other hand, are usually dispersed by water, after part of the mature infructescence drops from the rachis, floating downstream for a while by air trapped in the arachnoid indumentum among the perianths.



Fig. 6. Staminate inflorescences of *Cecropia pachystachya*. (Photograph by: Alvin Francis Lok Siew Loon).



Fig. 7. Pistillate inflorescences of *Cecropia pachystachya*. (Photograph by: Alvin Francis Lok Siew Loon).



Fig. 8. A small population of *Cecropia peltata* growing along Tyersall Avenue. (Photograph by: Alvin Francis Lok Siew Loon).



Fig. 9. A young branch of *Cecropia peltata* showing the lack of dense indumentum (trichilia) at the base of the petiole as compared to *Cecropia pachystachya* which displays this characteristic (Photograph by: Alvin Francis Lok Siew Loon).

PAST AND PRESENT RECORDS

Cecropia peltata has long been thought to be the species that has naturalised in Singapore. However after studying naturalised populations in Singapore and comparing their members with herbarium sheet specimens, we now know that there are at least two *Cecropia* species here and that most of the naturalised populations are in fact those of *Cecropia pachystachya* and not *Cecropia peltata* as was previously believed. This confusion about the identity of the naturalised species in Singapore was probably because previous workers were more concerned with the origins of plants grown in the Singapore Botanic Gardens, rather than examining the morphological features of the herbarium specimens. According to the records of the Herbarium, Singapore Botanic Gardens (SING), seeds of *Cecropia peltata* from Jamaica were imported to Singapore as early as 1902. This species “has been successfully grown in the gardens and produces seeds freely” and “seedlings appear in many parts of the gardens”. However, at present only one small wild population of *Cecropia peltata* has been found near the Botanic Gardens along the mid-point of Tyersall Avenue (Fig. 8) and close to one large *Cecropia peltata* tree cultivated inside the National Orchid Garden.

Cecropia peltata is also reported to be present in Indonesia and Peninsular Malaysia (Putz & Holbrook 1988). However, its identity has always been questioned in this region because congeners here may be either *Cecropia pachystachya* or *Cecropia peltata* (Berg & Rosselli, 2005). Putz & Holbrook (1988) traced the origins of the Malaysian material to the Bogor Botanic Garden in Java, Indonesia, which supposedly obtained its material from Brazil, which is rather unhelpful since *Cecropia pachystachya* and *Cecropia peltata* have overlapping ranges in Brazil. The question of interest is how *Cecropia pachystachya* arrived in Singapore. As we were unable to find any official record at SING of its origins, it may have been introduced by some other means. Putz & Holbrook (1988) noted that a *Cecropia peltata* plantation was initiated in 1953 at the Forest Research Institute Malaysia (FRIM), and we concur with their identification, so dispersal from the north may not be possible due to the immense distance involved. Another more likely possibility is that wild populations of *Cecropia pachystachya* in Singapore may have originated from an introduction at the Singapore Zoo in 1992 as food for sloths (Singapore Zoo, pers. comm.). This introduction coincides with the sudden population surge of *Cecropia pachystachya* at the SAF training areas at Mandai bordered by the Seletar Expressway, as well as in the Sembawang Air Base also adjacent to this area in the 1990s. This species is also found further north, to the woodlands areas, with the population densities decreasing further from the Mandai area, further supporting our hypothesis.

