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MANDAI MANGROVE, SINGAPORE: LESSONS FOR THE CONSERVATION OF SOUTHEAST ASIA'S MANGROVES

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ABSTRACT. — Vital for their diverse ecosystem services, Southeast Asian mangroves are the most biodiverse in the world and are critically threatened, yet they remain woefully understudied. A notable exception is Mandai mangrove in Northwest Singapore, a hotspot of research for decades, with an intensive contemporary research agenda. It provides not only a baseline of mangrove research for the region, but exemplifies the threats facing mangroves across Southeast Asia: changing sediments and currents, insect pests, genetic disconnection from other mangrove patches, land reclamation, and future sea level rise. Many of these threats are unique to mangrove ecosystems, but associated data gaps prohibit informed mangrove conservation across the region. Mandai mangrove is one of Southeast Asia's few mangrove sites with the baseline and contemporary research capable of elucidating these broad threats to the region's mangrove systems.

KEY WORDS. — deforestation, ecology, erosion, gene flow, reclamation, sea level rise, taxonomy, threat, wetland

INTRODUCTION

Massive habitat loss, environmental degradation, and unsustainable resource use continue to endanger Southeast Asian biodiversity (Sodhi & Brook, 2005; Koh & Sodhi, 2010; Miettenen et al., 2011), and the processes are exemplified by the colonisation of Singapore. The predicted rates of regional species loss by 2100 (13–85%) are alarming (Sodhi et al., 2010), while a distinct lack of data still hinders understanding of the drivers and scale of regional biodiversity loss (Sodhi et al., 2004). Facing such uncertainty and paucity of data, Singapore is often held up as an environmental warning to other rapidly developing Southeast Asian countries (e.g., Corlett, 1992; Turner et al., 1994; Castelleta et al., 2000; Sodhi et al., 2004) and cities around the world (e.g., Duncan et al., 2011). With local extinctions predicted to be as much as 73% of its native species (Brook et al., 2003), Singapore continues to present an extreme example of the impending "Southeast Asian biodiversity crisis" (Sodhi et al., 2004). Moreover, geographic access and resources have made Singapore's remaining natural ecosystems the subject of intensive study, which can inform conservation and management of regional mangroves experiencing rapid development.

Mangroves provide a range of crucial ecosystem and socioeconomic services (e.g., Moberg & Rönnbäck, 2003; Lacambra et al., in press) and Southeast Asia represents the centre of mangrove diversity (Spalding et al., 2010). Yet mangroves in the region are experiencing rapid deforestation and fragmentation (Valiela et al., 2001; Miettinen et al., 2011) due to land cover change, principally due to aquaculture and urbanisation (Duke et al., 2007). Mangrove loss has been particularly acute in Singapore, with declines from 63.4 km^2 in 1953 (Hilton & Manning, 1995) to 6.6 km^2 today (Yee et al., 2010). Mangroves are now among the most threatened ecosystems in the country (Hilton & Manning, 1995). Although there is broad recognition of the importance of mangrove conservation, the threats to mangroves remain understudied, fundamentally limiting management, rehabilitation, and conservation efforts.

Mandai mangrove, a small mangrove patch in northeast Singapore, offers critical insights on Southeast Asian mangrove ecology and threats to conservation. Despite its small size, Mandai is one of the more intensively studied mangroves in Southeast Asia, alongside sites such as Matang Mangrove Forest Reserve (Peninsular Malaysia), Ranong Biosphere Reserve (Thailand), and the Mekong River Delta (Vietnam). However, Mandai mangrove offers particular lessons for the fate of Southeast Asia's mangroves: a) it is a smaller, relatively isolated site that may be more representative of increasingly fragmented Southeast Asian systems; b) unlike sites such as Matang and Ranong, Mandai lacks any official protected status, so is more representative of the vast majority of mangrove outside (enforced) protected areas; c) Mandai clearly demonstrates the impacts of urbanisation on mangroves when compared against larger, protected systems; and d) the unique, contemporary research agenda at Mandai is addressing conservation threats unique to mangroves and of regional relevance. Mandai thus serves as a helpful regional baseline and an extreme example of the threats to mangroves facing rapid development.

In this article, we provide a description of the Mandai mangrove: its history, scientific legacies, current status, and threats to its future conservation, presented within the broader context of Southeast Asian mangrove conservation. We further discuss why much of the research at this site is regionally relevant, and how Mandai serves as an example of the impacts of urbanisation on mangrove conservation that are relevant to mangrove conservation across Southeast Asia (cf. Sodhi et al., 2004).

MANDAI MANGROVE

Mandai mangrove and mudflat (referred to here as Mandai mangrove) is one of Singapore's few remaining mangrove patches. It is situated on the northwest coast of Singapore, close to the Singapore-Johor Causeway (Fig. 1).

