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# Plant invasion in mangrove forests worldwide

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ABSTRACT

Plant invasion is a major threat to natural ecosystems, and mangrove forests are among the most threatened ecosystems in the world. However, since mangrove species primarily occur in the saline and intertidal environment that is inhospitable for most terrestrial and freshwater plants, it is commonly assumed that mangrove forests are resilient to plant invasion. Still, many salt tolerant aquatic and terrestrial plants as well as epiphytes are found to invade the mangrove forests, and we know little about those invasive plants, their functional traits, invasion patterns and pathways and their ecological consequences. In a survey of global literature, we found a total of 57 plants reportedly invasive in the world's mangrove forests. These plants possessed the traits of salinity tolerance, tolerance to anaerobic condition, high fecundity and rapid growth. About 19% of invasive plants were anthropogenically introduced for coastal land stabilization, and the rests were accidental introduction. Invaders were found to colonize along the forest edges or forest interior, but mostly in the raised lands. That is, the presence of diversified microhabitats such as raised land and intertidal mudflat might help both halophytic and non-halophytic plants to invade the mangrove forests. Some invaders (30%) were transient, but many (70%) could persist for a longer time; and these species could modify habitat conditions, impede natural regeneration of mangroves and disrupt their faunal assemblage. Together, plant invasion in mangrove forests is much more widespread and problematic than commonly perceived, underscoring the need for the integration of invasive plant management strategy into mangrove forest management.

## 1. Introduction

Mangrove forests—a forest that is dominated by halophytic plant communities and occur predominantly along the tropical and subtropical coastlines—offer important ecosystem functions and services (Barbier et al., 2011; Lee et al., 2014; Kelleway et al., 2017), but presently they are severely degraded (Giri et al., 2011; Feller et al., 2017). About 35% area of the world's mangrove forest was lost by the end of 20th century (Valiela et al., 2001; Alongi, 2002), with an estimated annual rates of mangrove deforestation of 1–3% between 1985 and 2005 (FAO, 2007). In the mid to late 21th century, however, the loss of mangrove forest has slowed down slightly (Spalding et al., 2010; Feller et al., 2017), with an estimated annual rates of mangrove deforestation of 0.2–0.7% between 2000 and 2012 (Hamilton and Casey, 2016). On the other hand, about 16% of mangrove species are presently experiencing threats to extinction (Polidoro et al., 2010). Anthropogenic land-use change such as conversion of mangrove forests to shrimp aquaculture, over-harvesting of mangrove resources, deforestation, and large natural disturbance are among the commonly highlighted causes of mangrove degradation (Biswas et al., 2009; Lewis et al., 2016; Richards and Friess, 2016); of which, shrimp aquaculture contributes disproportionately to mangrove destruction worldwide (Feller et al., 2017). However, the role of plant invasion to the degradation of mangrove forests has received little attention (Biswas et al., 2012). This is surprising, because biological invasion is a well-known threat to natural ecosystems (Secretariat of the Convention on Biological Diversity, 2006), and mangrove forests are among the most threatened ecosystems in the world (Valiela et al., 2001).

The conventional belief remains that mangrove forests are resilient to plant invasion, in part, because mangrove forests typically occur in

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the saline and intertidal environment where the potential terrestrial and freshwater plant invaders struggle to survive and reproduce (Lugo, 1998; Hurst and Boon, 2016). This belief may be partially correct, because despite many salt-tolerant aquatic and terrestrial plants as well as epiphytes can colonize and persist in mangrove forests (Biswas et al., 2007), many opportunistic invaders can also invade mangrove forests during periodic reduced soil and water salinity (Lugo, 1998; Biswas et al., 2012). Mangrove species typically grow in the saline intertidal zone (Tomlinson, 1986), but the spatial extent of a mangrove forest is not limited to the saline intertidal zone but includes other microhabitats such as raised lands (Harun-or-Rashid et al., 2009). For instance, the world's largest mangrove forest, the Sundarbans, has a spatial area of about 10,000 square kilometer, which comprises a mix of intertidal mudflat, raised lands, soft sand microhabitats and depressions (Giri et al., 2007). In an active delta, today's intertidal mudflat may turn into tomorrow's raised land due to coastal land accretion (Thomas et al., 2014). The intertidal mudflats are inundated twice daily, while raised lands are inundated only occasionally; and consequently, raised lands are expected to be relatively less saline with a reduced waterlogged condition.