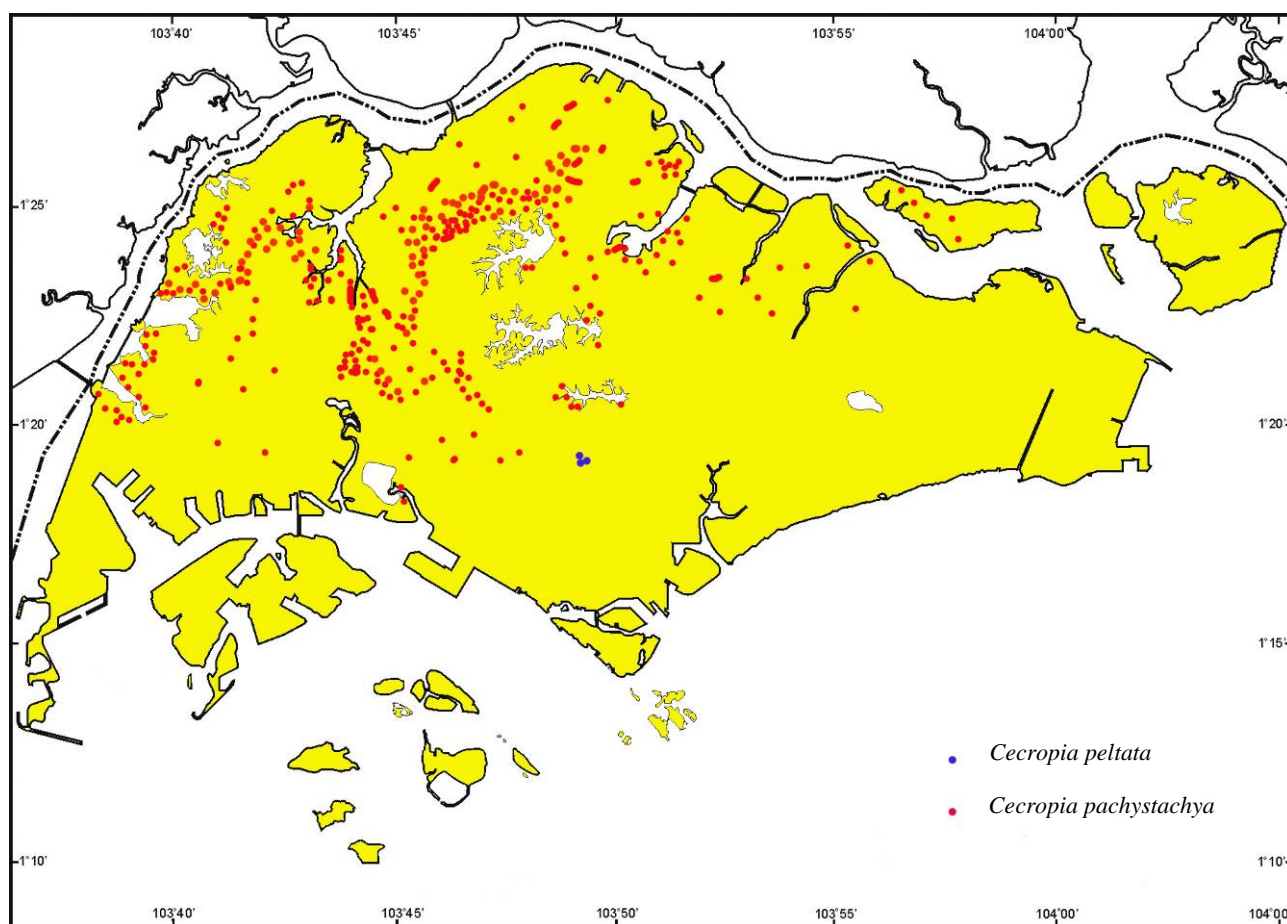


Fig. 10. Distribution of *Cecropia peltata* and *Cecropia pachystachya* around Singapore. (Photograph by: Alvin Francis Lok Siew Loon).

Certain plasticities in morphological features however still complicates things slightly, such as the presence and absence of trichilia in *Cecropia peltata* from Jamaica was found to be dependent on whether plant populations were associated with *Azteca* ants. Jamaican *Cecropia peltata* populations associated with *Azteca* ants, were found to have well-developed trichilia, while those without associations did not have trichilia (Fig. 9) (Berg & Rosselli, 2005). This plasticity further contributed to the previous ambiguity over the origins of the *Cecropia* specimens planted in Singapore. The Malaysian material examined by Putz & Holbrook (1988) showed a range of trichilia development. 80% of these specimens examined had fully developed trichilia, 8% had poorly developed trichilia, while the remaining 12% had no trichilia.