Prior to the colonial period, this mangrove supported seafaring peoples such as the Orang Seletar and the Orang Biduanda Kallang (Murphy & Sigurdsson, 1990). Communities at

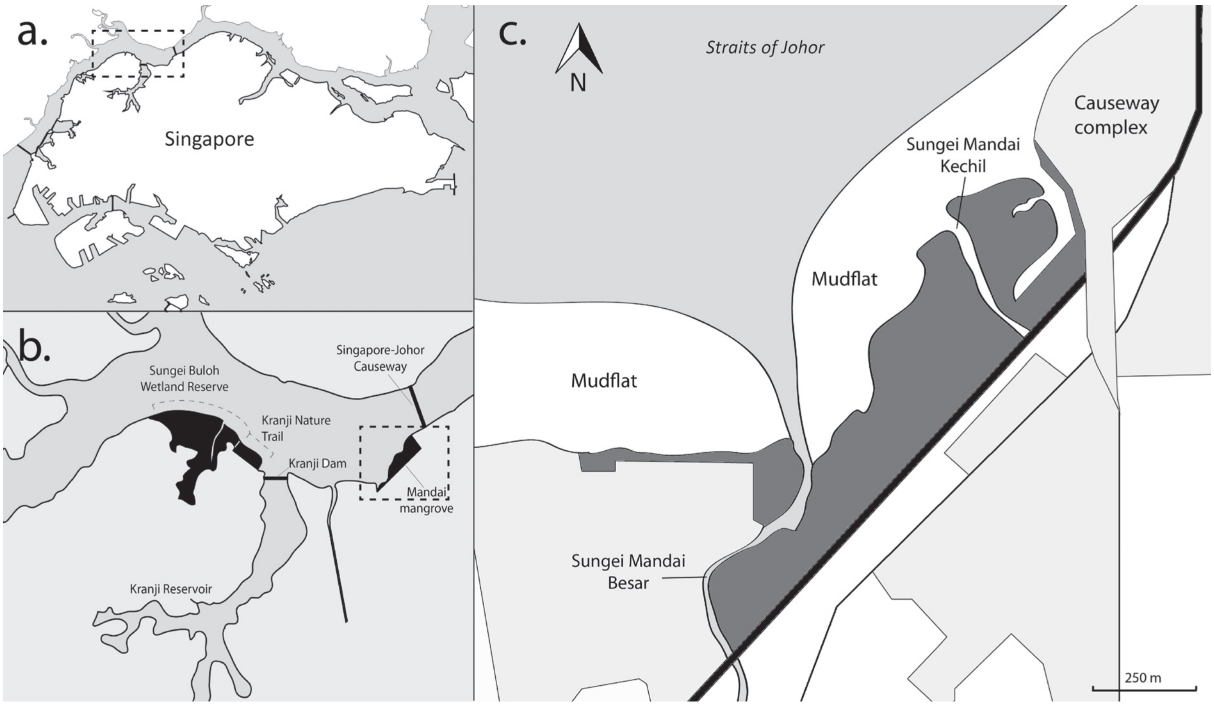

Fig. 1. Location of Mandai mangrove in Singapore (a); the coastal zone surrounding Mandai (b); site map of Mandai (c). Dark grey denotes mangrove, light grey denotes urban area. Black line denotes land formerly comprising the railway (c).

Kampong [=village] Mandai Besar, Kampong Mandai Kechil, and Kampong Lorong Fatimah continued to inhabit Mandai mangrove and the surrounding area until the late 1980s (Fig. 2) before their relocation into public housing. Remnants of the village can still be found within the mangrove (Fig. 3), which is still used by local fisherman, though artisanal fishing continues to decline (Ng & Low, 1994).

Mandai mangrove was once part of an extensive mangrove complex that stretched as far as Lim Chu Kang and Sungei Buloh to the west. Its deforestation was first principally associated with shrimp pond development; more recently the mangrove-fringed coastline of north-western Singapore has been progressively reclaimed for industry and freshwater reservoirs since Singapore's independence (Hilton & Manning, 1995). These pressures reduced Mandai mangrove to a patch of only 15.4 ha (Yee et al., 2010).

