

## The biological, ecological and conservation significance of freshwater swamp forest in Singapore

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**ABSTRACT.** The Nee Soon stream drainage in the Central Catchment Nature Reserve is virtually the last remaining fragment of primary freshwater swamp forest in Singapore. The forest type has been poorly studied in the Southeast Asia. The hydrology, water quality, as well as aquatic flora and fauna all have great theoretical and practical significance. The ecology and management of the Nee Soon freshwater swamp forest are reviewed, with remarks on their national, regional and global contexts. This review sets the scene for a three-year integrated conservation and management study completed in 2016.

**Keywords.** Biodiversity, climatology, hydrology, nutrient cycle, research gaps, tropical wetlands

### Introduction

Globally, freshwater swamp forests occur in Southeast Asia, Africa, and South America, with the largest proportion in the Amazon basin (Richards, 1996). In Southeast Asia, they are located throughout the region, often near large rivers such as the Mekong and Chao Phraya in Thailand, and the Irrawaddy in Myanmar, and in many smaller systems such as the Sedili rivers in Johor (Corner, 1978; Whitmore, 1984).

This unique forest formation is mostly restricted to the alluvial soil of flood plains, often on the landward side of mangrove forests or in areas with a high water table (Göltenboth et al., 2006). While freshwater swamp forests are often located in areas with a wet climate, they are also found in seasonally drier regions such as in west New Guinea and east Java (Whitmore, 1984).

In Southeast Asia, freshwater swamp forest is a rather understudied forest type, mainly owing to its inaccessibility and the occurrence of insect-borne diseases within them (Yamada, 1997). Other wetland habitats, such as mangrove and peat swamp forests, have tended to receive more attention (Dudgeon, 2000). Nevertheless, the freshwater swamp forests of Peninsular Malaysia were surveyed relatively comprehensively by Corner (1978), and additional work has been done in Cambodia (Theilade et al., 2011) and Singapore (Ng & Lim, 1992; Turner et al., 1996; Lim et al., 2011).

Freshwater swamp forest can be broadly characterised as forest that is subjected to flooding with relatively mineral-rich fresh water (Whitmore, 1984). As tropical freshwater swamp forest is a formation of tropical rainforest, several environmental conditions are common between freshwater swamp forests and other tropical rainforest formations (e.g. high humidity levels and solar irradiance; see Richards, 1996). However, beyond these commonalities, conditions found within freshwater swamp forests and other tropical rain forest formations can differ greatly. Flooding in inland, freshwater swamp forests is usually semi-permanent, irregular, or seasonal. Water depth also varies tremendously, ranging from a few centimetres to several metres. These physical factors, acting individually or synergistically, impact the ecology of freshwater swamp forests. Indeed, previous work by de Pádua Teixeira et al. (2011) concluded that drainage patterns were the most prominent factor in the spatial organisation of plants in the swamp forests of Brazil. Despite the variable nature of freshwater swamp forests, sufficient water is always present during the growing season, which ensures that organisms adapted to living in water or waterlogged soils flourish (Junk et al., 2011).

Freshwater swamp forests have several sources of water, including rain, rivers, and groundwater, whereas peat swamp forests obtain their water solely from rain (Richards, 1996; Göltenboth et al., 2006). The colour of the water in the freshwater swamp forest is often an indication of the levels of plant matter present in the water and soil.

### Management of freshwater swamp forests

Freshwater swamp forest soils are relatively nutrient-rich, unlike ombrotrophic swamp forests, which receive nutrients solely via rain (Yule & Gomez, 2009). In freshwater swamp forests, nutrients and alluvial soils are subsequently deposited within the forest via rain and water table fluctuations (Whitmore, 1984; Richards, 1996; Whitten et al., 2000; Göltenboth et al., 2006). The nutrient-rich soils in freshwater swamp forests have resulted in over-exploitation for agriculture, such as wetland rice cultivation (Richards, 1996; Whitten et al., 2000; Corlett, 2009) and oil palm plantations (Yule & Gomez, 2009). Indeed, Chokkalingam et al. (2007) reported that in southern Sumatra, fire of varying intensities was utilized to clear the swamp forest for agricultural purposes. The widespread and repeated fires there transformed a diverse and complex habitat into a habitat consisting of uniform stands of fire-resistant *Melaleuca* L. species thickets. Additionally, mismanagement of these ecosystems via extensive logging and

conversion to agriculture has led to severe degradation and loss of ecological and biological diversity (Rijksen & Peerson, 1991; Hansen et al., 2009; Yule, 2010).

The conceptual model presented in this review explores the direct and indirect effects of hydrology, physico-chemistry, stream morphology, and vegetation on the macroinvertebrate and fish communities.

The following sections will explore and review the hydrology, physico-chemistry, as well as both the aquatic flora and fauna in freshwater swamp forests in Southeast Asia. Owing to the dearth of studies investigating freshwater swamp forests specifically, the literature concerning peat swamp forests was also incorporated, as peat swamps are the habitat most similar to freshwater swamp forests in Southeast Asia.

### Hydrology in freshwater swamp forests

How water flows is a major determinant of geomorphological, biological and biogeomorphological processes and functions within aquatic ecosystems (Poff et al., 1997; Bunn & Arthington, 2002; Davidson et al., 2012; Fig. 1). By influencing geomorphology, flow plays a major role in determining spatial and temporal benthic community structure (Poff & Allan, 1995; Bunn & Arthington, 2002; Mims & Olden, 2013). For example, Leigh & Sheldon (2009) found that hydrological connectivity had a major effect on macroinvertebrate assemblages, with highly connected water bodies displaying greater macroinvertebrate diversity than isolated water bodies, which tended to have fewer diverse assemblages and were dominated by a handful of taxa. Similar effects have been noted in tropical systems where wet or monsoon season flooding has resulted in greater proportions of migratory species and changes in community assemblages (da Silva et al., 2010). On a smaller scale, changes in physical habitat caused by alterations in flow regime can increase habitat heterogeneity and thereby increase species diversity (Downes et al., 1998; Bunn & Arthington, 2002). Furthermore, a highly heterogeneous habitat is able to provide refugia for species during periods of disturbance such as flooding or drought (Bunn & Arthington, 2002; Negishi et al., 2002). In ecosystems where water availability can vary dramatically between seasons, such refugia can become extremely important (Brown, 2003; Leigh et al., 2010).

In some tropical systems there is pronounced seasonal variation in the hydrologic regime between the monsoon and dry seasons (Douglas et al., 2005; Mitsch et al., 2010), though with caveats for Singapore's meteorology as described below. When the monsoon season arrives, heavy rains can create flood pulses which integrate terrestrial and aquatic systems (Davidson et al., 2012). Junk et al. (1989) stressed the importance of seasonal flood pulses through effects such as over-bank flooding, which strongly influences biological community structure through allochthonous inputs and changing of the physical habitat (Douglas et al., 2005; Davidson et al., 2012). For example, in Brazilian floodplains da Silva et al. (2010) found that turbid and anoxic water conditions dominated in the high water season compared to low or falling water

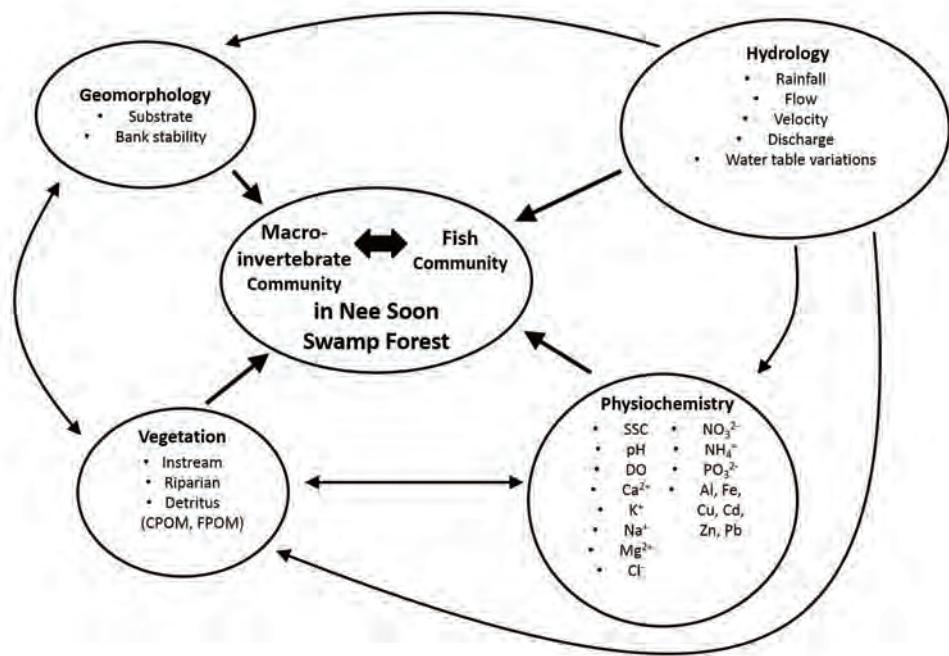
seasons, which had relatively well oxygenated and low turbid waters. The differences in seasonal hydrology impacted fish diversity, abundance and biomass, which were significantly higher in falling and low water seasons than during the high water season (da Silva et al., 2010). In tropical wetland forests similar changes have been documented in macroinvertebrate communities with stream physico-chemistry as well as insect assemblages, density and biomass reflecting fluctuations in seasonal rainfall (Ramirez et al., 2006). How rainfall impacts tropical wetlands, however, is varied and can depend on both regional and local biotic and abiotic factors.

