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An overview and checklist of non-native and cryptogenic vascular macrophytes in Singapore's fresh waters

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Abstract. Urban freshwater habitats (e.g., canals, reservoirs) are novel ecosystems that comprise a major portion of Singapore's freshwater landscape. Aquatic vegetation in urban habitats have important roles and functions, including regulating water quality and supporting biodiversity, although both their diversity and ecology remain poorly documented. In this paper, we compile a list of exotic macrophyte species that have been recorded in Singapore, mostly from urban fresh waters, including naturalised, casual, cultivated and cryptogenic species. We also discuss the potential risks and impacts, as well as the possible ecological functions and benefits provided by non-native macrophytes in Singapore's urban freshwater environments. In recent years, perceptions of macrophytes in urban waterways and water bodies have been changing and their environmental contributions are now receiving greater recognition. Nevertheless, further research is necessary to properly evaluate the various benefits and impacts of exotic vegetation in Singapore's fresh waters, particularly their ecological roles.

Key words. urban ecology, aquatic plants, ecological impacts, urban waterways, invasive species, diversity

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INTRODUCTION

Macrophytes, i.e., aquatic plants and macroalgae, are key components of many freshwater ecosystems and have a profound influence on ecosystem structure and functioning (Jeppesen et al., 1998; Rejmankova, 2011). In addition to being primary producers, macrophytes contribute to habitat complexity and provide refuge for aquatic fauna (Schriver et al., 1995; Thomaz & Cunha, 2010; Lusardi et al., 2018). Dense aquatic vegetation can also influence the hydrology and biogeochemistry of freshwater ecosystems, for example, by affecting hydraulic regimes (Chambers et al., 1991; Bal et al., 2011) and modulating the exchange of nutrients and compounds between plant tissues and the environment (Barko & James, 1998; Prasad et al., 2005). As such, the presence and degree of dominance of macrophytes can have a substantial influence on the ecological functioning and water quality of freshwater systems.

In the island city-state of Singapore, rapid urbanisation and development has resulted in the concretisation and diversion of many natural channels, as well as the creation of artificial, novel aquatic ecosystems (Corlett, 1992; Yeo & Lim, 2011; Blakely et al., 2014). Relatively less-disturbed forested freshwater habitats still persist mainly within the Central Catchment Nature Reserve and Bukit Timah Nature Reserve (Blakely et al., 2014; Davison et al., 2018; Davison & Chew, 2019), and are critical habitats for shade-loving native macrophyte species, including the locally endangered *Cyrtosperma merkusii* (Hassk.) Schott (Lok & Tan, 2008), *Lasia spinosa* (L.) Thwaites (Yee et al., 2019), and *Barclaya motleyi* Hook.f. (Lok et al., 2009), as well as the natural hybrid *Cryptocoryne* × *timahensis* Bastm. (Bastmeijer et al., 2001). However, urbanised waterways and water bodies now dominate the freshwater landscape, featuring a vast network (upwards of 8,000 km) of channelised drains and canals (Irvine et al., 2014), catchment reservoirs, stormwater ponds and decorative urban ponds throughout the city (Yeo & Lim, 2011; Chye, 2018; pers. obs.).

In contrast to forested habitats, urban freshwater habitats are typically highly exposed with little canopy cover and support primarily exotic, sun-loving macrophyte species. In many urban channels, the impervious concrete substratum largely prevents macrophytes from rooting, while high flow rates during downpours can wash away any plants that do attach successfully (Tan & Yeo, 2009), such as emergent (e.g., *Pontederia vaginalis* Burm.f. [formerly *Monochoria vaginalis* (Burm.f.) C.Presl ex Kunth; see Pellegrini et al., 2018], *Limnocharis flava* (L.) Buchenau) and sometimes submerged species (e.g., *Hydrilla verticillata* (L.f.) Royle), which may colonise sites where the surface has been compromised (i.e., cracked or uplifted concrete) or where organic sediment has built up over time (pers. obs.) (Fig. 1). Recently, efforts to ecologically rehabilitate urban waterways have culminated in the naturalisation of some urban channels and water bodies (Lim & Lu, 2016; Lim, 2019; Wilkinson et al., 2021; Kok, 2022). This has resulted in the creation of novel habitats for macrophytes (Baur et al., 2012; An et al., 2020), as well as the purposeful transplantation of some species for ornamental and biofiltration functions (Schaefer & Spirn, 2014; Sim et al., 2015). In these open environments, some species have also been reported to escape cultivation and establish at new sites, such as *Hydrocotyle verticillata* Thunb. (Lim et al., 2014), *Bacopa caroliniana* (Walter) B.L.Rob. (Chen et al., 2018), and *Echinodorus grandiflorus* (Cham. & Schltdl.) Micheli (Chen et al., 2021).

Presently, our understanding of the ecology of macrophytes in Singapore's waterways remains nebulous, despite recognition of their potential contributions to biodiversity and water quality. Furthermore, much of the attention on macrophytes in Singapore has focused on a small number of problematic weedy species that are also the subjects of reservoir management, e.g., *Hydrilla verticillata* and *Pontederia crassipes* Mart. (formerly *Eichhornia crassipes* (Mart.) Solms; see Pellegrini et al., 2018) without a more holistic overview on the ecology of this group. In this article, we present a checklist of non-native and cryptogenic macrophyte species that occur in the inland freshwater habitats of Singapore, particularly in urban canals, ponds, and reservoirs. Certain cultivated species were also included, especially those that are commonly planted in large quantities at managed habitats and which would thus have notable ecological significance. Additionally, we describe the life-forms of these various taxa, a key ecophysiological characteristic of aquatic species, that has not been referenced in other checklists. We highlight selected noteworthy species based on abundance, ecological significance, and/or (potential) impacts, which we assess and discuss.