Despite the reduction in spatial extent, Mandai mangrove provides critically important habitat for local flora and fauna, and continues to offer new discoveries of the region's mangrove zoology and ecology (e.g., Tanokuchi, 1989; Sodhi et al., 1997; Schubart et al., 2009). Mandai is one of the few mangroves in Singapore with an extensive mudflat exposed at low tide, where large patches of the critically endangered seagrass species *Halophila beccarii* can be found (Davison et al., 2008). Mandai is also one of the most floristically-diverse mangroves in Singapore. On the seaward fringe, common mangrove species include *Avicennia officinalis*, *A. alba*, *A. rumphiana*, and *Sonneratia alba*, with *Bruguiera cylindrica*, *B. gymnorrhiza*, and *Rhizophora apiculata* further landward (Lee & Murphy, 1990; Sodhi et al., 1997; Ng & Sivasothi, 1999). The mangrove flora transitions at higher landward elevations to upper intertidal mangrove species and associates such as *Excoecaria agallocha*, *Talipariti tiliaceum* (formerly *Hibiscus tiliaceus*), *Terminalia catappa*, and *Acanthus* spp. The back mangrove is home to several mangrove tree and associate species that are severely endangered in Singapore (as designated by Davison et al., 2008), including the trees *Sonneratia ovata*, *Intsia bijuga*, and *Lumnitzera racemosa* (all critically endangered), *Heritiera littoralis* and *Ceriops zippeliana* (both endangered), and the mangrove associates *Finlaysonia obovata* (Ang et al., 2010), *Merope angulata* (both critically endangered) and *Brownlowia tersa* (endangered). An extensive faunal community also exists in Mandai, spanning both vertebrate (e.g., fishes, birds, reptiles, amphibians) and invertebrate groups (e.g., insects, chelicerates, crustaceans, molluscs). The extensive mudflat is a major feeding area for birds (especially migrants) roosting at the nearby Sungei Buloh Wetland Reserve (Fig. 1b), such as waders, herons, and egrets (Murphy & Sigurdsson, 1990).

A LEGACY OF MANGROVE RESEARCH FROM MANDAI

The scientific importance of Mandai has "been recognised for many years by local and overseas scientists" (Briffett, 1991:

Fig. 2. Kampong within Mandai mangrove at high tide, Nov.1971. (Source: Singapore Press Holdings).

Table 1. Breakdown of peer-reviewed, international journal articles from Mandai by research field or taxa.

Class	Taxonomy	Morphology & physiology	Behaviour	Population	Ecology
Florideophyceae (algae)	–	1	–	–	–
Fungi	3	–	–	1	1
Vegetation	–	2	–	–	–
Polychaeta	1	–	–	–	–
Sipunculida	–	6	–	–	–
Insecta	7	–	–	2	–
Arachnida	–	–	–	1	–
Gastropoda	2	3	–	–	–
Malacostraca	6	2	2	–	1
Merostomata	–	–	–	2	–
Osteichthyes	–	–	–	1	–
Aves	–	–	1	1	1
Coastal management	2	–	–	–	–

283). An extensive literature review through the academic databases *Web of Science* and *Google Scholar* found 48 peer-reviewed journal articles between 1988 and 2011 where the majority of research was carried out at Mandai (Table 1). This number does not include an extensive body of research published in conference proceedings, undergraduate or doctoral theses, or research conducted before the late 1980s.

Fig. 3. Remnants of kampong structures within Mandai mangrove, e.g., housing platform (a) and stairs (b). (Photographs by: R. C. Leong).

Baseline benthic surveys. — Benthic fauna taxonomy and physiology have traditionally been a strong research area at Mandai over the last three decades (e.g., Ng, 1988, and others). A large proportion of the peer-reviewed literature pertaining to Mandai is based on the taxonomy and physiology of invertebrates; 18 of these articles have been published in the *Raffles Bulletin of Zoology*, reflecting the zoological research focus, and the importance of Mandai to researchers in Singapore and the local region. New discoveries emanating from Mandai include the description of two genera of Coleoptera (Sawada, 1989; Tanokuchi, 1989), two genera of mangrove crab (Ng, 1988; Ng & Schubert, 2002), and at least 20 new species within the orders Coleoptera (Sawada, 1989, 1991; Tanokuchi, 1989; Woolridge, 1990), Isopoda (Cookson & Cragg, 1991), Hemiptera (Polhemus & Cheng, 1982; Anderson, 2000; Yang & Murphy, 2011), and Lepidoptera (Murphy, 1989).

Various baseline benthic surveys are also being conducted by the National Parks Board, including the 'Comprehensive Marine Biodiversity Survey of Singapore', a nation-wide, three-year survey from 2010–2013 to catalogue Singapore's benthic diversity and abundance (NParks, 2009). This is one of the most rigorous and large-scale benthic surveys in the region, and includes Mandai as a key study location. Such baseline studies provide benchmarks for these understudied taxa, and provide data on critical bio-indicators. Benthic fauna can provide valuable insights into the impacts of urbanisation, such as changing sediment loads and pollution (e.g., Bedini & Piazzi, 2012).