The effect of flood pulses on tropical wetlands can vary because catchment hydrology is influenced by the amount of rainfall and speed of the run-off (Page et al., 2009; Yule, 2010). In tropical peat swamp forests the topography, biodiversity of the forest and its microtopography can buffer the speed of run-off and thus mitigate potential impacts further downstream (Page et al., 2009). On a microtopographical or local scale buffering is partly caused by the presence of hollows, roots, buttresses and pneumatophores (Page et al., 1999). However, what primarily influences rainfall run-off and hydrology in a tropical peat swamp forest is how water flows laterally through the peat and the hydraulic connectivity of the peat near to its surface (Page et al., 1999). If the water table is consistently high, the amount of peat able to be sequestered increases as well as the system's water holding capacity (Page et al., 1999). Alternatively, if the water table is low or if the swamp forest is being drained, the speed of the run-off can become faster because of peat oxidation and subsidence processes (Page et al., 1999, 2009). The impact that faster run-off can have on the catchment varies from flooding downstream to scouring of the soil, which can have an impact on water chemistry.

### Water quality in freshwater swamp forests

Gasim et al. (2007) conducted a detailed physico-chemistry study in the Bebar river in the Pahang peat swamp forests in Peninsular Malaysia where the authors documented low dissolved oxygen (DO) and pH, whilst the average stream flow was estimated at  $5 \times 10^5 \text{ m}^3$  daily. Indeed, the pH recorded ranged from 3.53 to 4.55 whilst DO ranged from 0.54 to  $1.76 \text{ mg L}^{-1}$ . The high organic content and high biological decomposition resulted in a high deoxygenation rate when compared with the reoxygenation rate (Das & Acharya, 2003; Gasim et al., 2007). Similarly, low levels of DO have been observed at the Beriah swamp forest in Perak ( $1.21\text{--}2.14 \text{ mg L}^{-1}$ ; Mashhor et al., 2004). A recent study by Gandaseca et al. (2015), determined the water quality of four rivers in peat swamp forests in Sarawak, Malaysia. The authors also documented low levels of DO ( $4.98\text{--}5.02 \text{ mg L}^{-1}$ ) and attributed this to the high levels of organic matter in the rivers.

Reported ranges of total dissolved solids (TDS) varied from 0.75 to  $15.75 \text{ mg L}^{-1}$ , whilst turbidity ranged from 1.5 to 17.15 NTU. Temporal investigations by Ramirez et al. (2006) on a tropical wet forest documented a decrease in streamwater pH throughout the year, from near neutral ( $\text{pH} > 6.0$ ) to near acidic ( $\text{pH} < 4.5$ ), while  $\text{NO}_3\text{-N}$  concentrations were high throughout the year and were independent of



**Fig. 1.** Conceptual diagram showing the effects of stream morphology, hydrology, vegetation and physico-chemistry on each other and on the macroinvertebrate and fish community in freshwater swamp forests, specifically in the Nee Soon freshwater swamp forest.

discharge. The authors identified that changes in pH were related to both streamwater level and monthly rainfall. Indeed, the decrease in pH was related to the inundation of the streams and an increase in overland flow (Ramírez et al., 2006). Furthermore, Ramírez et al. (2006) noted that discharge and pH changed most during the year and whilst pH decreased, stream discharge increased. The temporal variation in pH was attributed to the increases in the concentration of humic acids suspended in the water column during the wet season. Indeed, previous work by Winterbourn & Collier (1987) observed low pH levels in many New Zealand streams and attributed this to the large inputs of humic acids from surrounding watersheds. Alternatively, temporal variations in conductivity were small and were independent of discharge but were related to groundwater influence (Ramírez et al., 2006).

### Aquatic flora in freshwater swamp forests

The environmental conditions of a tropical freshwater swamp forest are similar to those of a tropical dryland rain forest, but in general, the tree canopy of the freshwater swamp forest is lower than that in the lowland dipterocarp forest (Corner, 1978; Theilade et al., 2011). The vegetation structure in freshwater swamp forests is often dependent on

the nutrients present in the water source and the flooding regime of the forest (Junk et al., 2011). For example, the nutrient-rich *várzea* forests in the lower Amazonian floodplains experience flooding caused by swollen rivers and have the highest species richness among wetland forests in the world (Junk et al., 2011). Alternatively, the vegetation of Brazilian blackwater *igapó* forests is dependent on heavy rains that determine the forests' flood height and duration. *Igapó* forests generally have fewer tree species than *várzea* forests and few herbaceous plant species (Junk et al., 2011). Furthermore, floating plants are rare or absent in this forest type. Freshwater swamp forests are generally less diverse floristically if compared to dryland forests and, as a result, are dominated by one or a few tree species (Corlett, 2009). Often the dominant plant types are used to categorise freshwater swamp forests and the four main types recognized in Southeast Asia are (1) mixed swamp forest; (2) *Melaleuca* species (Myrtaceae) swamp forest; (3) *Terminalia* L. species (Combretaceae) swamp forest; and (4) *Campnosperma* Thwaites species (Anacardiaceae) swamp forest (Göltenboth et al., 2006).

Floristically, freshwater swamp forests are not easily distinguishable from dryland forests at the taxonomic levels of family and genus (Whitmore, 1984). There are few plant species restricted only to freshwater swamp forest ecosystems and usually they tend to form clusters and have species-poor associations (Whitten et al., 2000). The diverse assemblage of forest types are influenced by several environmental factors, including the wide variation of soil content as well as the degree of water inundation (Yamada, 1997).

Depending on the degree of water inundation, a thin layer of peat may be present on the ground surface of freshwater swamp forests. However, the limited decomposition rate of organic matter often results in the development of a peat layer only a few centimetres thick (Whitmore, 1984). The slow decomposition rate is due to high phenolic concentrations in the leaves, which can be up to three times greater than those found in temperate forests (Coley & Barone, 1996). The high concentration of phenols is thought to be a response to the high levels of mammalian and invertebrate predation as well as fungal pathogens (Coley & Barone, 1996). The slow decomposition of organic matter under anoxic conditions causes the release of humic acid, which greatly lowers the pH of the water (Page et al., 1999; Göltenboth et al., 2006; Yule, 2010; Posa et al., 2011). This then affects the floral composition found in swamp forest streams and leads to specialisation of characteristics such as pneumatophores (Whitmore, 1984).

The waterlogged nature of freshwater swamp forests creates soft, unstable, and anoxic waterlogged soil that may have led to the evolution of special root adaptations in freshwater swamp forest trees that are morphologically similar to those found in a true mangrove forest (Corlett, 1986). Special root adaptations such as pneumatophores are common within freshwater swamp forests and work by Corner (1978) noted that pneumatophores typically occur in five forms. For example, in the genus *Sonneratia* L.f., they grow as upright, elongated, conical pegs whereas in the species *Lophopetalum multinervium* Ridl., they develop as erect planks (Corlett, 1986). Pneumatophores help provide stability and aid in gas exchange in the anoxic soil conditions (Corner, 1978).

Other adaptations include buttress roots, that provide stability in the unstable and soft substrates. Furthermore, many trees have lenticellate bark which aids in gas diffusion in anaerobic conditions (Whitten et al., 2000). Many of these root adaptations can be found in Southeast Asia's freshwater swamp forests including those in Singapore.