Differences in the variation of presence and absence of lamina lobation, long white hairs in the trichilia, together with the lengths of stipules have now been used to distinguish these two species. In Singapore, because of the lack of infection of *Azteca* ants in both species, trichilia is apparently absent in *Cecropia peltata* but still very distinctly present in *Cecropia pachystachya*. *Cecropia peltata* also has much shorter leaf stipules as compared to *Cecropia pachystachya*, which have stipules twice the length of *Cecropia peltata*. Barry John Conn and Juliasasi Tri Hadiyah who visited the Herbarium at the Singapore Botanic Gardens (SING) in 2009 have determined some previously labeled *Cecropia peltata* specimens as *Cecropia pachystachya*. All the specimens at the Herbarium, Raffles Museum of Biodiversity Research (SINU) previously labelled as *Cecropia peltata* have also been determined to be *Cecropia pachystachya*.

Generally most trees that have naturalised themselves in Singapore have been found to be *Cecropia pachystachya* with the exception of a single colony of *Cecropia peltata* at Tyersall Avenue, and are up to 25 m tall, but have been observed to flower at only 2 m in height. *Cecropia pachystachya* has large palmate, nearly circular leaves, up to 50–60 cm across, usually whitish on the undersides and subtended by a 1.2–4.3 cm thick and 20–53 cm long petiole. Trichilia were observed in all specimens examined in the field from the Mandai Road area, Central Catchment Nature Reserve, as well as the military training area adjacent to Old Jurong Road. The trichilia were observed at the base of the leaf petiole, fused into a single brown indumentum intermixed with short, white hairs. Records from the Herbarium, Singapore Botanic Gardens (SING; Table 1), has however shown specimens with trichilia patches which are not fused, as well as specimens which lack the trichilia altogether. In all naturalised specimens seen, stipules were white to pale green, subsericeous to pilose and exceeding 20cm suggesting they are *Cecropia pachystachya* in contrast to *Cecropia peltata* stipules that are sometimes subpersistent, strigose to hirtellose and only up to 12cm long (Fig. 9) (Berg & Rosselli,



Fig. 11. Ants found foraging for food bodies on the abaxial surface of the lamina. (Photograph by: Alvin Francis Lok Siew Loon).

2005). The staminate inflorescences (Fig. 6) of *Cecropia pachystachya* are usually erect, but sometimes deflexed, with a 3.0–6.7 cm long peduncle, 2.8–7.3 cm long, greenish-white spathe, 24–34 cm long spikes, and 0.9 cm long hairy stipes. The pistillate inflorescences (Fig. 7), similar to the staminate inflorescences, are also borne in pairs and are usually erect. However, they may also be pendulous, with a 10–17 cm long peduncle, 3.2–6.3 cm long spathe, and spikes 3.0–5.2 cm long.

In Singapore, naturalised *Cecropia pachystachya* have been observed to be regularly visited by the lesser dog-faced fruit bat (*Cynopterus brachyotis*) and a wide range of frugivorous and generalist bird species. They include the cream-vented bulbul (*Pycnonotus simplex*), red-eyed bulbul (*Pycnonotus brunneus*), yellow-vented bulbul (*Pycnonotus gaoivier*), pink-necked pigeon (*Treron vernans*), common myna (*Acridotheres tristis*), white-vented myna (*Acridotheres javanicus*), and the Philippine glossy starling (*Aplonis panayensis*). All the above species have been reported by Corlett (1998) as being good dispersers of seeds, with the exception for the pink-necked pigeon belonging to the genus *Treron* and family Columbidae which are known to be fig seed predators owing to their grinding gizzard action. Others workers, such as Balasubramanian (1996), have however found many viable seeds of *Manilkara hexandra* and *Zizyphus oenoplia* under *Treron bicincta* roosting sites, while Lambert (1989) has found that some fig seeds are able to survive the gut of these birds, indicating that *Treron* species are not absolutely seed predators and are still capable of seed dispersal. In light of these findings, more work needs to be done on whether *Cecropia* seeds are indeed able to survive the gut of *Treron* species in Singapore, instead of dismissing them as seed dispersers. All of the above listed are relatively common bird species, with a relatively large country-wide range and are not fastidious with regards to habitat type, possibly allowing *Cecropia pachystachya* to easily escape cultivation from the Singapore Zoological Gardens to other parts of Singapore. *Cecropia pachystachya* thrive in areas of high light intensity, and as such can be found in a few localities along the edge of MacRitchie Reservoir, in secondary forest areas and forest fringe areas in the Central Catchment Nature Reserve especially in the north, Singapore Armed Forces training areas adjacent to Old Jurong Road and Western Catchment Area, abandoned farmland areas near Neo Tiew Lane, and unmaintained parkland areas around Singapore (Fig. 10).