A mangrove forest could be vulnerable to plant invasion during the period of reduced water and soil salinity or throughout the year for the following reasons. First, the pool of potential invasive species for a mangrove forest may include salt- and anaerobic condition-tolerant aquatic and terrestrial species. This is because juxtaposition of aquatic, terrestrial and transitional habitats within a mangrove forest will support both aquatic and terrestrial species. By contrast, the pool of potential invasive species in a terrestrial or an aquatic system will include either terrestrial or aquatic species. Second, propagules of potential invasive species could reach a mangrove forest through multiple and often unpredictable pathways such as through hydrologic flow, anthropogenic transportation, wind and animal dispersal (Harun-or-Rashid et al., 2009). Third, environmental site conditions of a mangrove forest are spatially (i.e., presence of diversified microhabitats) and temporally (i.e., seasonal variation in soil and water salinity) variable (Feller et al., 2010), which creates and rejuvenates regeneration niches, potentially supporting both habitat specialist and generalist invasive species. Fourth, disturbance within a mangrove forest creates canopy openings where opportunist invaders can colonize and persist (Lugo, 1998). Disturbance in the upstream of a mangrove forest could also affect the sedimentation pattern in the downstream and may favour colonization and persistence of invasive species due to upstream-downstream hydrologic connectivity (Lugo, 1998; Soares, 1999; Lewis, 2005).

Pyšek and Richardson (2007) suggested that rapid growth rate, high fecundity, effective dispersal mechanisms, persistent seed bank, and tolerance to a wider range of environmental conditions are among the key trait for invaders. Zedler and Kercher (2004) suggested that hydrochory, floating ability, flood tolerance, and rapid growth rate are the key traits of an invasive plant species occupying the wetland habitat. Coastal mangroves are a special type of wetlands that is characterized by saline and variable environmental site conditions and inundation. It is likely that salinity tolerance and tolerance to anaerobic conditions are among the important traits of species occupying the mangrove habitat (Feller et al., 2010; Friess et al., 2012).

However, if mangrove forests are vulnerable to plant invasion, what are the traits of an invasive species that equip them to invade a mangrove forest? Earlier research on plant invasion in mangrove forests focused merely on the presence of invasive species, or on the relative performance of invasive species (Biswas et al., 2007; Cao et al., 2007; Fourqurean et al., 2010; Ren et al., 2014). While these studies offer valuable initial insights, there is a lack of serious evaluation on plant invasion in the world's mangrove forests. Importantly, no study has so far evaluated the traits of invasive plants in mangrove forests. Here, by surveying relevant global literature, we aim to present an overview of plant invasion in the world's mangrove forests. In particular, we address the following questions: (*i*) Which plant species commonly invade mangrove forests? (*ii*) What are their traits? (*iii*) Is the plant invasion in mangrove forests related to disturbance? (*iv*) What are the pathways of plant invasion? (*v*) What are the patterns (spatial and temporal) and processes of plant invasion? (*vi*) What are the consequences of plant invasion? We anticipate that both aquatic and terrestrial plants that invade mangroves possess some degree of tolerance to saline and anaerobic conditions in order to cope with the harsh mangrove environment. We also expect that plant invaders would have rapid growth rate and persistent propagule bank to take over and crowd out native communities. As discussed above, we expect that the invader's presence should be associated with disturbance, and the non-halophytic invaders should colonize within the raised lands. We did not hold any a priori expectation for invasion impacts or invasion pathways. Although salt marsh ecosystems are closely related to mangrove systems and are also threatened by invasive plants, we restrict this review to the mangrove forests.

## 2. Methods

### *2.1. Literature search*

To locate relevant papers, we searched the ISI Web of Knowledge™ and SCOPUS databases using different combinations of keywords ("mangrove", "estuarine invasion", "plant invasion", "biological invasion", "alien plant", "invasive plant", "weed", "exotic plant"). We conducted these searches in January 2018; and the result was last updated in April 16, 2018. We also tracked forward and backward citations of several important papers on the topic (Biswas et al., 2007; Cao et al., 2007; Fourqurean et al., 2010; Ren et al., 2014). In this process, we selected a total of 54 peer-reviewed papers, reporting 124 invasion events, for this study (Table 1). The geographic coverage of these papers include Africa, Asia, Australia, Europe, North America and South America (Fig. 1).