CHECKLIST OF NON-NATIVE & CRYPTOGENIC MACROPHYTE SPECIES

A compilation of 143 non-native and cryptogenic (i.e., of unknown origin) macrophytes in Singapore's waterways is presented in the Appendix, comprising 42 naturalised, 16 casual, 30 cryptogenic and 55 cultivated species. This list was derived from checklists of plants in Singapore by Chong et al. (2009) and Lindsay et al. (2022). First, we filtered the list from Lindsay et al. (2022) for non-native and cryptogenic vascular plant species, and then identified aquatic species based on their characteristic habitats and morphology. Nomenclature therefore mostly follows Lindsay et al. (2022) except for *Pontederia crassipes* and *Pontederia vaginalis* for which we follow Pellegrini et al. (2018). Species known only from cultivation were not included in Lindsay et al. (2022) therefore we checked the checklist of Chong et al. (2009) and included some species from there, supplemented with species that were reported in the NParks Flora and Fauna Web (2022) for the purpose of highlighting species that are commonly planted in managed freshwater habitats and may have ecological significance, e.g., these could potentially escape cultivation and establish themselves as casuals, as was the case for *Echinodorus grandiflorus* (Chen et al., 2021). Personal observations of two species, *Hygrophila polysperma* Anderson and *Sagittaria platyphylla* (Engelm.) J.G.Sm., that have escaped cultivation (i.e., should be considered casuals) but were not included in Lindsay et al. (2022) are also reported here. Although the non-native status for cryptogenic species (many of which are casual weeds) cannot be determined with certainty, we nevertheless included these in our list for several reasons. Firstly, many cryptogenic species thrive in open, urban or heavily human-influenced habitats, rather than in forested natural habitats, and are possibly naturalised from other parts of the region (Lok et al., 2010). Secondly, these species often possess superior dispersal capabilities that allow them to rapidly colonise new sites (Carlton, 1996). Thirdly, several of these cryptogenic species are known to be noxious weeds in multiple geographical regions around the world, e.g., *Hydrilla verticillata* and *Salvinia molesta* D.S.Mitch (Pieterse & Murphy, 1993). As such, the statuses of cryptogenic species should be monitored alongside the species known to be non-native.

Across the literature, different categories of plants have been classified as 'macrophytes' depending on their life-form and habitat type (Cook, 1999). Categorising 'emergent' macrophytes can be particularly controversial since many typically terrestrial species are opportunistic and often colonise waterlogged environments (e.g., *Dillenia suffruticosa* (Griff. ex Hook.f. & Thomson) Martelli), or are associated with freshwater habitats (e.g., large native ferns like *Angiopteris evecta* (Forst.) Hoffm. and *Alsophila latebrosa* Wall. ex Hook.). For our purposes, we adopt a relatively conservative definition of 'macrophyte' that includes submerged and floating hydrophytes, as well as herbaceous and shrub-like emergent macrophytes that are associated with aquatic habitats. The intention here is