Baseline ecological surveys. — Research at Mandai has increasingly addressed mangrove ecology and larger-scale issues with clear regional implications. Mandai-based ecological studies have especially highlighted the ecological importance of small mangrove fragments, which might otherwise be overlooked for conservation. Sodhi et al. (1997) conducted one of the first published mangrove avian ecology studies in Southeast Asia at Mandai, after Noske (1995) in western Peninsular Malaysia. Sodhi et al. (1997) recorded 60 species within Mandai and its surroundings, including locally threatened, mangrove-breeding and mangrove-dependent species. Despite its small area, Mandai (especially its mudflat) may play a critical role as a feeding area for the bird populations that roost in neighbouring mangrove areas such as Sungei Buloh (Murphy & Sigurdsson, 1990), an internationally recognised migratory bird habitat and a key link in the East Australasian Flyway (Wei et al., 2009). Mandai has also been a key site of Southeast Asian ecological research on vulnerable (as per Davison et al., 2008) horseshoe crab species; Mandai mudflat hosts the last known breeding populations of *Carcinoscorpius rotundicauda* and *Tachypleus gigas* on the main island of Singapore, due to surrounding habitat loss and urbanisation (Cartwright-Taylor et al., 2011). Research at Mandai and the immediate coastline have provided important data on population densities, distribution, size classes, and breeding behaviour (Cartwright-Taylor et al., 2009, 2011). These are among a number of case studies that highlight the ecological and regional importance of very small mangrove fragments. As Southeast Asian mangroves become increasingly fragmented, research on habitat connectivity and ecological communities at Mandai becomes increasingly important.

Biogeomorphology and the long-term sustainability of mangroves. — Mandai has also been the site of important quantitative research on Southeast Asian mangrove vegetation ecology, particularly related to the interactions between vegetation and their physically dynamic intertidal environment. Early topographic and vegetation surveys revealed zonation and links between species abundance and topography, tidal inundation frequency and soil characteristics (Lee & Murphy, 1990; Murphy & Lee, 1991). This work was the first to propose long-term changes in the morphology of Mandai as a potential threat to its persistence. The authors suggested ongoing changes in topography at Mandai, and potentially other sites due to erosion, bioturbation by *Thalassina* mud lobsters, and long-term marine transgression; indeed, intertidal surfaces are shaped by sediment, wave, current, and weather dynamics (Ellison, 2009; Friess et al., 2012). This seminal work has provided a biogeomorphic baseline for contemporary studies on changes to mangrove topography and diversity (discussed below).

In an editorial for *The Raffles Bulletin of Zoology*, Sodhi (1997) stated the importance of a sound taxonomic and natural history research foundation, on which to base ecological research that understands requirements for conservation. The work of these researchers, from D. H. Murphy and N. S. Sodhi onwards, shows that a larger-scale ecological and process viewpoint is critical in order to identify and combat the multiple threats to Mandai, and to Southeast Asian mangroves.

MANDAI AS AN EXAMPLE FOR UNDERSTANDING MANGROVE THREATS

Myriad threats to biodiversity have been identified in Southeast Asia, notably unsustainable harvesting and land cover conversion and associated fragmentation and isolation (Sodhi et al., 2004). Mangroves are subject to similar land conversion pressures as terrestrial forests, but also face a unique set of threats—changing hydrodynamics, altered sediment supply, and sea level rise (SLR). Such threats have yet to be meaningfully researched in the Southeast Asian context, which fundamentally limits long-term mangrove management, conservation, and rehabilitation in the region. As an extreme example of the threats faced by mangroves in the region, and considering its detailed historical baselines, Mandai provides unique insights and research opportunities for better understanding long-term mangrove management, impacts of urbanisation and responses to SLR. We review the leading threats to mangroves in Southeast Asia, providing a local assessment of these threats in relation to Mandai and, where relevant, link these to the contemporary Mandai-based research agenda.

Encroachment and conflicting coastal management objectives. — Although not unique to mangrove systems, poor resource management resulting in encroachment, deforestation and degradation remains a leading, immediate, and visible threat to mangroves in the region (e.g., Giri et al., 2008). Land conversion threats, primarily due to agriculture and aquaculture, are relatively well documented at multiple scales (Seto & Fragkias, 2007; Giri et al., 2008). However, given the increasing rates of population growth and urbanisation expected in many Southeast Asian countries (Wong, 2006), coastal habitats will be increasingly vulnerable and fragmented due to urban encroachment. Little is known about the maintenance of key ecosystem services (e.g., biodiversity, coastal protection, fisheries) within degraded and fragmented mangroves, and small fragments can be easily overlooked. However, previous studies in Singapore have shown that small habitat fragments are important to conserve as they act as refuge for threatened species, and a source for their recolonisation (Turner & Corlett, 1996).

The Mandai context. — The coastline surrounding Mandai shows extensive urban encroachment. GIS analysis (D. A. Friess, unpublished data) shows that 77.8% of the coastline between the Kranji Nature Trail mangrove and the Singapore-Johor causeway (a length of 4.42 km) has been modified for industry or reservoir construction. Designated a "reserve site" (URA, 2008), Mandai has no legal protection status to save it from further reclamation. The current status of warranting conservation "for as long as possible" suggests that this area faces the likelihood of conversion to industry or housing in the future.