### *2.2. Compilation of species-specific information*

We gathered species-specific information on functional traits, invasion patterns, invasion pathways and ecological consequences of invasion from each paper or from scattered literature and relevant database such as Global Invasive Species Database (2018), Invasive Species Compendium (CABI, 2018), USDA plants database (USDA, 2018), Plant directory of Center for Aquatic and Invasive Plants, University of Florida (UF-IFAS, 2018) and Hawaiian Ecosystem at Risk project (Hawaiian Ecosystems at Risk project, 2018). Some of these information were not explicit in many cases; therefore, we developed the following rules a priori that allowed us to identify and classify implicit information consistently.

(i) *Invasive plants:* We divided the recorded invasive plants into invasive alien species (Richardson et al., 2000) and invasive native species (Nackley et al., 2018). An invasive alien species is defined as an exotic/alien species occurring outside their native ranges due to intentional or accidental introduction (Richardson et al., 2000). These species often grow aggressively and cause ecological and environmental harm to native ecosystems. Whereas, an invasive native species is defined as 'a native species whose abundance increases in their original or expanded ranges' (Nackley et al., 2018). That is, an invasive native species are plants that grow in sites where they are not wanted and which usually have detectable economic or environmental effects (Richardson et al., 2000).

(ii) *Functional traits of invasive plants:* By matching the traits of an ideal invader (Pyšek and Richardson, 2007), traits of a wetland invader (Zedler and Kercher, 2004) and the traits of a mangrove species (Friess et al., 2012) we selected species' life form, longevity, relative growth rate, dispersal vector, fecundity, persistent propagule