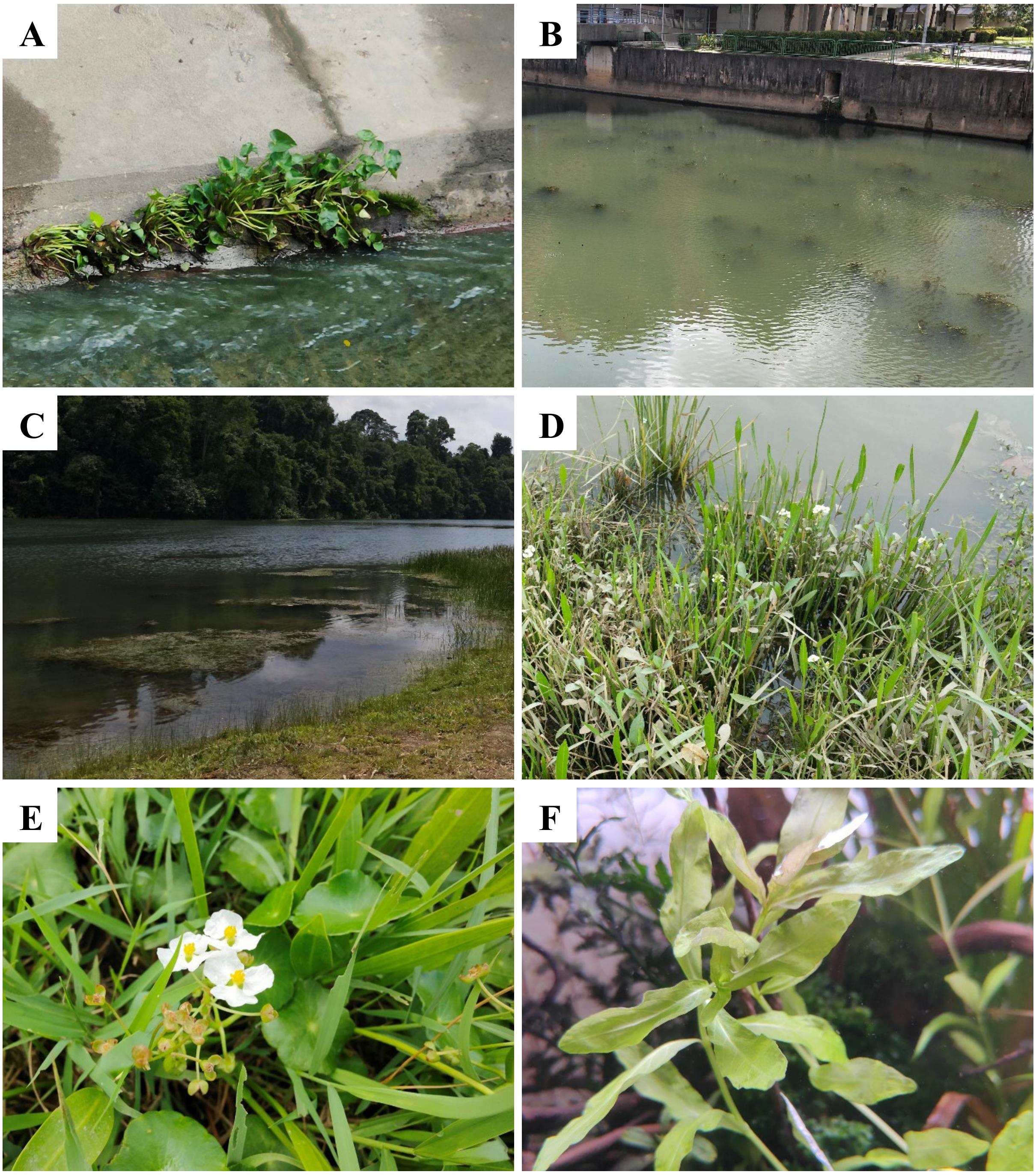

Fig. 1. Examples of non-native macrophyte occurrences in urban water bodies. (A) *Pontederia vaginalis* plants growing from a crack in a concrete canal in Bedok. (B) *Hydrilla verticillata* stands growing in a section of the canalised Kallang River. (C) Floating canopies of *Mayaca fluviatilis* at MacRitchie Reservoir. (D) Periodically inundated bank of the canalised Sungei Ulu Pandan. Several non-native macrophyte species were observed from the site, including *Alternanthera reineckii*, *Pontederia vaginalis*, and *Hydrocotyle verticillata*. (E) Flowers, fruits, and foliage of *Sagittaria platyphylla* and (F) submersed foliage of *Hygrophila polysperma*, for which specimens were collected for the first time in Singapore from the Sungei Ulu Pandan site. Voucher specimens for *S. platyphylla* and *H. polysperma* have been submitted to the Singapore Botanic Gardens Herbarium under voucher numbers SING 2022-808 and SING 2022-827 and barcodes SING 0364348 and SING 0364350, respectively. (Photographs by Darren Sim).

to highlight species that can potentially fulfil similar ecological niches as macrophytes, even if they are not obligately aquatic.

Although the flora of Singapore is relatively well-documented (Chong et al., 2011; Lindsay et al., 2022), counts of non-native vascular macrophyte species presented in this paper are likely to be an underestimate due to two reasons. Firstly, macrophyte communities in most of Singapore's vast lengths of waterways have yet to be comprehensively surveyed. This is especially the case for large urban canals, where it can be difficult to inspect the vegetation up close. For instance, an examination of flora at lower Sungei Ulu Pandan in 2017 found two previously unreported macrophyte species, *Sagittaria platyphylla* (Engelm.) J.G.Sm. and *Hygrophila polysperma* (Roxb.) T.Anderson, to have spontaneously established along the bank (Fig. 1D–F). Secondly, an ever-increasing number of non-native species are planted intentionally at managed waterways for ornamental purposes, making it a challenging task to curate a comprehensive list of non-native macrophytes. Vegetation surveys at representative waterways will be necessary to obtain a clearer picture of macrophyte biodiversity.

LIFE-FORM, ECOLOGICAL AND HABITAT CHARACTERISTICS

As alluded to earlier, non-native macrophytes occur mainly in exposed urban freshwater environments, a sharp contrast to native macrophytes that usually grow in shaded less-disturbed freshwater habitats. For each macrophyte life-form category, we highlight some main ecological and habitat characteristics that the non-native macrophytes within that category have in common.

Submerged. This category includes species with vegetative parts that grow completely submerged in the water, either rooted to the substrate or suspended in the water (Fig. 2A). These are rarely sighted in canals and drains but are more frequent in standing water bodies such as reservoirs and ponds or at lotic sites with deep, slow-moving water, in which case they can form dense stands. Only two species are reported to form large populations. The first, *Hydrilla verticillata*, a now-cosmopolitan species with origins in Asia (Cook & Lüönd, 1982; Langeland, 1996), is the most common and occurs in several reservoirs, ponds and in some canals (Yeo & Lim, 2011; pers. obs.), and the other is *Mayaca fluviatilis* Aubl., a Neotropical species found in MacRitchie and Lower Peirce Reservoirs (Niissalo & Leong-Škorničková, 2019) (Fig. 1C). Both species exhibit rapid growth rates and tend to form thick underwater canopies. The cryptogenic weeds *Utricularia gibba* L. and *Utricularia aurea* Lour. have also been observed in some reservoirs and ponds (pers. obs.).

Free-floating. This category includes species that grow freely floating on the water surface, with roots suspended in the water (Fig. 2B). This life-form is most frequently observed in ponds, and occasionally in reservoirs and slow-flowing waterways with near-stagnant sections. Known for their rapid growth rates and the potential to cover entire water surfaces if left unchecked, common species with this life-form include water hyacinth (*Pontederia crassipes* Mart.), water spangle (*Salvinia molesta*), and duckweeds (*Spirodela polyrhiza* (L.) Schleid., *Wolffia globosa* (Roxb.) Hartog & Plas). Some emergent species may develop floating growth forms, i.e., buoyant structures and modified stems, leaves or roots (Schweingruber et al., 2020), that allow them to creep over the water surface, potentially forming large, free-floating mats or islands if detached from the shore, which has been observed locally for *Ludwigia adscendens* (L.) H.Hara (Fig. 2F) and *Persicaria barbata* (L.) H.Hara (pers. obs.), and can potentially also occur in *Hanguana anthelminthica* (Blume ex Schult. & Schult.f.) Masam. (Leong-Škorničková & Niissalo, 2017).

Floating-leaved. This category includes species that grow rooted in the substrate but with leaves extending upwards and floating on the water surface (Fig. 2C). Membranous submerged leaves usually also develop underwater (Schweingruber et al., 2020). This life-form is sometimes observed in the shallows of reservoirs and ponds, and in rural streams with natural substratum. Most wild specimens were originally intentionally introduced as ornamentals, although populations of *Nelumbo nucifera* Gaertn and *Nymphaea* sp. have been observed outside of cultivation in Kranji Reservoir (Fig. 2C) and Clementi Forest (Fig. 2D), respectively. As such, we suggest to change the status of *Nelumbo nucifera* from 'Cultivated' to 'Casual', and similarly for the *Nymphaea* sp. once the identity of the population can be confirmed.

Emergent. This category generally includes species that can grow partially submerged in water but with most vegetative parts exposed in air (Fig. 2E). This life-form is the least clearly defined and includes species with varying degrees of aquatic adaptation. Many species are also able to adapt to fully submerged environments by altering their morphology, e.g., *Mayaca fluviatilis* gradually transitions from a compact, scale-leaved form to a larger, needle-leaved form when immersed in water. This life-form is typically found along riverbanks or in the littoral zones of reservoirs, ponds and other lentic habitats. Species such as *Typha* spp., *Thalia* spp. and *Cyperus* spp. are commonly planted as ornamentals in aquatic environments (NParks Flora & Fauna Web, 2022*)*. In canals and drains, *Pontederia vaginalis* and *Limnocharis flava* may occur as opportunists. In marshy, water-logged areas, helophytic species from the families Araceae (e.g., *Alocasia macrorrhizos* (L.) G.Don, *Colocasia esculenta* (L.) Schott) and Poaceae (e.g., *Arundo donax* L., *Urochloa mutica* (Forssk) T.Q.Nguyen) tend to be more dominant, especially around reservoirs, e.g., the surrounding forest around MacRitchie Reservoir and at Kranji Marshes near Kranji Reservoir.