Until recently, the Singapore-Malaysia railway line ran along the back of Mandai (Fig. 1c) and was owned by Malaysian authorities. The resultant poor accessibility may have historically protected the mangrove patch from development. However, the railway land was returned to Singapore ownership through a land-swap deal with Malaysia on 1 Jul.2011 (PMO, 2011), removing this protective barrier and potentially opening up Mandai to development.

Considering the extensive modification of all accessible coastline areas surrounding Mandai, the barrier removal has introduced an acute threat of future reclamation. However, from a trajectory of continued encroachment, Mandai is now an important case study of coastal management decision-making, giving an unprecedented opportunity to conserve small forest patches within a large-scale management plan. The Nature Society Singapore and other interested parties envisage a bold plan where 173.7 ha of relinquished land is created into a "Green Corridor" that links existing green spaces together, including Mandai mangrove (NSS, 2011). The Green Corridor is a unique starting point to begin discussions on how newly-accessible and even relatively small land parcels can be better conserved by their incorporation into the national planning process.

Sea level rise. — Long-term mangrove persistence is linked to physical variables such as surface elevation, which controls the frequency of tidal inundation (e.g., Woodroffe, 1990). Predicted accelerated SLR is a serious potential threat to coastal wetlands globally (e.g., Nicholls, 2004) as tidal inundation increases beyond a threshold of species-specific tolerance to flooding (Friess et al., 2012). Very little information exists on the potential response of Southeast Asian mangroves to SLR, with the exception of incipient studies at Mandai.

Historically, mangroves have kept pace with changes in sea levels and maintained their relative position in the tidal frame through two mechanisms. Over the long-term, intertidal habitats may migrate to higher elevations landwards, though this is impossible in urbanised environments and regions lined with coastal defences, such as Singapore and broad lengths of the Thai-Malay Peninsula. In these cases, the seaward margin of the mangrove retreats upslope, though the landward margin is constrained by a fixed barrier, resulting in "coastal squeeze" (Gilman et al., 2006a). The survival of mangroves under such constraints is thus dependent on sediment deposition, accumulation, and subsequent increases in vertical surface elevation. Many components contribute to surface elevation change (summarised by Friess et al., 2012), such as below-ground organic matter accumulation by root production (e.g., McKee, 2010). A particular key input to positive vertical elevation change is mineral sediment input from river catchments and the surrounding coastal zone (Bird, 2000). Unfortunately, fluvial sediment input is limited in many coastal areas due to dam construction (e.g., Thampanya et al., 2006; Newton et al., 2012). Quantitative research on the impact of dam construction on mangrove surface elevations—and ultimately resilience to SLR—is unavailable for Southeast Asian mangroves.

The Mandai context. — A causeway connecting Singapore and Malaysia was constructed in 1913 (Bird et al., 2004), blocking tidal exchange between the west and east Straits of Johor. The causeway has thus disconnected Mandai and associated mangroves in the west from the Johor Estuary, which drains a large area of southern Peninsular Malaysia and is an important source of sediment. Second, local sediment sources (Kranji River) close to Mandai have been reduced by river damming (Bird et al., 2004). Murphy (1990) suggested that sediment starvation may be impacting Mandai, though no quantitative information is currently available for this site as such an impact is likely to occur over decadal timescales. An impact on Mandai is expected however, as it has been observed indirectly at the neighbouring Sungei Buloh Wetland Reserve. Bird et al. (2004) showed how a general accretionary trend of mangrove seaward expansion onto new mudflats fronting Sungei Buloh between 1946 and 1969 reversed to mangrove retreat in the latter half of the 20th century, potentially due to changing hydrodynamic patterns and reduced sediment input caused by the damming of the Kranji river in 1972 (Murphy & Lee, 1991). With sea levels predicted to rise significantly throughout the 21st century, and local river damming reducing fluvial sediment input, Mandai mangrove may be at great risk of increased inundation.

Contemporary studies of fine-scale surface elevation change at Mandai are helping to determine the susceptibility of this mangrove patch to SLR, and elucidate the geomorphological mechanisms that may influence the response of other mangrove patches in the region. Long-term surface change is monitored at Mandai using Surface Elevation Tables, a technique that measures millimetre vertical changes in the mangrove surface (see Cahoon et al., 2002 for methodology), and can be compared to scenarios of SLR (sensu Krauss et al., 2010 in Micronesia) or incorporated into geomorphological models that predict habitat change and vulnerability. Mandai is one of the few sites in Asia where net surface elevation change is being monitored with high accuracy. Thus, Mandai is starting to fill a large geographical data gap (Cahoon et al., 2006) and providing data that can contribute to regional- or continental-scale information on SLR vulnerability.