### Aquatic fauna in freshwater swamp forests

Previous work by Whitten et al. (2000) has documented that the fauna of freshwater swamp forests is as diverse as that found in lowland terra firma forests. However, research in this area is still very lacking (Göltenboth et al., 2006). Nonetheless, Posa et al. (2011) documented that approximately 23–32% of all species of mammals and birds in Peninsular Malaysia and Borneo have been recorded from peat swamp habitats. The proportions of snakes (7–18%) and amphibians (19–23%) are somewhat lower, but nevertheless, the results collated by Posa et al. (2011) do show that peat swamp forests provide habitats for a considerable proportion of the region's fauna.

Additionally, freshwater swamp forests support a number of rare, specialized and threatened species. Posa et al. (2011) found that 45% of mammals and 33% of birds recorded in freshwater swamp forests had an IUCN Red List status of near threatened, vulnerable or endangered. Additionally, Phillips (1998) documented the importance of swamp forests in conserving primates such as proboscis monkeys (*Nasalis larvatus*) and the Bornean banded langur (*Presbytis chrysomelas*). Previous work from Johnson et al. (2005) at Gunung Palung National Park in western Kalimantan, documented a higher density of Bornean orang-utan nests and individuals than in lowland forest. In addition, Cheyne et al. (2009) observed a number of endangered felids (e.g. the flat-headed cat, *Prionailurus planiceps*; the Sunda clouded leopard, *Neofelis diardi*; and the marbled cat, *Pardofelis marmorata*) within swamp forests, whilst Bezuijen et al. (2001) documented swamp forests to be favoured habitat for the endangered false gharial (*Tomistoma schlegelii*).

These results already suggest that freshwater swamp forests are extremely important for conservation, but it must also be remembered that there has been a general bias towards charismatic mammalian species in biodiversity research (Clark & May, 2002). Conversely, invertebrate, fish, amphibian and reptilian research has usually been under-represented (see Wells & Yule, 2008; Yule, 2010), despite the fact that these groups are often much more diverse than mammals, making up some of the dominant animal groups in the forest (Clark & May, 2002). Thus, the importance of freshwater swamp forests in preserving overall faunal diversity has in fact been understated thus far.

Freshwater fish serve as a good example of the importance of freshwater swamp forests to less well known groups. They have been documented as exhibiting extremely high endemicity to swamp forests, up to the point that 33% of known freshwater fish species are associated with peat swamps (Ng et al., 1994; Kottelat et al., 2006). Additionally, Posa et al. (2011) found that out of 219 fish species collated from peat swamps, 80 species are restricted to this ecosystem, while 31 species are point endemic

species found only in single locations. Furthermore, the critically endangered *Betta persephone*, *B. miniopinna* and *B. spilotogena* are listed on the IUCN Red List as highly threatened by extinction as a result of declines in area of occupancy, extent of occurrence and quality of habitat. Additionally, there are 17 species of swamp forest fish on the IUCN Red List classified as vulnerable or endangered, 12 of which are point endemics (Posa et al., 2011). Comprehensive studies of freshwater swamp forest fish have been carried out in only a few regions such as Thailand, central Sumatra, Peninsular Malaysia and the Riau Archipelago (e.g. Ng et al., 1992; Tan & Tan, 1994; Vidthayananon, 2002; Tan & Kottelat, 2009), and all indications point to even greater fish diversity in unexplored locations.

Far less is known about the invertebrates of swamp forests, as most swamp invertebrates have not been extensively studied and furthermore, organisms are rarely identified to the species level. Johnson (1968) did note that Coleoptera, Hemiptera and Diptera may be abundant and diversified in small blackwater pools but in most blackwater habitats, freshwater macroinvertebrates are rather scarce and have poor diversity, with Cheng & Fernando (1969) listing only six hemipteran species from Malaysian blackwaters. Although there seem to be few if any invertebrate species specific to or characteristic of swamp forest (e.g. Ng et al., 1992; Abang & Hill, 2006), rotifer and decapod crustacean species have been found in these habitats (see Ng et al., 1992). For instance, a total of 133 rotifer species were identified from five coastal peat swamps on Phuket Island, Thailand (Chittapun et al., 2007), whilst Wowor et al. (2009) found four species of the freshwater *Macrobrachium* prawns occurring in acidic peat habitats.

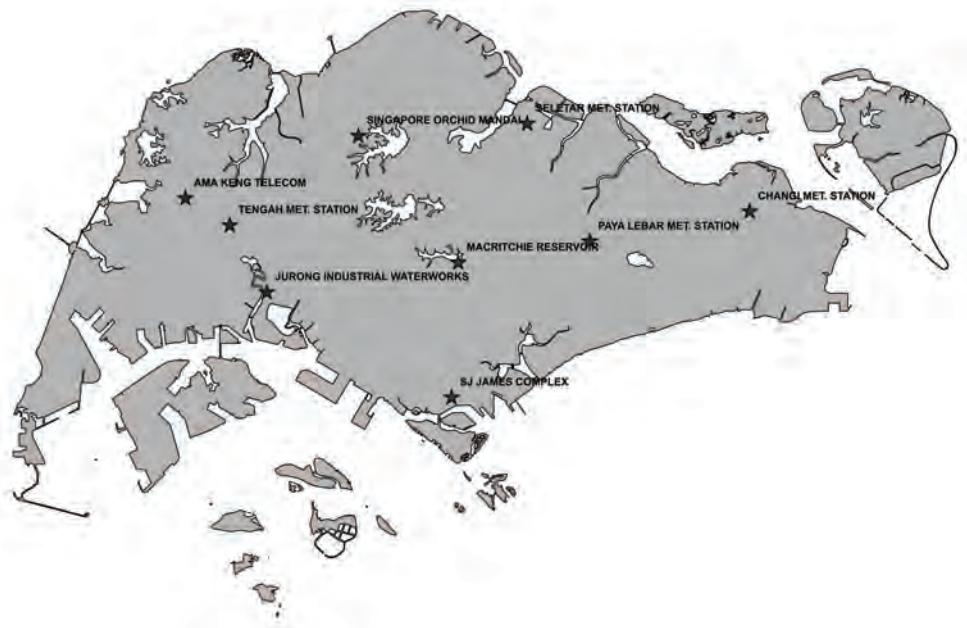
## General climatology of Singapore

### *Historical trends in precipitation*

Nine rain gauges in Singapore (Fig. 2; Liong & Raghavan, 2004), selected for their data comprehensiveness and relevance to Nee Soon freshwater swamp forest, provided the daily rainfall data from 1961 until 2007 used for the present study. From some of the stations the time series was incomplete. Table 1 provides the periods of data availability for the nine stations considered.

### *Historical trends in temperature*

The trends in daily temperature observations for Singapore reveal evidence of a warming trend since 1970 that is consistent with broader evidence of global warming and other temperature trend analyses in the region. Daily maximum and minimum temperature data are available from four observation stations in Singapore, for varying periods (shown in Table 4). The station-averaged absolute change values compared to baseline 1961–1990 show the rise in surface temperatures since 1961–1990, as recorded at all stations.

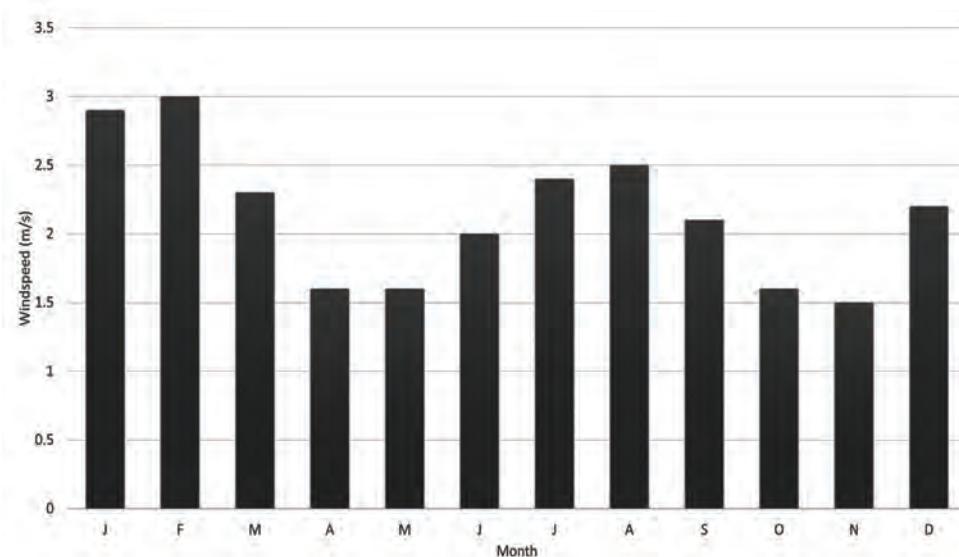


**Fig. 2.** Geographical locations of selected meteorological stations in Singapore.

#### *Historical trends of wind*

The strength and direction of the winds over Singapore are influenced by the monsoon (Nieuwolt, 1981; National Environment Agency, 2007). Northeasterly winds prevail during the Northeast Monsoon which occurs from December to early March, with wind speeds sometimes reaching 30 to 40 km/h in January and February. During the Southwest Monsoon (June to September), southeast to southwest winds prevail over Singapore (with more consistent southwest winds over the Indian continent). Periods between monsoon seasons (Pre-Southwest Monsoon: April and May, Post-Southwest Monsoon: October and November) receive less wind. The highest extreme gust speeds come from thunderstorms, whereas higher extreme mean wind speeds come from non-thunderstorm events (Choi, 1999).