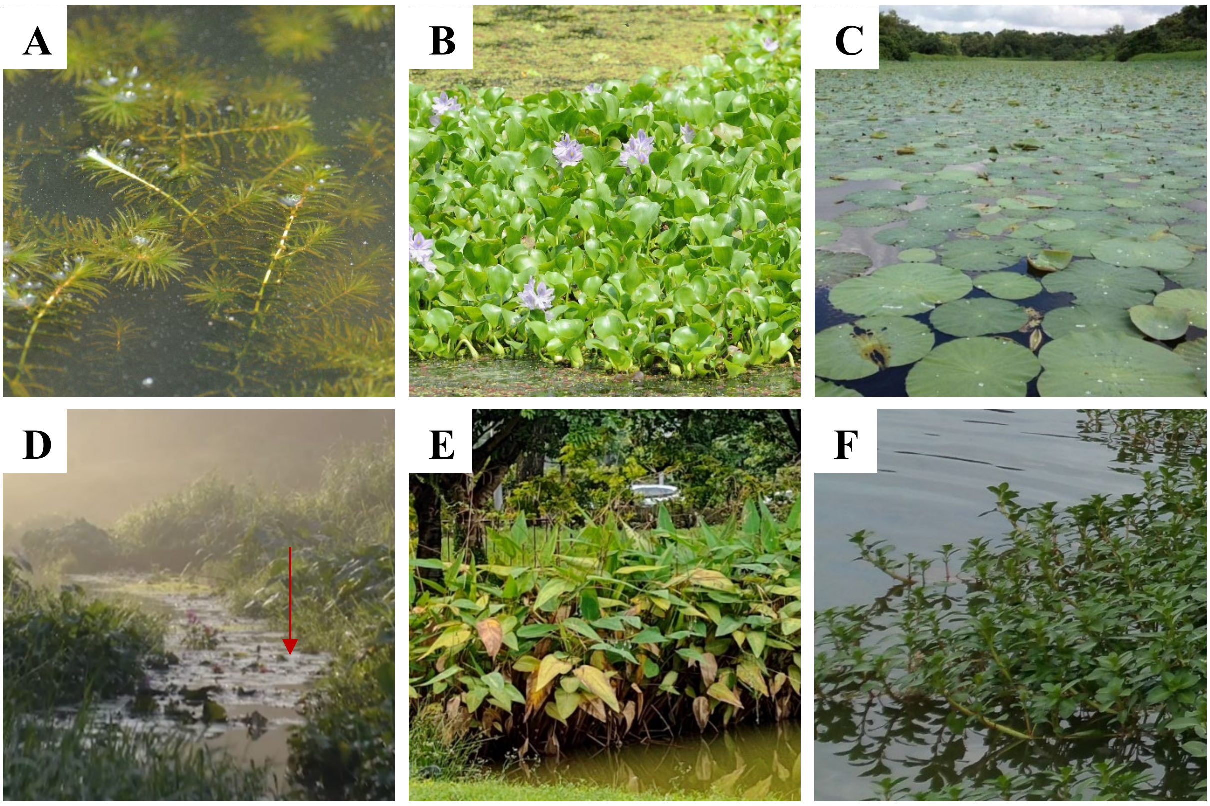

Fig. 2. Examples of different macrophyte life-forms at freshwater sites around Singapore, including both naturalised and cultivated exotics. (A) Submerged *Hydrilla verticillata* and (B) free-floating *Pontederia crassipes* growing in ponds at Sungei Buloh Wetland Reserve. (C) Floating-leaved *Nelumbo nucifera* growing in Kranji Reservoir and (D) *Nymphaea* sp. growing in a freshwater stream at Clementi Forest. (E) Emergent *Thalia* sp. in a pond at the Gardens by the Bay. (F) *Ludwigia adscendens* is a creeping emergent species that adapts to a floating habit when growing on the surface of reservoirs and ponds. (Photographs A and B by Tan Heok Hui, C and F by Maxine Mowe, D by Kong Man Jing, E by Darren Sim).

ORIGINS AND PATHWAYS OF INTRODUCTION

Pioneer non-native macrophyte populations are surmised to have first entered local waterways via pathways commonly associated with the introduction of non-native terrestrial plants as well as other aquatic organisms in Singapore. Species such as *Pontederia crassipes* may have been first introduced as animal fodder or vegetable crops, with present naturalised populations being legacy remnants from past agricultural practices (Wee & Corlett, 1986). Many ornamental macrophytes are intentionally planted in urban water bodies and waterways for their aesthetic value, and there is a risk of populations escaping cultivation and naturalising in Singapore, as has been observed for *Hydrocotyle verticillata* (Lim et al., 2014) and *Echinodorus grandiflorus* (Chen et al., 2021).

More recently, some commonly traded aquarium species have been sighted in urban freshwater habitats, such as *Mayaca fluviatilis* in MacRitchie and Lower Peirce Reservoirs (Niissalo & Leong-Škorničková, 2019), *Ammania crassicaulis* Guill. & Perr. in Bishan-Ang Mo Kio Park (Chen et al., 2019) and the spontaneous occurrence of *Hygrophila polysperma* and *Sagittaria platyphylla* in Sungei Ulu Pandan reported here. These species were likely introduced into urban habitats as discarded aquarium specimens or as 'hitchhikers' alongside other aquatic releases by members of the public or traders (Yeo & Chia, 2010; Magalhães et al., 2017), as has been reported in many other parts of the world (e.g., Hussner et al., 2010; Martin & Coetzee, 2011; June-Wells et al., 2012). Singapore's status as an international hub for the aquarium trade (Brunel, 2009; Belle et al., 2011), combined with the local popularity of the aquarium hobby (Ng et al., 2010), has already been implicated in the introduction of non-native fish species into waterways (Yeo & Chia, 2010; Tan et al., 2020). Recent years have also seen particular interest in aquatic plants for 'aquascaping' (Awang, 2020), a style within the aquarium hobby that emphasises their aesthetic values, which could in turn facilitate entry via the aquarium release pathway. Likewise, these factors facilitate the entry of non-native plants presently as well as in the future.