Cecropia peltata has been nominated as one of the “100 of the World’s Worst Invasive Alien Species” by the Global Invasive Species Database (2005) that is managed by the Invasive Species Specialist Group (ISSG) of the International Union for Conservation of Nature and Natural Resources (IUCN) Species Survival Commission and has also been given a high risk status and a score of 9 by the Pacific Island Ecosystems at Risk or PIER (PIER, 2007), and is today naturalised in Cameroon, Zaire, Java, Malaysia, and the Ivory Coast (Berg & Rosselli, 2005), as well as being invasive in Hawaii and French Polynesia (PIER, 2007), where it competes with native pioneer species. Strangely, even with high invasive tendencies, *Cecropia peltata* has not been able to escaped far from its source of introduction, since its introduction to Singapore Botanic Gardens in 1902. In contrast, the less invasive *Cecropia pachystachya* which is listed as a weed in the Hawaiian Ecosystems at Risk or HEAR (HEAR, 2007), seems to be the only *Cecropia* species that has

Table 1. Previous collections of *Cecropia* species deposited in the Herbarium, Singapore Botanic Gardens (SING, with bar code no.) or Herbarium, Raffles Museum of Biodiversity Research, National University of Singapore (SINU, with accession no.).

S/No.	Species	Specimen location	Accession/Barcode No.	Collector	Collector's Number	Date	Locality
1	<i>Cecropia peltata</i>	SING	127538	Mohd Nur	s.n.	1918	Botanic Gardens, near fence C
2	<i>Cecropia peltata</i>	SING	127539	Mohd Nur	1854	1 Mar.1918	Arboretum
3	<i>Cecropia peltata</i>	SING	127535	Mohd Nur	144	21 Aug.1918	Botanic Gardens, Lawn E
4	<i>Cecropia peltata</i>	SING	127537	Mohd Nur	s.n.	10 Jun.1924	Arboretum
5	<i>Cecropia peltata</i>	SING	127534	Mohd Nur	s.n.	13 Jun.1924	Arboretum
6	<i>Cecropia peltata</i>	SING	127536	Mohd Nur	s.n.	19 Jun.1924	Arboretum
7	<i>Cecropia peltata</i>	SING	127532	C. X. Furtado	144	18 Jun.1930	Botanic Gardens, Lawn E
8	<i>Cecropia peltata</i>	SING	127533	C. X. Furtado	144	18 Jun.1930	Botanic Gardens, Lawn E
9	<i>Cecropia peltata</i>	SING	127540	W. L. Chew	19	8 Nov.1957	Botanic Gardens
10	<i>Cecropia pachystachya</i>	SING	127531	K. Sidek	S60	18 May.1967	Botanic Gardens, Botanic quarters
11	<i>Cecropia pachystachya</i>	SINU	2007001807	Y. C. Wee	s.n.	29 May.1979	—
12	<i>Cecropia pachystachya</i>	SINU	2007001806	J. F. Maxwell	79 - 59	10 Dec.1979	Botanic Gardens Quarters
13	<i>Cecropia pachystachya</i>	SING	46	E. Tang	566	8 May.1995	Lorong Gambas
14	<i>Cecropia pachystachya</i>	SINU	2007001809	H. T. W. Tan, T. S. S. Khoo, A. H. B. Loo & E. S. C. Seah.	s. n.	1996	Locality unknown
15	<i>Cecropia pachystachya</i>	SINU	2007001804	C.C. Lim	LCC. 7.	1999	Mandai Road
16	<i>Cecropia pachystachya</i>	SINU	2007001802	C.C. Lim	LCC. 5.	1999	Mandai Lake Road
17	<i>Cecropia pachystachya</i>	SINU	2007001801	C.C. Lim	LCC. 1.	1999	Mandai Lake Road
18	<i>Cecropia pachystachya</i>	SINU	2007001803	C.C. Lim	LCC. 8.	23 Mar.1999	Yishun Ave 2
19	<i>Cecropia pachystachya</i>	SINU	2007001805	C.C. Lim	LCC. 7.	23 Mar.1999	Yishun Ave 2
20	<i>Cecropia peltata</i>	SING	44783	S. Lee	LA 6	29 May.2007	Sembawang/Lentor Ave
21	<i>Cecropia pachystachya</i>	SING	113787	T. P. Ng	SING 2008-411	7 Oct.2008	Mandai Road
22	<i>Cecropia pachystachya</i>	SING	113788	T. P. Ng	SING 2008-412	7 Oct.2008	Mandai Road