The source of Fig. 3 (monthly mean wind speed (m/s) in Singapore) is the National Environment Agency (2012); see also Meteorological Services Division (2016). Overall, the wind speed at Changi is weaker than at the other three stations. The wind speed during the Northeast Monsoon is stronger (by 1–3 m/s, according to the site) than in other seasons. Maxima in the monthly mean wind speed tend to occur in January and February during the Northeast Monsoon, while minima tend to occur in April and May during the pre-Southwest Monsoon.



**Fig. 3.** Monthly mean wind speeds ( $\text{m sec}^{-1}$ ) in Singapore (derived from National Environment Agency, 2012).

### Freshwater swamp forests: a Singapore perspective

#### Background

Prior to the establishment of modern Singapore, freshwater swamp forests were estimated to have occurred at all upper river reaches of Singapore, covering about 74 km<sup>2</sup> or about 13% of the island (Yee et al., 2011; O'Dempsey, 2014). However, with rapid urbanisation and industrialisation from the 1900s, vast forested areas were cleared for agricultural and industrial purposes. In 1932, Corner (1978) studied one such area—a patch of original swamp-forest in Jurong, which was completely transformed into a pineapple plantation the year after. In this patch of more than 6 ha, Corner (1978) found many plant species that only existed in Jurong but not in Mandai, or any other Singapore swamp forests. This suggested that Jurong could have represented a unique phytogeographical area (Corner, 1978; Yamada, 1997). However, no extensive surveys of faunal species were conducted in the freshwater swamp forest in Jurong before its clearance. Like this patch in Jurong, vast natural areas in Malaysia and Singapore were or are often cleared for development before surveys can be conducted on their existing flora and fauna (Ng & Lim, 1992).

The clearing of Jurong, Mandai, and Pulau Tekong swamp forests has left the Nee Soon freshwater swamp forest as the last remnant of primary freshwater swamp forests on Singapore Island (Corlett, 1992; Ng & Lim, 1992; Turner, 1996; Turner et al., 1996; Yeo & Lim, 2011). Nee Soon is relatively intact but dominated by primary and old secondary vegetation, covering about 87 ha of land (Corner, 1978; Ng & Lim, 1992; Turner et al., 1996). Named after a wealthy Chinese-Peranakan merchant,

**Table 1.** Total Annual Precipitation for nine stations in Singapore and percentage change relative to 1961–1990.

Period	Station Average (mm) (1961–2010)	Precipitation Stations (mm)								
		Mandai (1961– 2010)	Amakeng (1961– 2010)	Tengah (1961– 2010)	Jurong (1977– 2010)	Seletar (1961– 2010)	Mac- Ritchie (1961– 2010)	St James (1961– 2010)	Paya Lebar (1961– 2010)	Changi (1961– 2010)
1961–1990	2235	2403	2219	2359	2419	2309	2263	2162	2142	2022
1961–2010	2377	2555	2382	2517	2560	2451	2453	2292	2273	2105
1990–2010	2557	2709	2596	2715	2622	2585	2708	2468	2434	2172
2001–2010	2689	2810	2779	2906	2792	2712	2840	2573	2494	2295
Change compared to baseline 1961–1990 (in %)										
1961–2010	6.3	6.3	7.4	6.7	5.8	6.2	8.4	6.0	6.1	4.1
1990–2010	14.4	12.7	17.0	15.0	8.4	11.9	19.7	14.1	13.6	7.4
2001–2010	20.3	16.9	25.2	23.2	15.4	17.5	25.5	19.0	16.4	13.5

**Table 2.** Average Maximum Daily Precipitation for nine stations in Singapore and percentage change relative to 1961–1990.

Period	Station Average (mm) (1961–2010)	Precipitation Stations (mm)								
		Madai (1961–2010)	Amakeng (1961–2010)	Tengah (1961–2010)	Jurong (1977–2010)	Seletar (1961–2010)	MacRitchie (1961–2010)	St James (1961–2010)	Paya Lebar (1961–2010)	Changi (1961–2010)
1961–1990	116.2	110.3	105.5	123.1	119.9	110.8	116.4	116.6	127.5	131.5
1961–2010	102.3	120.2	108.2	122.5	120.7	125.9	119.9	119.4	127.4	130.4
1990–2010	124.2	130.2	110.5	119.8	118.9	140.9	123.8	121.5	125.3	127.5
2001–2010	164.2	159.1	132.8	142.2	130.2	170.7	149.2	136.2	139.3	155.7
Change compared to baseline 1961–1990 (in %)										
1961–2010	3.47	8.98	2.60	-0.49	0.70	13.59	2.97	2.45	-0.05	-0.88
1990–2010	6.89	18.08	4.69	-2.68	-0.78	27.17	6.35	4.22	-1.76	-3.10
2001–2010	25.74	44.30	25.88	15.56	8.60	54.07	28.21	16.85	9.22	18.37

**Table 3.** List of stations and the availability of observed daily rainfall data.

Station name	Station code	Availability	Periods with missing data
Paya Lebar	S6	1961–2007	
MacRitchie Reservoir	S7	1961–2007	
Ama Keng Telecom	S11	1961–2007	
Tengah	S23	1961–2007	
Changi	S24	1967–2007	December 1969, October 1971, November 1971
Seletar	S25	1967–2007	April 1, 1969 to March 31, 1970
St. James Complex	S31	1961–2007	February 1983
Jurong Industrial Waterworks	S39	1964–2007	
Singapore Orchids Mandai	S40	1966–2007	

**Table 4.** Average Surface Temperature for four stations in Singapore during the recent past and absolute changes relative to 1961–1990. (Source: Liong, S.Y. & Raghavan, V.S., 2014)

Period	Station Average (°C) 1961–2010	Meteorological Stations (°C)			
		Tengah (1971–2010)	Seletar (1971–2011)	PayaLebar (1961–2010)	Changi (1984–2010)
1961–1990	27.3	27.7	27.7	27.3	25.8
1961–2010	27.5	27.7	27.9	27.6	27.2
1990–2010	27.7	27.7	28.1	28.1	27.6
2001–2010	27.7	27.6	28.1	28.4	27.8
Change compared to baseline 1961–1990 (°C)					
1961–2010	0.17	0.02	0.21	0.33	1.43
1990–2010	0.42	0.05	0.42	0.80	1.86
2001–2010	0.33	-0.04	0.39	1.07	2.02

Lim Nee Soon (1879–1936), the Nee Soon freshwater swamp forest is located in the Central Catchment Nature Reserve, surrounded by the Executive Golf Course in the north, Seletar Expressway and Old Upper Thompson Road in the east, Upper and Lower Peirce reservoirs in the south, and the southern-most tributary of the Upper Seletar Reservoir and the northern-most tributary of the Upper Peirce Reservoir in the west (Yeo & Lim, 2011). This area incorporates areas that were previously part of the Chan Chu Kang forest reserve (Corlett, 1992), which has allowed it to preserve much old-growth vegetation. The Nee Soon freshwater swamp forest is thus the last remnant of a larger swamp forest which was previously found along the entire Seletar drainage, including the areas surveyed by Corner in Mandai (Corner, 1978; Ng & Lim, 1992; O'Dempsey & Chew, 2013). It has probably only survived to the present day by virtue of being both included in the Central Catchment Nature Reserve as well as being used as a training area for the Singapore Armed Forces and the presence of military shooting ranges nearby (Ng & Lim, 1992). According to Corlett (2011), the freshwater swamp forest is concentrated within several shallow valleys that drain towards the Seletar River while the elevated areas between the valleys support patches of dryland forest.