Provided with a suitable environment, many non-native macrophyte species are highly competent colonisers in the absence of competitors owing to their propensity for clonal growth and species traits such as phenotypic plasticity (Fleming & Dibble, 2015). Subsequent dispersal typically occurs via hydrochory, relying on water movements to disperse seeds or, far more frequently, plant fragments. Hence, macrophytes can easily form new populations at multiple points within any continuous waterway or connected water body. Furthermore, mechanical measures (i.e., pulling or pruning) to remove macrophytes may inadvertently facilitate dispersal by creating more viable fragments (Sidorkewicj et al., 2000), which should be accounted for if the spread of these macrophytes is deemed to be undesirable.

RISK OF INVASION INTO NATURAL HABITATS

Many of the recorded non-native and cryptogenic (henceforth referred to together as 'non-native') macrophytes in Singapore are known to be invasive in other geographical regions, and there are valid concerns that these plants could threaten native biodiversity or cause other undesirable effects should their populations expand unchecked. For instance, *Hydrilla verticillata* and *Pontederia crassipes* are known to be highly problematic cosmopolitan weeds with high invasive potential (Langeland, 1996; Villamagna & Murphy, 2010), and can occur at high densities in certain water bodies and waterways in Singapore (Wee & Corlett, 1986; Tan et al., 2010a; Yee et al., 2019). The Neotropical *Mayaca fluviatilis* has been evaluated to be potentially invasive in Sri Lanka and Australia (Yakandawala & Dissanayake, 2010; Madigan & Vitelli, 2012), and its non-native range also appears to be expanding, with additional recent sightings in Malaysia and China (Jacobsen et al., 2016; Su et al., 2020).

In Singapore, non-native macrophyte populations may occur in sites that are proximate to or share connections with natural waterways. Although this proximity raises the risk of non-native macrophytes dispersing into natural freshwater habitats, few such incursions of non-native macrophytes have been reported, except for isolated patches of *Mayaca fluviatilis* observed in forest streams of the MacRitchie drainage where silt had accumulated under exposed canopy gaps (pers. obs.). Forest streams within the Central Catchment Nature Reserve in particular have thus far managed largely to resist invasion despite their connectivity with Upper Peirce and MacRitchie Reservoirs, which support large stable populations of *Hydrilla verticillata* and *Mayaca fluviatilis* respectively (Niissalo & Leong-Škorničková, 2019).

Strong contrasts in environmental conditions, especially of light, might be a key factor preventing non-native macrophytes from colonising less-disturbed habitats, a pattern that has also been observed in other regions (e.g., Evangelista et al., 2017; Kankanamge et al., 2019; Mouton et al., 2019). Similarly, in Singapore, non-native species thrive in reservoirs and ponds, which are generally exposed, unshaded environments with higher pH and conductivity values (Yeo & Lim, 2011; Clews et al., 2014). Urban waterways also share these characteristics (Yeo & Lim, 2011; Blakely et al., 2014), which could facilitate the colonisation of emergents like *Pontederia vaginalis* and *Limnocharis flava*. Conversely, natural habitats such as forest streams and freshwater swamp forest are deeply shaded by forest cover, while water conditions tend towards lower temperature, pH and conductivity values (Yeo & Lim, 2011; Blakely et al., 2014). As such, many non-native macrophytes may be incompatible with the natural habitats in Singapore, especially the faster-growing, potentially invasive species such as *Hydrilla verticillata*, *Mayaca fluviatilis* and *Pontederia crassipes*. Further research would be required to confirm the factors contributing to this apparently strong biological filtering effect.

CAUSE FOR CONCERN OR A SUBTLE BENEFACTOR?

Considering their apparent incompatibility with shaded, forested freshwater habitats, non-native macrophyte populations pose little threat to Singapore's natural freshwater ecosystems and their constituent native biota—as long as they remain little-disturbed/fairly intact. Likewise, non-native macrophytes in urban waterways are generally expected to have little ecological impact on native biota, since these waterways are populated mainly by non-native species (Tan et al., 2010b; Yeo & Chia, 2010; Tan et al., 2020). Nevertheless, macrophyte stands in urban waterways may still cause undesirable impacts when their populations are unchecked.

In the 1970s, dense infestations of floating macrophytes plagued certain reservoirs, covering large swathes of the water surface, e.g., *Pontederia crassipes* at Kranji Reservoir in 1975 and *Salvinia molesta* at Upper Peirce Reservoir in 1978 (Wee & Corlett, 1986; Wee & Yeoh, 1989; Tan et al., 2010a; Public Service Division, 2015). Such massive infestations could have impacted water quality by limiting gaseous exchange at the water surface and depleting dissolved oxygen (Chamier et al., 2012), while also interfering with environmental aesthetic value and promoting mosquito breeding (Kant & Srivastava, 2004; Jayan & Sathyanathan, 2012), thereby necessitating their removal by extensive mechanical harvesting (Public Utilities Board, 2017). Dense stands of submerged macrophytes in reservoirs and ponds may cause other problems; *Hydrilla verticillata* and *Mayaca fluviatilis* can form underwater canopies that hinder boat travel, clog intake pipes and stagnate water flow, which could potentially promote mosquito breeding or interfere with reservoir operations (Kant & Srivastava, 2004; Gettys et al., 2014). Furthermore, these canopies tend to trap algal scum, rubbish and other debris, which can be especially unsightly (Public Utilities Board, 2017).