Wave and current erosion. — Hydrodynamic thresholds prohibit the survival of both naturally recruited seedlings (Balke et al., 2011; Friess et al., 2012) and mature trees. The former is important for the establishment of a mangrove system, while the latter controls long-term mangrove resilience. In many systems, natural mangrove erosion and retreat due to hydrodynamic pressures is related to large wave fetch lengths (e.g., Thampanya et al., 2006), though increasingly erosion can be caused by anthropogenic factors such as shipping traffic. Busy shipping lanes such as the Malacca Straits have caused significant erosion of mangroves on the western coast of Peninsular Malaysia, particularly at the Tanjong Piai National Park after the opening of a new port at Tanjong Pelepas (Chong, 2006; D. A. Friess, pers. obs.). However, there is little academic literature on the distribution of erosion, or mechanisms that control erosion (especially ship-derived) on the patch scale.

The Mandai context. — Mandai has experienced severe seaward erosion in recent years (Fig. 4), and scouring and sediment erosion can be seen around numerous trees, particular *Avicennia* spp. (Fig. 5a). Erosion here may at first be surprising, since the Straits of Johor provide a fetch length of only a few hundred metres. At Mandai, erosion could be caused by higher boat traffic along this coastline (Bird et al., 2004) or altered current hydrodynamics after causeway construction. The exposure of roots and poor anchoring makes large trees susceptible to toppling during subsequent high-wind events (Fig. 5b).

Contemporary research at Mandai includes high-resolution mapping efforts that are investigating the distribution of dead and uprooted trees at the site-scale in order to better understand this important stressor (Leong, 2012). To our knowledge, this is one of the only mangrove studies to quantitatively monitor the spatial distribution of tree erosion. The results will allow the assessment of the relative importance of factors such as surface elevation, distance from shore, and species in controlling erosion, especially for mangroves such as those along the west coast of Peninsular Malaysia that are heavily affected by shipping traffic.

Insect pest damage. — Insect herbivory of propagules, seedlings and foliage can be an important disturbance mechanism in the mangrove forest, and may even affect forest structure (Farnsworth & Ellison, 1997). Insect infestations have had such an impact that entire stands of *Avicennia marina* were almost completely defoliated by the larva of *Nephopterix syntaractis* within three months in Hong Kong (Anderson & Lee, 1995). Such pest attacks are further exemplified by records of site-scale herbivory of *Rhizophora mucronata* propagules and seedlings by the scale insect *Aulacapsis marina* in Bali, Indonesia (Ozaki et al., 1999) and other Southeast Asian mangroves including Palawan, Philippines and Matang, Malaysia (Takagi & Williams, 1998). Multiple stressors such as insect damage, wave erosion, and sea level rise may interact or accumulate to reduce ecosystem health, and hence overall mangrove resilience (Gilman et al., 2006b; Gilman et al., 2008). We currently have little quantitative information about interactions between pest attacks and other such stressors.

The Mandai context. — In Singapore mangroves, various insect-herbivory studies have shown the link between herbivory and mangrove mortality. Murphy (1985) found massive mortality of mangrove saplings from tortricid moth (*Lasiognatha leveri*) attack in Singapore mangroves, particularly Mandai. Rhizophoraceae are also known to have higher mortality rates from herbivory of scolytid beetles (*Ips subelongatus*) (Murphy, 1990). Furthermore, polyphagism of certain insects on various mangrove species was found in a number of Singapore mangroves including Mandai (Murphy, 1990). Mandai mangrove may be especially vulnerable to insect damage due to the additive effect of existing stressors such as erosion. The previous studies by Murphy, as well as the other baseline faunal and floral studies previously conducted at Mandai may begin to provide information to answer this question.