#### *Physical environment of Nee Soon freshwater swamp forest*

The ground surface of most places in Nee Soon freshwater swamp forest is covered by a shallow layer of peat and there is some variation in the microtopography of the forest (Taylor et al., 2001; Corlett, 2011). Because the water table is so close to the soil surface, periodic to semi-permanent flooding can be observed (Yeo & Lim, 2011). In addition, depressions in the topography are often saturated with water, forming small pools and slow-flowing streams (Turner et al., 1996; Taylor et al., 2001). Usually, the clear water in the swamp forest is stained a dark-tea colour, a result of tannin leaching from slowly decomposing plant matter under waterlogged soil conditions (Yeo & Lim, 2011). Some of the larger streams have bed deposits of coarse-grained sand that probably originates from the Triassic Period Bukit Timah granite formation that constitutes most of the basement rock below the swamp (Taylor et al., 2001).

Soil analysis conducted at the Nee Soon freshwater swamp forest in the mid-1990s revealed that the first 5 cm of the soil layer was rich in organic matter (approaching 80% to 90% loss-on-ignition by mass), though the content decreased rapidly beyond that depth to less than 50% loss-on-ignition by mass (Turner et al., 1996). Hence, the lower layer of soil is not considered to be peat, which has more than 90% loss-on-ignition by mass. The anaerobic and waterlogged conditions found in the soil of the Nee Soon freshwater swamp forest reduce its rate of decomposition, contributing to the richness in its organic matter (Turner et al., 1996).

Additionally, leaf litter in the Nee Soon freshwater swamp forest was found to have a lower level of nutrients such as nitrogen, potassium and phosphorus compared to the top 5 cm of soil. This could be caused by the draining of nutrients from the leaf litter into the soil (Turner et al., 1996).

The pH of swamp forest streams and soil water is between 4.6 and 5.5, more acidic compared to typical forest streams, and could become more acidic 5 cm below the surface of the soil (Turner et al., 1996; Yeo & Lim, 2011). This could be a result of

the thin layer of peat present in the swamp forest causing the release of humic acid, the mechanisms of which were explained above.

#### *Ecology of Nee Soon freshwater swamp forest*

Through the collation of data from published articles—mostly from the *Gardens' Bulletin Singapore* and *The Raffles Bulletin of Zoology*, as well as unpublished data retrieved from the National Parks Board (NParks), the number of faunal species recorded in the Nee Soon freshwater swamp forest was determined to be at least 346. However, this is probably a highly conservative figure, and it is likely that this is only a small proportion of the species present in the forest.

A series of field surveys was conducted in the 1990s, and their results published in 1997 in the *Gardens' Bulletin Singapore* (Chan & Corlett, 1997). This contributed immensely to the inventory of biodiversity knowledge in Singapore, especially in the Bukit Timah and Central Catchment Nature reserves. Among the groups surveyed were vascular plants, fish, prawns, crabs, butterflies, stick and leaf insects, semi-aquatic bugs, dragonflies and damselflies, and water beetles.

Based on our compilation of known faunal species in the Nee Soon freshwater swamp forest, insects and birds make up the largest proportion of animals recorded. Molluscs and annelids, on the other hand, make up only 3% of the total number of species which have been documented in this forest patch.

While the Nee Soon freshwater swamp forest has lost much of its original vertebrate fauna, it is still a very important site for the conservation of Singapore's remaining forests (Corlett, 1992). In fact, Yeo & Lim (2011) commented that Nee Soon freshwater swamp forest supports the highest diversity of native freshwater organisms in the country, reflecting its high conservation value and in particular supporting freshwater fish, amphibians, reptiles, freshwater prawns and crabs and bird species (Ng & Lim, 1992; Yeo & Lim, 2011). Many species, especially primary freshwater fish, have their main populations in Singapore located in the Nee Soon freshwater swamp forest and some others can be found nowhere else in Singapore, or even globally, such as the swamp forest crab, *Parathelphusa reticulata* (Davison et al., 2008; Cumberlidge et al., 2009; Lim et al., 2011). This makes the Nee Soon freshwater swamp forest a vital refugium for many forest or swamp-adapted species in Singapore, and gives it a very high conservation value (Ng & Lim, 1992; Lim et al., 2011).

#### *Freshwater flora of the Nee Soon freshwater swamp forest*

Parts of the Nee Soon forest were cleared during the late 19<sup>th</sup> and early 20<sup>th</sup> century for rubber and pepper plantations (Turner et al., 1996). Other parts have been drained or turned into reservoirs (Ng & Lim, 1992). The remaining vegetation consists of a mixture of primary and secondary forest (Corner, 1978; Ng & Lim, 1992). Given its history, the species composition and structure differ across the forest, suggesting a mixed swamp forest. Many of the tree species in parts of the forest, such as *Palaquium xanthochymum* (de Vriese) Pierre ex Burck and *Xylopia fusca* Maingay ex Hook.f. & Thomson, exhibit adaptations to flooding, including buttress roots, prop roots, and pneumatophores whereas some areas are dominated by plant species similar to those

of a dryland forest (Corner, 1978). In addition, Corner (1978) noted that the vegetation of the Mandai Swamp Forest, of which the Nee Soon freshwater swamp forest is the largest surviving remnant, was intermediate between a freshwater swamp forest and a peat swamp forest. Corner (1978) further suggested that patches of substrate that contain peat mats and decaying organic matter may transition to a full peat swamp forest at some point in the future (Ng & Lim, 1992).

Studies are lacking on the aquatic flora of the Nee Soon freshwater swamp forest; nevertheless, the investigations of Lok et al. (2009) documented the occurrence of the locally rare forest water lily, which they called *Barclaya kunstleri* Ridl. (Nymphaeaceae) but which is treated as a synonym of *Barclaya motleyi* Hook.f. by Kiew (2015). This was noted as occurring within the forest at least until 1954 but now it appears to be extinct at Nee Soon and only present in Singapore at Bukit Timah.

#### *Aquatic fauna structure of Nee Soon freshwater swamp forest*

The fauna of the Nee Soon freshwater swamp forest is rich and highly diverse. Insects and birds make up the largest proportion of animals, whilst molluscs and annelids make up a total of 3% of the species documented from Nee Soon. Additionally, Ng & Lim (1992) and Yeo & Lim (2011) have documented that 71% of the amphibians, 28% of the reptiles, 47% of freshwater prawn and 57% of freshwater crab species known in Singapore still exist in the Nee Soon freshwater swamp forest. The forest also contains the highest proportion of threatened native freshwater fish and crustaceans in Singapore (Ng, 1997; Ng & Lim, 1997).

It is also the only area in Singapore where 11 out of 26 known species of native freshwater fish can be found, including species such as the dwarf snakehead (*Channa gachua*), which was thought to be extinct in Singapore for 20 years before being rediscovered in 1989 (Ng & Lim, 1989), as well as the black snakehead (*Channa melasoma*), which was first recorded from Singapore only in 1990 (Ng & Lim, 1990). Some other fish species in the Nee Soon freshwater swamp forest that cannot be found elsewhere in Singapore include the spotted eel-loach (*Pangio muraeniformis*) and the grey-banded loach (*Nemacheilus selangoricus*), while many other fish species known from the Nee Soon freshwater swamp forest are also forest specialists that are only found within such habitats.

The Nee Soon freshwater swamp forest is also a vital area for conservation of freshwater invertebrates (Ng & Lim, 1992) in Singapore, as it was found to have the highest diversity of water beetles in the country (Balke et al., 1997), whilst odonate diversity was also found to be very high with eight species being exclusively found in the Nee Soon freshwater swamp forest (Murphy, 1997). Additionally, the forest also has the highest diversity of semi-aquatic bugs (Gerromorpha) in Singapore, with 83% of Singapore's Gerromorpha species having been recorded in the swamp forest (Yang et al., 1997). The forest is also a stronghold for freshwater decapods, with multiple species of freshwater shrimp, such as *Macrobrachium platycheles* (which was originally described from the area), having thriving populations there. Perhaps the most important decapod found within the Nee Soon freshwater swamp forest is the endemic swamp forest crab, *Parathelphusa reticulata*. It was described from the

swamp almost thirty years ago (Ng, 1990) and today, the entire world's population of *P. reticulata* is still confined to the Nee Soon freshwater swamp forest. Hence, if Nee Soon freshwater swamp forest were to be lost or modified, this species could potentially be rendered globally extinct.