Despite the abovementioned detriments and costs, non-native macrophytes may yet offer various environmental and socio-economic benefits. Fast-growing weedy species like *Pontederia crassipes* and *Hydrilla verticillata* have potential applications as bioremediation tools due to their ability to incorporate large quantities of nutrients into their biomass (Evans & Wilkie, 2010; Wang et al., 2012), which can then be harvested to effectively remove nutrients from the waterways in question, particularly in reservoirs. Many macrophytes also efficiently take up heavy metal and organic pollutants (Vardanyan & Ingole, 2006; Rai, 2009), and would have a positive effect on water quality, especially in municipal reservoirs. Studies have shown that the dominance of aquatic vegetation in reservoirs and lakes can alter phytoplankton community structure, suppress phytoplankton abundance and reduce the occurrences of algal blooms (Takamura et al., 2003; Song et al., 2019; Sim et al., 2021). Offering another perspective, non-native macrophytes could also present an opportunity for the ecological rehabilitation of urban or novel freshwater habitats, which are otherwise incompatible with native macrophytes. Non-native macrophytes can thrive in urban or otherwise human-modified open environments where few native macrophytes would do well (Parker & Hay, 2005; Figueiredo et al., 2015), thereby enhancing aquatic biodiversity by modifying hydraulic regimes and providing habitats for native wildlife (Dorotovičová, 2013; Figueiredo et al., 2015)—such floating plant mats have been reported to be an important habitat for the critically endangered grey-headed swamphen (*Porphyrio poliocephalus viridis* (Latham), formerly *Porphyrio porphyrio viridis* Begbie) (Lok & Subaraj, 2008). Additionally, non-native macrophytes could potentially offer new ecosystem services, particularly the regulation of water quality in lentic habitats (Everard & Moggridge, 2012; Finlay & Vogt, 2016), in environments where native species have thus far been unable to establish to any significant degree. As such, a more nuanced approach to non-native macrophyte management could be warranted in these scenarios to balance both their negative qualities and their potential benefits.

At this juncture, our understanding of macrophyte ecology in Singapore freshwater habitats remains largely superficial. Nevertheless, macrophytes have recently seen greater incorporation into the management of urban waterways and water bodies (Lim & Lu, 2016; Chye, 2018; Yeo, 2020), particularly via floating wetland installations in large water bodies (Wong et al., 2013; Sim et al., 2015; Sajan, 2021) and the naturalisation of existing canals (Sim et al., 2015; Lim & Lu, 2016; Lim, 2019; Wilkinson et al., 2021; Kok, 2022). Since many specific details of macrophyte ecology are unresolved, e.g., interactions between native and non-native species and their contribution to tropic food webs, further research will be necessary to evaluate the ecological roles of both native and non-native macrophytes, and in turn inform macrophyte-waterway management strategies. To facilitate such efforts, it will be necessary to cultivate a deeper understanding of the roles that macrophytes can play in our urban freshwater landscape.

CONCLUSIONS

The modified freshwater habitats of Singapore's urban landscape have been colonised by numerous macrophytes, including many non-native and cryptogenic species. However, to date, much about their ecology remains poorly understood. Recent years have seen a growing number of new non-native macrophyte introductions, which could have been facilitated by demand for ornamental plants in landscaping and the popularity of the local aquarium hobby. Many introduced species are recognised as being potentially invasive based on assessments from other geographical regions, although they have thus far exhibited little ability to expand into natural freshwater habitats here, possibly due to environmental incompatibility. Although there are clear negative consequences to unchecked macrophyte growth in many urban environments, managed aquatic vegetation can in some circumstances provide useful services. Further research into the diversity and ecology of urban aquatic vegetation would be required to better understand the extents of their impacts and benefits and to devise optimal management strategies.

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APPENDIX

Table A1: Checklist of vascular macrophytes recorded as being non-native or cryptogenic in Singapore. Status follows Lindsay et al. (2022) except for those marked with a plus-sign (+) which are first reported in this paper or with an asterisk (*) which is a new status proposed based on our observations. Native range information was cross-referenced from Lok et al. (2010), NParks Flora & Fauna Web (2022), and the POWO (2022) database. Life-form: **Su**: Submerged; **FF**: Free-floating; **FL**: Floating-leaved; **Em**: Emergent.

Family	Species	Status	Life-form	Native range
Pteridaceae	*Adiantum capillus-veneris* L.	Naturalised	Em	N. to S. America
	Ceratopteris thalictroides (L.) Brongn.	Cryptogenic	Em/Su/FF	Pantrop.
	Pityrogramma calomelanos (L.) Link	Naturalised	Em	Trop. America
Salviniaceae	*Azolla pinnata* R.Br. ssp. *asiatica* R.M.K.Saunders & K.Fowler	Naturalised	FF	Asia to New Guinea
	Salvinia molesta D.S.Mitch.	Naturalised	FF	Trop. America
Acanthaceae	*Hygrophila auriculata* (Schumach.) Heine	Casual	Em/Su	Trop. Asia
	Hygrophila phlomoides Nees	Casual	Em/Su	New Guinea
	Hygrophila polysperma (Roxb.) T. Anderson	Casual+	Em/Su	SE. Asia
	Justicia gendarussa Burm.f.	Naturalised	Em	Trop. Asia
	Justicia procumbrens L.	Naturalised	Em	Trop. & Subtrop. Asia
Acoraceae	*Acorus calamus* L.	Naturalised	Em	Eurasia
Alismataceae	*Echinodorus grandiflorus* (Cham. & Schltdl.) Micheli	Casual	Em/Su	S. America
	Limnocharis flava (L.) Buchenau	Naturalised	Em	Trop. America
	Sagittaria platyphylla (Engelm.) J.G. Sm.	Casual+	Em/Su	N. to C. America
Amaranthaceae	*Alternanthera philoxeroides* (Mart.) Griseb.	Naturalised	Em/FF/Su	Trop. America
	Alternanthera sessilis (L.) DC.	Cryptogenic	Em	Trop. Asia to Trop. Australia
Araceae	*Alocasia macrorrhizos* (L.) G.Don	Naturalised	Em	Trop. Asia to Trop. Australia
	Colocasia esculenta (L.) Schott	Casual	Em	Asia to Pacific
	Dieffenbachia seguine (Jacq.) Schott var. *seguine*	Casual	Em	Trop. America
	Lemna perpusilla Torr.	Naturalised	FF	Cent. America
	Lemna aequinoctialis Welw.	Naturalised	FF	Pantrop.
	Pistia stratiotes L.	Naturalised	FF	Pantrop.
	Spirodela polyrhiza (L.) Schleid.	Cryptogenic	FF	Cosmopolitan
	Typhonium flagelliforme (Roxb. ex G.Lodd.) Blume	Cryptogenic	Em	Asia to Trop. Australia
	Wolffia globosa (Roxb.) Hartog & Plas	Cryptogenic	FF	Trop. & Subtrop. Asia