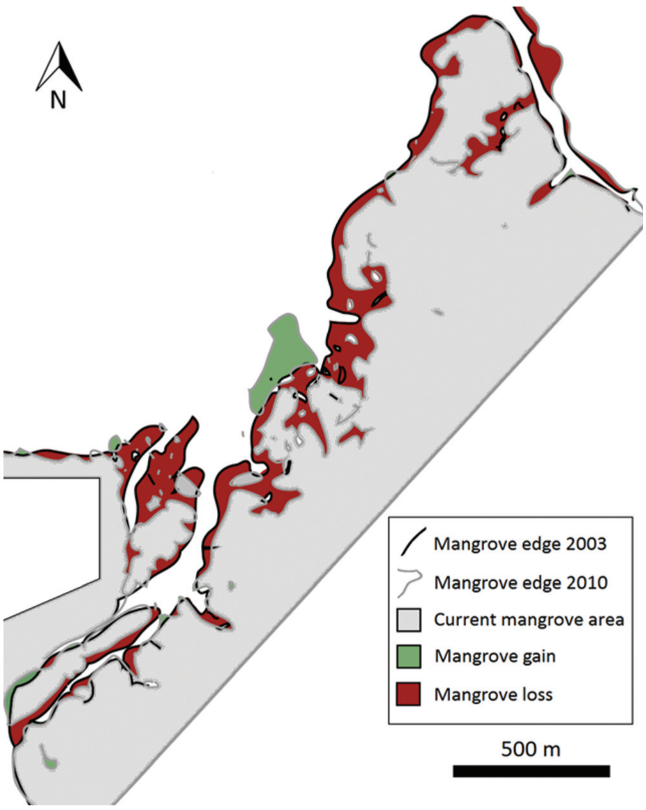

Fig. 4. Change in areal extent of mangrove at Mandai between 2003 and 2010. A large increase in mangrove cover in one location is due to the vegetative spread of a *Sonneratia* patch. Polygons extracted from Google Earth™ Imagery.

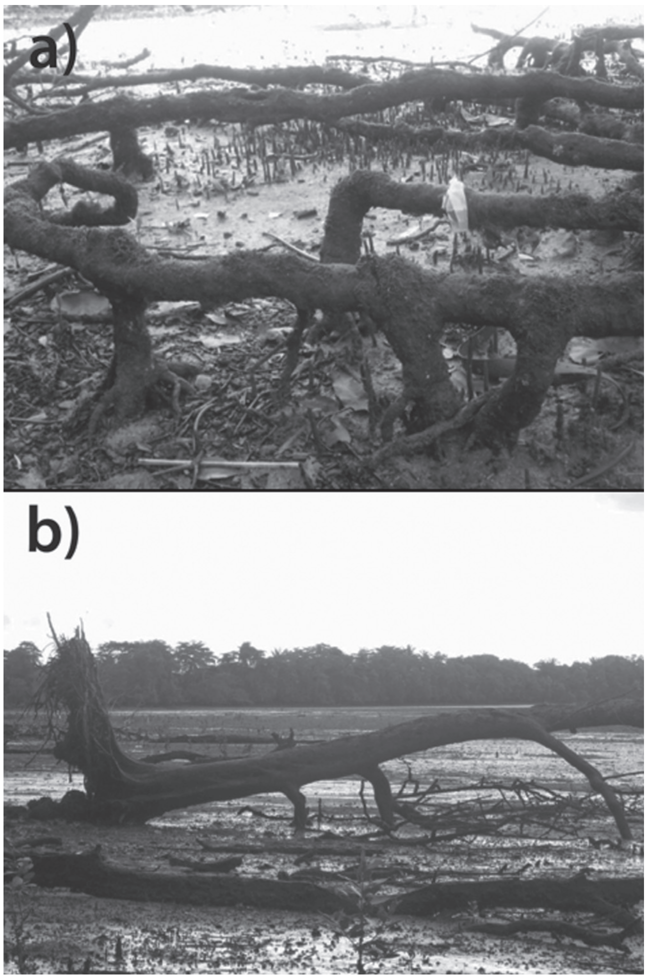

Fig. 5. (a) Example of sediment scouring, erosion and root exposure. (Photograph by: R. R. Y. Oh). (b) Uprooted individuals of *Avicennia* spp. on Mandai's seaward fringe. (Photograph by: C. R. Leong).

Genetic isolation due to habitat loss and fragmentation. — Genetic erosion is a major negative outcome of habitat fragmentation (Aguilar et al., 2008); restricted gene flow between isolated populations directly impacts reproductive success and short-term viability of the remnant populations due to genetic drift and inbreeding (Cascante, 2002; Aguilar et al., 2006). Genetic erosion may also have long-term evolutionary consequences due to the loss of alleles crucial for environmental adaptation (Young et al., 1996). While the factors influencing genetic isolation in terrestrial forests are generally relevant to non-terrestrial forests, specific factors affecting mangroves have yet to be meaningfully studied in Southeast Asia. Three major factors limit gene flow in mangroves:

1. Lack of pollen import from other mangrove populations. — Mangrove trees are largely insect-pollinated, with the exception of *Bruguiera gymnorrhiza*, *Lumnitzera littorea* (bird-pollinated), and *Sonneratia* spp. (bat-pollinated) (Tomlinson, 1986). The movement of insect pollinators could be hindered by as little as 100 m of open landscape (Powell & Powell, 1987). A reduction in allogamous fertilisation could lead to inbreeding, loss of genetic diversity, and genetic erosion.

2. Local loss of pollinators. — While some pollinators (specifically vertebrates) may be able to traverse the inhospitable anthropogenic matrix, reduction in habitat size and quality at Mandai could cause local extirpation of such pollinator populations. Small, isolated mangrove fragments may have insufficient resources to support larger animal pollinators, possibly resulting in mortality and emigration, and eventually local collapse of pollinator populations. This could only be avoided if the pollinators are habitat generalists capable of utilising alternative habitats around the mangrove (e.g., olive-backed sunbird, *Nectarinia jugularis*; Sodhi et al., 2005).