## Conclusions

Nee Soon freshwater swamp forest constitutes Singapore's last remaining patch of primary freshwater swamp forest. From the viewpoint of species richness alone, this makes the conservation of the Nee Soon freshwater swamp forest a top priority. Its large number of plant and animal taxa, currently found nowhere else in Singapore, only emphasises its conservation value. Finally, given that Nee Soon freshwater swamp forest houses a large proportion of Singapore's overall flora and fauna, conservation of this habitat undoubtedly has larger-scale, positive effects for biodiversity conservation in Singapore (Ng & Lim, 1992; Turner et al., 1996), accomplishing conservation of biodiversity from species to landscape scales.

Owing to the nature of its ecosystem and drainage, the Nee Soon freshwater swamp forest is extremely sensitive to external disturbances (Ng & Lim, 1992). Furthermore, many of the species or groups of species found here are rather specialised and thus, disturbance of the Nee Soon freshwater swamp forest and its surrounding areas would pose a great threat to these unique groups. Therefore, it is important to maintain Nee Soon freshwater swamp forest in its current state, as well as ensure that it is not affected adversely by development. These are amongst the reasons for conducting a long-term research project to intensify knowledge of the freshwater swamp forest system (Davison et al., 2018).

### *Gaps in research*

Singapore has been gradually building up knowledge on freshwater biodiversity, which includes the area in the Nee Soon freshwater swamp forest (Kottelat & Whitten, 1996; Ng & Lim, 1997). The several biodiversity surveys conducted during the 1990s in the nature reserves of Singapore further contributed to this store of information. However, the knowledge of wildlife in Singapore is still inconsistent between groups.

Several surveys have been conducted to record vascular plant species in Singapore, including specifically from freshwater swamp forests such as Nee Soon (Corner, 1978; Turner et al., 1996). As such, vascular plants are comparatively well studied. Among the different groups of plants, angiosperms are by far the most extensively studied plant group. Nevertheless, information on diversity of plants is probably still incomplete as demonstrated by continuing discoveries in Nee Soon and its vicinity (Chong et al., 2018).

In terms of the understanding of fauna in Singapore, several groups have been covered extensively. For example, much is known about the freshwater fish in Singapore, and our understanding of this group is among the best in the region (Ng & Lim, 1997). The surveys of the 1990s also improved our knowledge of several other groups of animals.

However, even in highly studied areas, many species, such as freshwater organisms, have only been found in recent years. This shows that streams in Singapore are still insufficiently surveyed (Kottelat & Whitten, 1996).

Also, several groups of organisms present in Nee Soon freshwater swamp forest are still underrepresented. While much more is known of the angiosperms of Singapore, other groups including the macrofungi, fresh water algae and lichens are understudied (Ng et al., 2011). Amongst the fauna, many forest and soil arthropods, as well as various protozoan species, are highly unstudied (Ng et al., 2011).

Extinction in Singapore has proceeded at an alarming rate largely due to habitat loss (Brook et al., 2003). Currently, only about 0.25% of land area in Singapore is designated as protected nature reserves and 50% of our native species are harboured in this area. Between 36% and 78% extinction has been inferred amongst various taxonomic groups (Brook et al., 2003).

A forest cannot be conserved without deep knowledge of the majority of its species, and more work should be devoted to surveying these groups. A deeper understanding of the organisms present in the Nee Soon freshwater swamp forest could greatly aid its conservation. Singapore has many specialist species of animals and plants and a large proportion of which occur or occurred within the Nee Soon freshwater swamp forest. We have lost some of these species already, and in order to protect the rest, we require an improved understanding of their needs and interactions within the ecosystem.

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## References

- Abang, F. & Hill, D.S. (2006). The invertebrate fauna. In: Abang, D. & Das, I. (eds) *The Biodiversity of a Peat Swamp Forest in Sarawak*, pp. 87–98. Kota Samarahan: Universiti Malaysia Sarawak.

- Balke, M., Hendrich, L. & Yang, C.M. (1997). Water beetles (Insecta: Coleoptera) in the nature reserves of Singapore. *Gard. Bull. Singapore* 49(2): 321–331.
- Bezuijen, M.R., Webb, G.J.W., Hartoyo, P. & Samedi. (2001). Peat swamp forest and the false gharial *Tomistoma schlegelii* (Crocodylia, Reptilia) in the Merang River, eastern Sumatra, Indonesia. *Oryx* 35: 301–307.
- Brook, B.W., Sodhi, N.S. & Ng, P.K.L. (2003). Catastrophic extinctions follow deforestation in Singapore. *Nature* 424: 420–424.
- Brown, B.L. (2003). Spatial heterogeneity reduces temporal variability in stream insect communities. *Ecol. Lett.* 6(4): 316–325.
- Bunn, S.E. & Arthington, A.H. (2002). Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environ. Manage.* 30(4): 492–507.
- Chan, L. & Corlett, R.T. (eds) (1997). Biodiversity in the Nature Reserves of Singapore. Proceedings of the Nature Reserves Survey Seminar, Singapore, December 1997. *Gard. Bull. Singapore* 49(2): i–iv, 147–425.
- Cheng, L. & Fernando, C.H. (1969). A taxonomic study of the Malayan Gerridae (Hemiptera: Heteroptera) with notes on their biology and distribution. *Orient. Insects* 3: 97–160.
- Cheyne, S.M., Morrogh-Bernard, H. & MacDonald, D.W. (2009). First flat-headed cat photo from Sabangau peat-swamp forest, Indonesian Borneo. *Cat News* 51: 16.
- Chittapun, S., Pholpunthin, P. & Segers, H. (2007). Diversity of rotifer fauna from five coastal peat swamps on Phuket Island, southern Thailand. *ScienceAsia* 33: 383–387.
- Choi, E.C.C. (1999). Extreme wind characteristics over Singapore – an area in the equatorial belt. *J. Wind Eng. Ind. Aerod.* 83: 61–69.
- Chokkalingam, U., Suyanto, Permana, R.P., Kurniawan, I., Mannes, J., Darmawan, A., Khususyiah, N. & Susanto, R.H. (2007). Community fire use, resource change, and livelihood impacts - The downward spiral in the wetlands of southern Sumatra. *Mitig. Adapt. Strat. Gl.* 12(1): 75–100.
- Chong, K.Y., Lim, R.C.J., Loh, J.W., Neo, L., Seah, W.W., Tan, S.Y. & Tan, H.T.W. (2018). Rediscoveries, new records, and the floristic value of the Nee Soon freshwater swamp forest, Singapore. *Gard. Bull. Singapore* 70 (Suppl. 1): 49–69.
- Clark, J.A. & May, R.M. (2002). Taxonomic bias in conservation research. *Science* 297: 191–192.
- Coley, P.D. & Barone, J.A. (1996). Herbivory and plant defenses in tropical forests. *Annu. Rev. Ecol. Syst.* 27: 305–335.
- Corlett, R.T. (1986). The mangrove understory - some additional observations. *J. Trop. Ecol.* 20(1): 93–94.
- Corlett, R.T. (1992). The Ecological Transformation of Singapore, 1819–1990. *J. Biogeogr.* 19(4): 411–420.
- Corlett, R.T. (2009). *The Ecology of Tropical East Asia*. New York: Oxford University Press.
- Corlett, R.T. (2011). Terrestrial ecosystems. In: Ng, P.K.L., Corlett, R.T. & Tan, H.T. (eds) *Singapore Biodiversity: An Encyclopedia of the Natural Environment and Sustainable Development*, pp. 44–51. Singapore: Raffles Museum of Biodiversity Research, Department of Biological Sciences, National University of Singapore.
- Corner, E.J.H. (1978). *The freshwater swamp-forest of south Johore and Singapore*. *Gard. Bull. Singapore*, Suppl. 1. Singapore: Botanic Gardens, Parks & Recreation Department.
- Cumberlidge, N., Ng, P.K.L., Yeo, D.C.J., Magalhães, C., Campos, M.R., Alvarez, F., Naruse, T., Daniels, S.R., Esser, L.J., Attipoe, F.Y.K., Clotilde-Ba, F.-L., Darwall, W., McIvor, A., Baillie, J.E.M., Collen, B. & Ram, M. (2009). Freshwater crabs and the biodiversity crisis – Importance, threats, status, and conservation challenges. *Biol. Conserv.* 142(8): 1665–1673.