Family	**Species**	**Status**	**Life-form**	**Native range**
Araliaceae	*Hydrocotyle verticillata* Thunb.	Casual	Em/Su	N. to S. America
Asteraceae	*Sphagneticola trilobata* (L.) Pruski	Naturalised	Em	Trop. America
Balsaminaceae	*Hydrocera triflora* (L.) Wight & Arn.	Naturalised	Em	Trop. Asia
Brassicaceae	*Cardamine hirsuta* L.	Casual	Em	Eurasia to N. Africa
Campanulaceae	*Lobelia chinensis* Lour.	Naturalised	Em	Cont. Asia
Cannaceae	*Canna indica* L.	Naturalised	Em	Trop. America
Commelinaceae	*Murdannia nudiflora* (L.) Brenan	Cryptogenic	Em	Trop. & Subtrop. Asia
Cyperaceae	*Cyperus odoratus* L.	Naturalised	Em	Pantrop.
	Cyperus sphacelatus Rottb.	Naturalised	Em	S America to trop. Africa
	Mapania macrocephala ssp. *longifolia* (Boeckeler) D.A.Simpson	Casual	Em	Australasia
Fabaceae	*Aeschynomene americana* L.	Naturalised	Em	Trop. America
	Aeschynomene indica L.	Naturalised	Em	Cent. America
	Neptunia plena (L.) Benth.	Naturalised	Em/FF	Trop. America
Hydrocharitaceae	*Blyxa aubertii* Rich.	Cryptogenic	Su	SE. Asia
	Blyxa japonica (Miq.) Maxim. ex Asch. & Gürke var. *alternifolia* (Miq.) C.D.K.Cook & Lüönd	Cryptogenic	Su	SE. Asia to Japan
	Hydrilla verticillata (L.f.) Royle	Cryptogenic	Su	Eurasia, Australia, Africa
	Najas indica (Willd.) Cham.	Cryptogenic	Su	Trop. & Subtrop. Asia
	Najas malesiana W.J.de Wilde	Cryptogenic	Su	SE Asia to N. Australia
Lamiaceae	*Pogostemon auricularius* (L.) Hassk.	Cryptogenic	Em/Su	Trop. & Subtrop. Asia
Lentibulariaceae	*Utricularia aurea* Lour.	Cryptogenic	Su	Trop. & Subtrop. Asia, Trop. Australia
	Utricularia bifida L.	Cryptogenic	Em/Su	Trop. & Subtrop. Asia
	Utricularia caerulea L.	Cryptogenic	Em/Su	Trop. Africa, Asia, Australia
	Utricularia gibba L.	Cryptogenic	Su	Pantrop.
	Utricularia minutissima Vahl	Cryptogenic	Em/Su	Asia to Australia
Lythraceae	*Ammannia baccifera* L.	Naturalised	Em/Su	India
	Ammannia crassicaulis Guill. & Perr.	Naturalised	Em/Su	Africa
Nelumbonaceae	*Nelumbo nucifera* Gaertn.	Casual*	Em/FL/Su	India to East Asia
Onagraceae	*Ludwigia adscendens* (L.) H.Hara	Cryptogenic	Em/FF	Trop. Asia, Autralia, America

Family	Species	Status	Life-form	Native range
	Ludwigia hyssopifolia (G.Don) Exell	Cryptogenic	Em	S. America
	Ludwigia octovalvis (Jacq.) P.H.Raven	Cryptogenic	Em	Pantrop.
	Ludwigia peruviana (L.) H.Hara	Naturalised	Em	S. America
	Ludwigia prostrata Roxb.	Cryptogenic	Em	Trop. & Subtrop. Asia
Pandanaceae	*Pandanus amaryllifolius* Roxb.	Casual	Em	Trop. Asia
Plantaginaceae	*Bacopa caroliniana* (Walter) B.L.Rob.	Naturalised	Em/Su	Trop. America
	Bacopa monnieri (L.) Wettst.	Cryptogenic	Em/Su	Pantrop.
	Limnophila chinensis (Osbeck) Merr. ssp. *aromatica* (Lam.) T. Yamaz.	Cryptogenic	Em/Su	Trop. & Subtrop. Asia, Trop. Australia
	Limnophila chinensis (Osbeck) Merr. ssp. *chinensis*	Cryptogenic	Em/Su	Trop. & Subtrop. Asia, Trop. Australia
	Limnophila laxa Benth.	Cryptogenic	Em/Su	SE. Asia
	Limnophila sessiliflora (Vahl) Blume	Cryptogenic	Em/Su	Trop. & Subtrop. Asia
	Limnophila villosa Blume	Cryptogenic	Em/Su	SE. Asia
Poaceae	*Arundo donax* L.	Casual	Em	Trop. & Subtrop. Asia
	Coix lacryma-jobi L.	Naturalised	Em	Trop. Asia
	Cynodon dactylon (L.) Pers.	Naturalised	Em	Africa
	Eriochloa meyeriana (Nees) Pilg.	Naturalised	Em	Africa, Arab Peninsula
	Panicum brevifolium L.	Casual	Em	Trop. Africa and Asia
	Panicum laxum Sw.	Naturalised	Em	Trop. & Subtrop. America
	Panicum repens L.	Naturalised	Em	Trop. & Subtrop. Asia, Africa
	Paspalum conjugatum P.J.Bergius	Naturalised	Em	Trop. & Subtrop. America
	Paspalum virgatum L.	Naturalised	Em	Trop. & Subtrop. America
	Rottboellia cochinchinensis (Lour.) Clayton	Naturalised	Em	Trop. & Subtrop. Asia, Africa, Australia
	Saccharum spontaneum L.	Naturalised	Em	Africa, Asia, Australia, Italy
	Setaria barbata (Lam.) Kunth	Naturalised	Em	Trop. & Subtrop. Asia, Africa
	Setaria palmifolia (J.Koenig) Stapf	Casual	Em	Trop. & Subtrop. Asia, Australia
	Stenotaphrum secundatum (Walter) Kuntze	Naturalised	Em	Africa
	Thysanolaena latifolia (Roxb. ex Hornem.) Honda	Naturalised	Em	Trop. & Subtrop. Asia
	Urochloa mutica (Forssk.) T.Q.Nguyen	Naturalised	Em	Africa
	Urochloa piligera (F.Muell. ex Benth.) R.D.Webster	Naturalised	Em	Sulawesi, Australia