3. Lack of propagule import. — Mangrove genetic diversity further relies on propagule-mediated gene flow (seed dispersal). Wetland species are unique in that their propagules are hydrochoric, that is, dispersed by water. Potential dispersal is defined primarily by propagule buoyancy and flotation period, with genus-specific differences from <20 days (*Lumnitzera* spp.) to one year (*Rhizophora* spp.) (summarised by Friess et al., 2012). Propagule import can be limited by two mechanisms: a) habitat loss and fragmentation that increases the distance between patches beyond a species-specific dispersal threshold; and b) the construction of artificial barriers that limit propagule exchange between habitat patches. In Colombia, barrier construction resulted in genetic disconnection and inbreeding in an *Avicennia germinans* population after only four decades, due to limited inter-patch propagule exchange (Salas-Leiva et al., 2009).

The Mandai context. — Habitat fragmentation and the relative isolation of Mandai provide an ideal research opportunity to understand the processes of propagule/pollinator disconnection and subsequent genetic erosion. Once part of a significantly larger mangrove system (Ng & Sivasothi, 1999), Mandai mangrove has since been reduced to a small patch, isolated from both Sungei Buloh Wetland Reserve and the Kranji Nature Trail mangrove to the west. The fragmentation of Mandai is a situation increasingly common to mangrove patches across Southeast Asia, which poses diverse challenges to genetic connectivity.

Most invertebrate pollinators are likely to have a constricted home range within the vicinity of Mandai mangrove. The highly industrialised area with little natural habitat surrounding Mandai could be inhospitable to such pollinators, acting as an effective barrier to pollen transfer between trees in Mandai and other neighbouring mangroves. The isolated nature of Mandai mangroves means that insect pollinators foraging there are unlikely to be bringing pollen from other mangrove patches at some distance away. Collapse of pollinator populations could lead to inbreeding depression, decreased seed set, and lower reproductive success, all of which would contribute towards genetic erosion.

Genetic connectivity between Mandai and neighbouring mangrove populations could be further hindered by a decrease in the rate of propagule exchange. The presence of the Singapore–Johor causeway obstructs propagule import into Mandai from north-eastern Singapore (including Pulau [=island] Ubin and Pulau Tekong), east Malay Peninsula, and the larger South China Sea region, thus placing greater importance on propagule exchange between Mandai and other mangrove populations to the west to maintain sufficient gene flow. Contemporary research is now focusing on: a) variables that may affect propagule exchange, namely buoyancy and dispersal; and b) molecular studies to elucidate the degree and direction of genetic erosion. Both studies are the first to use novel tools such as hydrodynamic modelling and genetic markers to investigate landscape-level connectivity between mangrove fragments in Southeast Asia. Similar to SLR, constrained gene flow is a threat with long-term implications for mangrove sustainability, though only now are we amassing the data required to make informed management decisions.

CONCLUSIONS

The important mangrove resource held in Mandai is threatened by multiple interacting stressors. The threats we describe here are not static, and continue to evolve: sediment supply will continue to decrease as small estuaries in southern Peninsular Malaysia are progressively reclaimed, sea level will continue to increase over the short- and long-term (Nicholls et al., 2011), and land use decisions in the surrounding landscape will continue to be made. Additional research is required to better understand these threats, monitor changes over time, and identify the relative importance of each threat to Mandai. These types of data are critical to guiding long-term management decisions, including efforts to reduce or mitigate threats and inform rehabilitation measures (e.g., Chou, 1994). Research on Mandai, based on its historical baselines, previous and current physical/ecological research, can guide regional knowledge on how to manage similar mangrove patches in an urban setting. Singapore can already provide examples to the region of how to successfully manage coastal habitats such as coral reefs and rocky shores alongside landfill sites and major port developments (Todd & Chou, 2005; Chou & Tun, 2007). With increased urbanisation and population growth across Southeast Asia, conflicts between mangroves and urban coastal development are going to expand further. Singapore has traditionally been viewed as a model for habitat destruction (Sodhi et al., 2004), though remaining habitat patches such as Mandai could prove to be a model for how to most effectively balance the needs of urban development and habitat conservation.

While data alone do not yield conservation outcomes, we have been cautioned against "building castles without putting too much effort into our foundation, which is derived from sound field natural history" (Sodhi, 1997). For decades, Mandai has been an internationally important site for zoological research, and increasingly for research on mangrove communities in the 21st century. Mandai presents new opportunities for regionally-relevant empirical research, to better inform effective coastal management practices and mangrove rehabilitation at both the local and regional level.

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