- da Silva, H.P., Petry, A.C. & da Silva, C.J. (2010). Fish communities of the Pantanal wetland in Brazil – evaluating the effects of the upper Paraguay river flood pulse on baía Caiçara fish fauna. *Aquat. Ecol.* 44(1): 275–288.
- Das, J. & Acharya, B.C. (2003). Hydrology and assessment of lotic water quality in Cuttack City, India. *Water Air Soil Poll.* 150: 163–175.
- Davidson, T.A., Mackay, A.W., Wolski, P., Mazebedi, R., Murray-Hudson, M. & Todd, M. (2012). Seasonal and spatial hydrological variability drives aquatic biodiversity in a flood-pulsed, sub-tropical wetland. *Freshwater Biol.* 57(6): 1253–1265.
- Davison, G.W.H., Ng, P.K.L. & Ho, H.C. (eds). (2008). *The Singapore Red Data Book-Threatened Plants & Animals of Singapore*, 2<sup>nd</sup> ed. Singapore: Nature Society (Singapore).
- Davison, G.W.H., Cai, Y., Li, T.J. & Lim, W.H. (2018). Integrated research, conservation and management of Nee Soon freshwater swamp forest, Singapore: hydrology and biodiversity. *Gard. Bull. Singapore* 70 (Suppl. 1): 1–7.
- de Pádua Teixeira, A., Assis, M.A. & Luize, B.G. (2011). Vegetation and environmental heterogeneity relationships in a Neotropical swamp forest in southeastern Brazil (Itirapina, SP). *Aquat. Bot.* 94: 17–23.
- Douglas, M.M., Bunn, S.E. & Davies, P.M. (2005). River and wetland food webs in Australia's wet-dry tropics: general principles and implications for management. *Mar. Freshwater Res.* 56(3): 329–342.
- Downes, B.J., Lake, P.S., Schreiber, E.S.G. & Glaister, A. (1998). Habitat structure and regulation of local species diversity in a stony, upland stream. *Ecol. Monogr.* 68(2): 237–257.
- Dudgeon, D. (2000). Riverine biodiversity in Asia – a challenge for conservation biology. *Hydrobiologia* 418(1): 1–13.
- Gandaseca, S., Rosli, N., Idris, M.H., Ahmed, O.H. & Pazi, A.M.M. (2015). Effects of converting tropical peat swamp forest into oil palm plantation on water quality. *Am. J. Appl. Sci.* 12: 525–532.
- Gasim, M.B., Ismail, B.S., Toriman, E., Islam Mir, S. & Chek, T.C. (2007). A physico-chemical assessment of the Bebar River, Pahang, Malaysia. *Global J. Environ. Res.* 1: 7–11.
- Göltenboth, F., Langenberger, G. & Widmann, P. (2006). 17 – Special forest ecosystems. In: Göltenboth, F., Timotius, K., Milan, P. & Margraf, J. (eds) *Ecology of Insular Southeast Asia*, pp. 385–399. Amsterdam: Elsevier.
- Hansen, M.C., Stehman, S.V., Potapov, P.V., Arunarwati, B., Stolle, F. & Pittman, K. (2009). Quantifying changes in the rates of forest clearing in Indonesia from 1990 to 2005 using remotely sensed data sets. *Environ. Res. Lett.* 4(3): 034001.
- Johnson, A.E., Knott, C.D., Pamungkas, B., Pasaribu, M., & Marshall, A.J. (2005). A survey of the orangutan (*Pongo pygmaeus wurmbii*) population in and around Gunung Palung National Park, West Kalimantan, Indonesia based on nest counts. *Biol. Conserv.* 121(4): 495–507.
- Johnson, D.S. (1968). Malayan blackwaters. In: Misra, R. & Gopal, B. (eds) *Proceedings of Symposium on Recent Advances in Tropical Ecology*, part 1, pp. 303–310. Varanasi: International Society for Tropical Ecology.
- Junk, W.J., Bayley, P.B. & Sparks, R.E. (1989). The flood pulse concept in river-floodplain systems. *Can. Spec. Publ. Fish. Aquat. Sci.* 106: 110–127.
- Junk, W.J., Piedade, M.T.F., Schongart, J., Cohn-Haft, M., Adeney, J.M. & Wittmann, F. (2011). A Classification of Major Naturally-Occurring Amazonian Lowland Wetlands. *Wetlands* 31(4): 623–640.

- Kiew, R. (2015). Nymphaeaceae. In: Kiew, R., Chung, R.C.K., Saw, L.G. & Soepadmo, E. (eds) *Flora of Peninsular Malaysia*, ser. 2, Seed Plants, vol. 5, pp. 207–219. Kepong: Forest Research Institute Malaysia.
- Kottelat, M. & Whitten, T. (1996). *Freshwater biodiversity in Asia, with special reference to fish*. World Bank Technical Paper 343. Washington, D.C.: The World Bank.
- Kottelat, M., Britz, R., Hui, T.H. & Witte, K.-E. (2006). *Paedocypris*, a new genus of Southeast Asian cyprinid fish with a remarkable sexual dimorphism, comprises the world's smallest vertebrate. *P. Roy. Soc. B.* 273(1589): 895–899.
- Leigh, C. & Sheldon, F. (2009). Hydrological connectivity drives patterns of macroinvertebrate biodiversity in floodplain rivers of the Australian wet dry tropics. *Freshwater Biol.* 54(3): 549–571.
- Leigh, C., Burford, M.A., Sheldon, F. & Bunn, S.E. (2010). Dynamic stability in dry season food webs within tropical floodplain rivers. *Mar. Freshwater Res.* 61(3): 357–368.
- Lim, K.K.P., Yeo, D.C.J. & Ng, P.K.L. (2011). Nee Soon freshwater swamp forest. In: Ng, P.K.L., Corlett, R.T. & Tan, H.T.W. (eds) *Singapore biodiversity: an encyclopedia of the natural environment and sustainable development*, pp. 52–63. Singapore: Editions Didier Millet in association with Raffles Museum of Biodiversity Research.
- Liong, S.Y. & Raghavan, V.S. (2014). *Quarterly Reports on High Resolution Regional Climate Change Impact Study, Vol I, as a part of the Coastal Inundation Risk Map Study for Singapore*. Submitted to the Building and Construction Authority, Govt. of Singapore. Confidential (non-disclosure agreement).
- Lok, A.F.S.L., Ang, W.F., Lee, S.M.L., Tan, H.H. & Tan, H.T.W. (2009). The status and distribution of *Barclaya* (Nymphaeaceae) in Singapore. *Nat. Singapore* 2: 237–245.
- Mashhor, M., Ahyaudin, A., Riley, J., Abu Hassan, A. & Asyraf, M. (2004). *Tropical Peat Swamps – Safe-Guarding a Global Natural Resource*, 1<sup>st</sup> ed. Penerbit Universiti Sains Malaysia, Pulau Pinang.
- Meteorological Services Division (2016). *Climate of Singapore*. <http://www.weather.gov.sg/climate-climate-of-singapore/>. Accessed 17 Feb. 2016.
- Mims, M.C. & Olden, J.D. (2013). Fish assemblages respond to altered flow regimes via ecological filtering of life history strategies. *Freshwater Biol.* 58(1): 50–62.
- Mitsch, W.J., Nahlik, A., Wolski, P., Bernal, B., Zhang, L. & Ramberg, L. (2010). Tropical wetlands: seasonal hydrologic pulsing, carbon sequestration, and methane emissions. *Wetlands Ecol. Manag.* 18(5): 573–586.
- Murphy, D.H. (1997). Odonata biodiversity in the Nature Reserves of Singapore. *Gard. Bull. Singapore* 49: 333–352.
- National Environment Agency (2007). *Climatology of Singapore*. <http://app.nea.gov.sg/cms/htdocs/article.asp?pid=1088>. Accessed 2 Dec. 2015 (now defunct).
- National Environment Agency (2012). *The weather and climate of Singapore, 2012*. Singapore: National Environment Agency.
- Negishi, J.N., Inoue, M. & Nunokawa, M. (2002). Effects of channelisation on stream habitat in relation to a spate and flow refugia for macroinvertebrates in northern Japan. *Freshwater Biol.* 47(8): 1515–1529.
- Ng, P.K.L. (1990). *Parathelphusa reticulata* spec. nov., a new species of freshwater crab from blackwater swamps in Singapore (Crustacea: Decapoda: Brachyura: Gecarcinucoidea). *Zool. Meded.* 63(18): 241–254.
- Ng, P.K.L. (1997). The conservation status of freshwater prawns and crabs in Singapore with emphasis on the nature reserves. *Gard. Bull. Singapore* 49: 267–272.