escaped cultivation and is now found in many places around Singapore (Fig. 10), while in contrast *Cecropia peltata* has only managed to spread across a road after more than a century of introduction (Fig. 10). The possible reasons for the success of *Cecropia pachystachya* in Singapore, is the ability to pollinate without the need for pollinators and the possible preferential liking for its fruits by frugivorous birds of this species over those of *Cecropia peltata* and lastly because they lack their natural predators. In Singapore, this species is now very common in habitats that were once dominated by *Macaranga* species. It is possible that *Cecropia pachystachya* are now out-competing the native *Macaranga* species, as they are more gregarious in flowering and fruiting than our native *Macaranga* species.

The *Cecropia pachystachya* in Singapore are not found to be associated with the *Azteca* ants they are normally associated with in their natural range. This is evident because many Müllerian bodies were still attached at the trichilia of the plants inspected, which would otherwise been quickly harvested by worker *Azteca* ants if present. Further examination by means of cutting open the hollow stems, revealed that none of the plants inspected were infested with any species of ant. This indicates that firstly, *Azteca* ant species were not co-introduced with the *Cecropia* plants and



Fig. 12. An ant tending to mealy bugs on the petiole of a *Cecropia pachystachya* tree. (Photograph by: Alvin Francis Lok Siew Loon).



Fig. 13. A *Euproctis* caterpillar found on a *Cecropia* tree at the Mandai area. (Photograph by: Alvin Francis Lok Siew Loon).

secondly, our native myrmecophytic ant species are not specialized and have not “learnt” to utilise the hollow stems by excavating the prostomata. Rather, loosely associated ant species have been noted with *Cecropia pachystachya* at many localities around Singapore. These ants are often observed foraging for food bodies under the leaf surfaces (Fig. 11), or tending to mealy bugs on the plants surfaces (Fig. 12). Although large arboreal herbivorous mammal predators, such as sloths, are not present here, leaves of *Cecropia pachystachya* have been found to be consumed by a large diversity of insects including grasshoppers, scale-insects, mealy bugs, and caterpillars (Fig. 13)

CONCLUSIONS

Since the introduction of *Cecropia peltata* to the Singapore Botanic Gardens in 1902, this species has somehow not been able to escape cultivation even though it has been listed as “100 of the World’s Worst Invasive Alien Species” by the Global Invasive Species Database (2005). In contrast, the less invasive *Cecropia pachystachya* which was introduced much later (around the 1960s), has since spread widely through Singapore. The identity of the naturalised species of *Cecropia* found in Singapore was for a long time assumed to be *Cecropia peltata*, owing to misidentification of certain herbarium records from the Herbarium, Singapore Botanic Gardens (SING) as well as the debate on the origins of the plants. However, upon close examination of herbarium sheets in both SINU and SING herbarium as well as from field observations have led to the naturalised species being identified as *Cecropia pachystachya*. Even though this two species could be sufficiently distinguished morphologically from herbarium sheets here as well as field collected material, it would still be wiser to develop and use DNA technology to more accurately differentiate these two species, owing that these two species of *Cecropia* are very similar morphologically and compounded by morphological plasticities due to intraspecific geographical variation as well as interactions with *Azteca* ants.

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