**Table 1**
List of reported invasive plants in mangrove forests.

| Invasive alien or invasive native? | Family | Species | Aquatic or terrestrial origin? | Invaded region | Native range | Reference |
|---|---|---|---|---|---|---|
| Invasive native | Pteridaceae | *Acrostichum aureum* | Aquatic | Tijuca, Brazil; Sundarbans, Bangladesh; Matang Mangrove and Rejang Mangrove, Malaysia | Americas, Tropical Africa, Asia | Soares (1999), Biswas et al. (2007), Jawa and Srivastava (1989), Srivastava and Shaffie (1979) |
| Invasive alien | Asteraceae | *Ageratum conyzoides* | Terrestrial | Huizhou Mangrove, China | Tropical America | Cao et al. (2007) |
| Invasive alien | Amaranthaceae | *Amaranthus tricolor* | Terrestrial | Huizhou Mangrove, China | Tropical Asia | Cao et al. (2007) |
| Invasive native | Poaceae | *Arundo donax* | Terrestrial | Sundarbans, Bangladesh | Eastern Asia | Biswas et al. (2007) |
| Invasive alien | Poaceae | *Axonopus compressus* | Terrestrial | Huizhou Mangrove, China | Tropical America | Cao et al. (2007) |
| Invasive alien | Asteraceae | *Bidens frondosa* | Terrestrial | Huizhou Mangrove, China | North America | Cao et al. (2007) |
| Invasive alien | Asteraceae | *Bidens pilosa* | Terrestrial | Huizhou Mangrove, China | Americas | Cao et al. (2007) |
| Invasive alien | Rhizophoraceae | *Bruguiera gymnorhiza* | Aquatic | Florida, USA; Hawaii, USA | Asia pacific | Ruiz et al. (2000), Allen (1998) |
| Invasive alien | Casuarinaceae | *Casuarina equisetifolia* | Terrestrial | Florida, USA | Asia, Oceania | Ruiz et al. (2000), U.S. Fish and Wildlife Service. (1999) |
| Invasive native | Lamiaceae | *Clerodendrum inerme* | Terrestrial | Sundarbans, Bangladesh | Tropical Australasia | Biswas et al. (2007) |
| Invasive alien | Asteraceae | *Conyza bonariensis* | Terrestrial | Huizhou Mangrove, China | Tropical America | Cao et al. (2007) |
| Invasive alien | Asteraceae | *Crassocephalum crepidioides* | Terrestrial | Huizhou Mangrove, China | Tropical Africa | Cao et al. (2007) |
| Invasive native | Araceae | *Cryptocoryne ciliate* | Aquatic | Sundarbans, Bangladesh | Tropical Asia | Biswas et al. (2007) |
| Invasive alien | Loranthaceae | *Dendropthoe falcata* | Terrestrial | Sundarbans, Bangladesh | Tropical Africa, Australasia | Biswas et al. (2007) |
| Invasive native | Fabaceae | *Derris trifoliata* | Aquatic | Sundarbans, Bangladesh | Australasia | Biswas et al. (2007) |
| Invasive alien | Pontederiaceae | *Eichhornia crassipes* | Aquatic | Huizhou Mangrove, China; Sundarbans, Bangladesh; Florida, USA; Sri Lanka | Brazil | Cao et al. (2007), Biswas et al. (2007), Biswas et al. (2012), Lugo (1998), Dahdouh-Guebas et al. (2005) |
| Invasive alien e | Poaceae | *Eleusine indica* | Terrestrial | Huizhou Mangrove, China | Australasia, Tropical America | Cao et al. (2007) |
| Invasive native | Fabaceae | *Entada rheedii* | Terrestrial | Sundarbans, Bangladesh | Africa | Biswas et al. (2007) |
| Invasive alien | Asteraceae | *Eupatorium catarium* | Terrestrial | Huizhou Mangrove, China | South America | Cao et al. (2007) |
| Invasive alien | Asteraceae | *Eupatorium odoratum* | Terrestrial | Sundarbans, Bangladesh | Americas | Biswas et al. (2007) |
| Invasive alien | Euphorbiaceae | *Euphorbia hirta* | Terrestrial | Huizhou Mangrove, China | India | Cao et al. (2007) |
| Invasive native | Euphorbiaceae | *Excoecaria indica* | Terrestrial | Sundarbans, Bangladesh | Old world tropics | Biswas et al. (2007) |
| Invasive native | Flagellariaceae | *Flagillaria indica* | Terrestrial | Sundarbans, Bangladesh | Asia, Polynesia, Australia, Old world tropics | Biswas et al. (2007) |
| Invasive alien | Asteraceae | *Helianthus tuberosu* | Terrestrial | Huizhou Mangrove, China | North America | Cao et al. (2007) |
| Invasive alien | Malvaceae | *Hibiscus tilliaceus* | Terrestrial | Sundarbans, Bangladesh | Old world tropics | Biswas et al. (2007) |
| Invasive alien | Apocynaceae | *Hoya parasitica* | Terrestrial | Sundarbans, Bangladesh | Asia | Biswas et al. (2007) |
| Invasive native | Poaceae | *Imperata cylindrical* | Aquatic | Sundarbans, Bangladesh | Asia | Biswas et al. (2007) |
| Invasive native | Convolvulaceae | *Ipoemea fistulosa* | Aquatic | Sundarbans, Bangladesh | Tropical Americas | Biswas et al. (2007) |
| Invasive alien | Convolvulaceae | *Ipomoea cairica* | Aquatic | Huizhou Mangrove, China | Pan tropics | Cao et al. (2007) |
| Invasive alien | Convolvulaceae | *Ipomoea purpurea* | Aquatic | Shenzhen Bay, China | North and south Americas | Ren et al. (2014) |
| Invasive alien | Verbenaceae | *Lantana camara* | Terrestrial | Huizhou Mangrove, China | Tropical America | Cao et al. (2007) |
| Invasive alien | Combretaceae | *Lumnitzera racemosa* | Aquatic | Tonga; Florida, USA | Asia, east Africa, pacific islands | Clarke and Thaman (1993), Fourqurean et al. (2010) |
| Invasive native | Asteraceae | *Micania scandens* | Terrestrial | Sundarbans, Bangladesh | Tropical America | Biswas et al. (2007) |
| Invasive alien | Asteraceae | *Mikania micrantha* | Terrestrial | Mai Po, Hong Kong, China, Tamsui River, Taiwan, China; Florida USA | Tropical America | Chen and Ma (2015), Kong et al. (2000), Maja et al. (2008), Chen et al. (2009a), Zhang and Zhang (2008), Yu and Yang (2011), Mao et al. (2011), Miao et al. (2012) |
| Invasive alien | Fabaceae | *Mimosa pudica* | Terrestrial | Huizhou Mangrove, China | Tropical America | Cao et al. (2007) |
| Invasive alien | Arecaceae | *Nypa fruticans* | Aquatic | Niger River Delta, Nigeria | Indo-pacific | Isebor et al. (2003), Numbere (2018), Little et al. (2018) |
| Invasive alien | Poaceae | *Panicum repens* | Terrestrial | Shenzhen Bay, China | Tropical and subtropical regions worldwide | Ren et al. (2014) |
| Invasive alien | Poaceae | *Paspalum dilatatum* | Terrestrial | Huizhou Mangrove, China | South America | Cao et al. (2007) |
| Invasive alien | Passifloraceae | *Passiflora foetida* | Terrestrial | Huizhou Mangrove, China | Tropical America | Cao et al. (2007) |
| Invasive alien | Poaceae | *Phragmites australis* | Aquatic | Minjiang River Estuarine Wetlands, China | North America | Wang et al. (2016) |
| Invasive alien | Plantaginaceae | *Plantago virginica* | Terrestrial | Huizhou Mangrove, China | North America | Cao et al. (2007) |
| Invasive native | Fabaceae | *Pongamia pinnata* | Terrestrial | Sundarbans, Bangladesh | Australasia | Biswas et al. (2007) |