Family	Species	Status	Life-form	Native range
Polygonaceae	*Persicaria barbata* (L.) H.Hara var. *gracilis* (Danser) H.Hara	Cryptogenic	Em/FF	Trop. Asia
	Persicaria hydropiper (L.) Delarbre	Casual	Em	Asia to Australia
	Persicaria odorata (Lour.) Sojak	Casual	Em	SE Asia
	Persicaria orientalis (L.) Spach	Naturalised	Em	Asia to Australia
	Pontederia crassipes Mart.	Naturalised	FF	Trop. America
	Pontederia hastata L.	Cryptogenic	Em	Trop. & Subtrop. Asia
	Pontederia vaginalis Burm.f.	Cryptogenic	Em	Trop. & Subtrop. Asia, Trop. Australia

Table A2: Checklist of cultivated-only non-native vascular macrophytes in Singapore, including species that are frequently planted at urban freshwater sites. Life-form: **Su**: Submerged; **FF**: Free-floating; **FL**: Floating-leaved; **Em**: Emergent. *Casual populations of *Nymphaea* sp. have been observed but have not yet been identified to species level.

Family	Species	Life-form	Native range
Equisetaceae	*Equisetum hyemale* L.	Em	Eurasia, N. America
	Equisetum ramosissimum Desf.	Em	Europe
	Equisetum scirpoides Michx.	Em	Europe
Marsileaceae	*Marsilea crenata* C.Presl	Em/Su	SE. Asia to Australia
Pteridaceae	*Adiantum raddianum* C.Presl	Em	Trop. America
Salviniaceae	*Salvinia auriculata* Aubl.	FF	Trop. America
Acoraceae	*Acorus gramineus* Aiton	Em	Trop. & Subtrop. Asia
Alismataceae	*Echinodorus palifolius* (Nees & Mart.) J.F.Macbr.	Em/Su	Trop. America
	Sagittaria latifolia Willd.	Em	N. to S. America
	Sagittaria sagittifolia L.	Em/Su	Eurasia
Amaryllidaceae	*Crinum album* (Forssk.) Herb.	Em	SW. Arab. Peninsula
	Crinum jagus (J.Thomps.) Dandy	Em	Trop. Africa
	Crinum moorei Hook.f.	Em	S. Africa
	Hymenocallis speciosa (L.f. ex Salisb.) Salisb.	Em	Caribbean
Araceae	*Alocasia cucullata* (Lour.) G.Don	Em	Trop. & Subtrop. Asia
	Anubias barteri Schott var. *glabra* N.E.Br.	Em/Su	Trop. Africa
	Montrichardia arborescens (L.) Schott	Em	Trop. America
	Typhonodorum lindleyanum Schott	Em	E. Africa to Madagascar
	Zantedeschia aethiopica (L.) Spreng.	Em	S. Africa
	Zantedeschia albomaculata (Hook.) Baill.	Em	S. Africa
Araliaceae	*Hydrocotyle javanica* Thunb.	Em	Trop to Subtrop. Asia
	Hydrocotyle umbellata L.	Em/Su	N. to S. America
Brassicaceae	*Nasturtium officinale* W.T.Aiton	Em/Su	Eurasia to N. Africa
Campanulaceae	*Lobelia cardinalis* L.	Em/Su	N. America
Cannaceae	*Canna glauca* L.	Em	Trop. America
Cyperaceae	*Cyperus alternifolius* L.	Em	Africa
	Cyperus papyrus L.	Em	Africa

Family	Species	Life-form	Native range
	Isolepis cernua (Vahl) Roem. & Schult.	Em	Widespread
	Rhynchospora latifolia (Baldwin ex Elliott) W.W.Thomas	Em	N. America
Hydrocharitaceae	*Ottelia alismoides* (L.) Pers.	Su	Trop. Asia to Trop. Australia
Iridaceae	*Iris laevigata* Fisch.	Em	S. Sibera to Japan
Lamiaceae	*Mentha arvensis* L.	Em	Eurasia
Lythraceae	*Trapa natans* L.	Su/FF	Eurasia, Africa
Marantaceae	*Calathea crocata* (É.Morren & Joriss.) Borchs. & S.Suárez	Em	Brazil
	Schumannianthus benthamianus (Kuntze) Veldkamp & I.M.Turner	Em	SE Asia
	Thalia dealbata Fraser ex Roscoe	Em	N. and C. America
	Thalia geniculata L.	Em	Trop. America and Africa
Nymphaeaceae*	*Nymphaea capensis* Thunb.	FL/Su	Africa
	Nymphaea nouchali Burm.f.	FL/Su	Trop. Africa, Asia, Australia
	Nymphaea pubescens Willd.	FL/Su	Trop. & Subtrop. Asia, Trop. Australia
	Nymphaea rubra Roxb. ex Salisb.	FL/Su	Trop. Asia
	Victoria amazonica (Poepp.) Klotzsch	FL/Su	S. America
	Victoria cruziana A.D.Orb.	FL/Su	S. America
Onagraceae	*Ludwigia sedoides* (Bonpl.) H.Hara	Su/FF	Trop. America
Plantaginaceae	*Micranthemum micranthemoides* (Nutt.) Wettst.	Em/Su	N. America
Poaceae	*Chrysopogon zizanioides* (L.) Roberty	Em	SE Asia
	Cymbopogon citratus (DC.) Stapf	Em	Trop. Asia
	Cymbopogon nardus (L.) Rendle	Em	Trop. Asia
	Setaria sphacelata (Schumach.) Stapf & C.E.Hubb.	Em	Africa
	Tripsacum dactyloides (L.) L.	Em	N. to S. America
	Zizania latifolia (Griseb.) Hance ex F.Muell.	Em	Subtrop. to Temp. Asia
Pontederiaceae	*Pontederia azurea* (Sw.) Kunth	Su/FF/Em	Trop. America
	Pontederia cordata L.	Em	N. to S. America
Saururaceae	*Houttuynia cordata* Thunb.	Em	Trop. & Subtrop. Asia