- Ng, P.K.L. & Lim, K.K.P. (1989). Rediscovery of the Dwarf Snakehead, *Channa gachua* (Hamilton, 1822) (Channidae) in Singapore. *Raffles B. Zool.* 37(1): 172–174.
- Ng, P.K.L. & Lim, K.K.P. (1990). The Black Snakehead, *Channa melasoma* (Bleeker, 1851) (Channidae): First record from Singapore. *Raffles B. Zool.* 38(1): 21–24.
- Ng, P.K.L. & Lim, K.K.P. (1992). The conservation status of the Nee Soon freshwater swamp forest of Singapore. *Aquatic Conserv.* 2(3): 255–266.
- Ng, P.K.L. & Lim, K.K.P. (1997). The diversity and conservation status of fishes in the nature reserves of Singapore. *Gard. Bull. Singapore* 49(2): 245–265.
- Ng, P.K.L., Tay, J.B. & Lim, K.K.P. (1994). Diversity and conservation of blackwater fishes in Peninsular Malaysia, particularly in the North Selangor peat swamp forest. *Hydrobiologia* 285(1–3): 203–218.
- Ng, P.K.L., Tay, J.B., Lim, K.K.P. & Yang, C.M. (1992). *The conservation of the fish and other aquatic fauna of the North Selangor Peat Swamp Forest and adjacent areas*. Kuala Lumpur: Asian Wetland Bureau and World Wildlife Fund.
- Ng, P.K.L., Corlett, R.T. & Tan, H.T.W. (eds) (2011). *Singapore biodiversity: an encyclopedia of the natural environment and sustainable development*. Singapore: Editions Didier Millet.
- Nieuwolt, S. 1981. The climates of continental Southeast Asia. In: Takahashi, K. & Arakawa, H. (eds) *World Survey of Climatology: The Climates of Southern and Western Asia*, vol. 9, pp. 1 – 66. Oxford & New York: Elsevier Scientific Publishing Co.
- O'Dempsey, T. (2014). Singapore's changing landscape since c. 1800. In: Barnard, T.P. (ed.), *Nature Contained: Environmental Histories of Singapore*, pp. 17–48. Singapore: NUS Press.
- O'Dempsey, T. & Chew, P.T. (2013). The freshwater swamp forests of Sungei Seletar Catchment: a status report. In: Leong, T.M. & Ho, H.C. (eds) *Proceedings of Nature Society, Singapore's Conference on "Nature Conservation for a Sustainable Singapore" – 16 October 2011*, pp. 121–166. Singapore: Nature Society (Singapore).
- Page, S.E., Rieley, J.O., Shotyk, O.W. & Weiss, D. (1999). Interdependence of peat and vegetation in a tropical peat swamp forest. *Philos. T. Roy. Soc. B* 354(1391): 1885–1897.
- Page, S.E., Hosciilo, A., Wösten, H., Jauhainen, J., Silvius, M., Rieley, J.O., Ritzema, H., Tansey, K., Graham, L., Vasander, H. & Limin, S. (2009). Restoration ecology of lowland tropical peatlands in Southeast Asia: current knowledge and future research directions. *Ecosystems* 12: 888–905.
- Phillips, V.D. (1998). Peatswamp ecology and sustainable development in Borneo. *Biodivers. Conserv.* 7: 651–671.
- Poff, N.L. & Allan, J.D. (1995). Functional organization of stream fish assemblages in relation to hydrological variability. *Ecology* 76(2): 606–627.
- Poff, N.L., Allan, J.D., Bain, M.B., Karr, J.R., Prestegaard, K.L., Richter, B.D., Sparks, R.E. & Stromberg, J.C. (1997). The natural flow regime. *BioScience* 47(11): 769–784.
- Posa, M.R.C., Wijedasa, L.S. & Corlett, R.T. (2011). Biodiversity and conservation of tropical peat swamp forests. *BioScience* 61(1): 49–57.
- Ramirez, A., Pringle, C.M. & Douglas, M. (2006). Temporal and spatial patterns in stream physicochemistry and insect assemblages in tropical lowland streams. *J. N. Am. Benthol. Soc.* 25(1): 108–125.
- Richards, P.W. (1996). *The Tropical Rain Forest – An Ecological Study*, 2<sup>nd</sup> ed. Cambridge: Cambridge University Press.
- Rijken, H.D. & Peerson, G. (1991). Food from Indonesia's swamp forest – Ideology or rationality. *Landscape Urban Plan.* 20: 95–102.

- Tan, H.H. & Kottelat, M. (2009). The fishes of the Batang Hari drainage, Sumatra, with description of six new species. *Ichthyol. Explor. Freshwat.* 20: 13–69.
- Tan, H.S. & Tan, H.H. (1994). The freshwater fishes of Pulau Bintan, Riau Archipelago, Sumatra, Indonesia. *Tropical Biodiversity* 2: 351–361.
- Taylor, D., Yen, O.H., Sanderson, P.G. & Dodson, J. (2001). Late Quaternary peat formation and vegetation dynamics in a lowland tropical swamp, Nee Soon, Singapore. *Palaeogeogr. Palaeocl.* 171(3–4): 269–287.
- Theilade, I., Schmidt, L., Chhang, P. & McDonald, J.A. (2011). Evergreen swamp forest in Cambodia – floristic composition, ecological characteristics, and conservation status. *Nord. J. Bot.* 29(1): 71–80.
- Turner, I.M. (1996). Species loss in fragments of tropical rain forests. A Review of the Evidence. *J. Appl. Ecol.* 33(2): 200–209.
- Turner, I.M., Boo, C.M., Wong, Y.K., Chew, P.T. & Ibrahim, A. (1996). Freshwater swamp forest in Singapore, with particular reference to that found around the Nee Soon Firing Ranges. *Gard. Bull. Singapore* 48(1): 129–157.
- Vidthayanan, C. (2002). *Peat Swamp Fishes of Thailand*. Bangkok: Office of Environmental Policy and Planning.
- Wells, A. & Yule, C.M. (2008). The caddisflies (Trichoptera) from a tropical peat swamp in Selangor, Peninsular Malaysia, including two new species. *Aquat. Insect.* 30: 69–76.
- Whitmore, T.C. (1984). *Tropical Rain Forests of the Far East*, 2<sup>nd</sup> ed. Oxford: Oxford University Press.
- Whitten, T., Damanik, S.J., Anwar, J. & Hisyam, N. (2000). *Freshwater-Swamp Forests*. Hong Kong: Periplus Editions.
- Winterbourn, M.J. & Collier, K.J. (1987). Distribution of benthic invertebrates in acid, brown water streams in the South Island of New Zealand. *Hydrobiologia* 153: 277–286.
- Wowor, D., Muthu, V., Meier, R., Balke, M., Cai, Y. & Ng, P.K.L. (2009). Evolution of life history traits in Asian freshwater prawns of the genus *Macrobrachium* (Crustacea: Decapoda: Palaemonidae) based on multilocus molecular phylogenetic analysis. *Mol. Phylogenet. Evol.* 52: 340–350.
- Yamada, I. (1997). *Tropical Rain Forests of Southeast Asia – A Forest Ecologist's View*. Honolulu: University of Hawaii Press.
- Yang, C.M., Lua, H.K. & Yeo, K. (1997). Semi-aquatic bug (Heteroptera: Gerromorpha) fauna in the Nature Reserves of Singapore. Proceedings of the Nature Reserves Survey Seminar. *Gard. Bull. Singapore* 49: 313–319.
- Yee, A.T., Corlett, R.T., Liew, S.C. & Tan, H.T.W. (2011). The vegetation of Singapore – an updated map. *Gard. Bull. Singapore* 63(1–2): 205–212.
- Yeo, D.C.J. & Lim, K.K.P. (2011). Freshwater ecosystems. In: Ng, P.K.L., Corlett, R.T. & Tan, H.T. (eds) *Singapore Biodiversity – An Encyclopedia of the Natural Environment and Sustainable Development*, pp. 52–63. Singapore: Raffles Museum of Biodiversity Research, Department of Biological Sciences, National University of Singapore, Singapore.
- Yule, C.M. (2010). Loss of biodiversity and ecosystem functioning in Indo-Malayan peat swamp forests. *Biodivers. Conserv.* 19(2): 393–409.
- Yule, C.M. & Gomez, L.N. (2009). Leaf litter decomposition in a tropical peat swamp forest in peninsular Malaysia. *Wetlands Ecol. Manag.* 17(3): 231–241.