(*continued on next page*)

**Table 1** (*continued*)

| Invasive alien or invasive native? | Family | Species | Aquatic or terrestrial origin? | Invaded region | Native range | Reference |
|---|---|---|---|---|---|---|
| Invasive alien | Rhizophoraceae | *Rhizophora mangle* | Aquatic | Hawaii Islands, Hawaii-Puerto Rico, USA | Atlantic coast, Western Africa | Allen (1998), Cox and Allen (1999), Fourqurean et al. (2010), Chimner et al. (2006) |
| Invasive alien | Rhizophoraceae | *Rhizophora stylosa* | Aquatic | Moorea, French Polynesia | Atlantic coast, Western Africa | Clarke and Thaman (1993) |
| Invasive native | Poaceae | *Saccahrum spontaneum* | Terrestrial | Sundarbans, Bangladesh | Indian subcontinent | Biswas et al. (2007) |
| Invasive native | Celastraceae | *Salacia prinoides* | Terrestrial | Sundarbans, Bangladesh | Asia | Biswas et al. (2007) |
| Invasive native | Apocynaceae | *Sarcolobus globosus* | Terrestrial | Sundarbans, Bangladesh | Tropical Asia | Biswas et al. (2007) |
| Invasive alien | Anacardiaceae | *Schinus terebinthifolius* | Terrestrial | Florida, USA | South America | Donnelly et al. (2008), U.S. Fish and Wildlife Service. (1999), Gordon (1998) |
| Invasive alien | Plantaginaceae | *Scoparia dulcis* | Terrestrial | Huizhou Mangrove, China | Neotropics | Cao et al. (2007) |
| Invasive alien | Lythraceae | *Sonneratia apetala* | Aquatic | Huizhou Mangrove, Shenzhen Bay, Leizhou Bay, China | Coastal Indian Ocean | Cao et al. (2007), Ren et al. (2014), Chen et al. (2013), Li et al. (2004a), Li et al. (2004b), Wang and Zan (2001), Han et al. (2003), Liang et al. (2005), Zeng et al. (2008), Wang et al. (2008b), Pan et al. (2006), Zhu (2012) |
| Invasive alien | Poaceae | *Spartina alterniflora* | Aquatic | Shankou, Guangxi, Qi'ao Island, Shenzhen, China | Atlantic and Gulf coast of North America | Chen et al. (2007), Chen et al. (2009b), Chen et al. (2013), Ren et al. (2014), Wan et al. (2014), Callaway and Josselyn (1992), Hong et al. (2005), Wang et al. (2008a), Zhang et al. (2008), Chen et al. (2012), Wu et al. (2013), Wang et al. (2014), Wen et al. (2014) |
| Invasive alien | Poaceae | *Spartina anglica* | Aquatic | Australia | Atlantic and Gulf coast of North America | Nightingale and Weiller (2005), Bridgewater and Cresswell (1999) |
| Invasive alien | Poaceae | *Spartina townsendii* | Aquatic | Australia | Atlantic and Gulf coast of North America | Nightingale and Weiller (2005) |
| Invasive native | Myrtaceae | *Syzygium fruticosum* | Terrestrial | Sundarbans, Bangladesh | Asia | Biswas et al. (2007) |
| Invasive alien | Tamaricaceae | *Tamarix indica* | Terrestrial | Sundarbans, Bangladesh | Eurasia and Africa | Biswas et al. (2007) |
| Invasive native | Typhaceae | *Typha angustata* | Aquatic | Sundarbans, Bangladesh | Eurasia | Biswas et al. (2007) |
| Invasive alien | Asteraceae | *Wedelia trilobata* | Terrestrial | Huizhou Mangrove, China | Tropical America | Cao et al. (2007), Ren et al. (2014) |

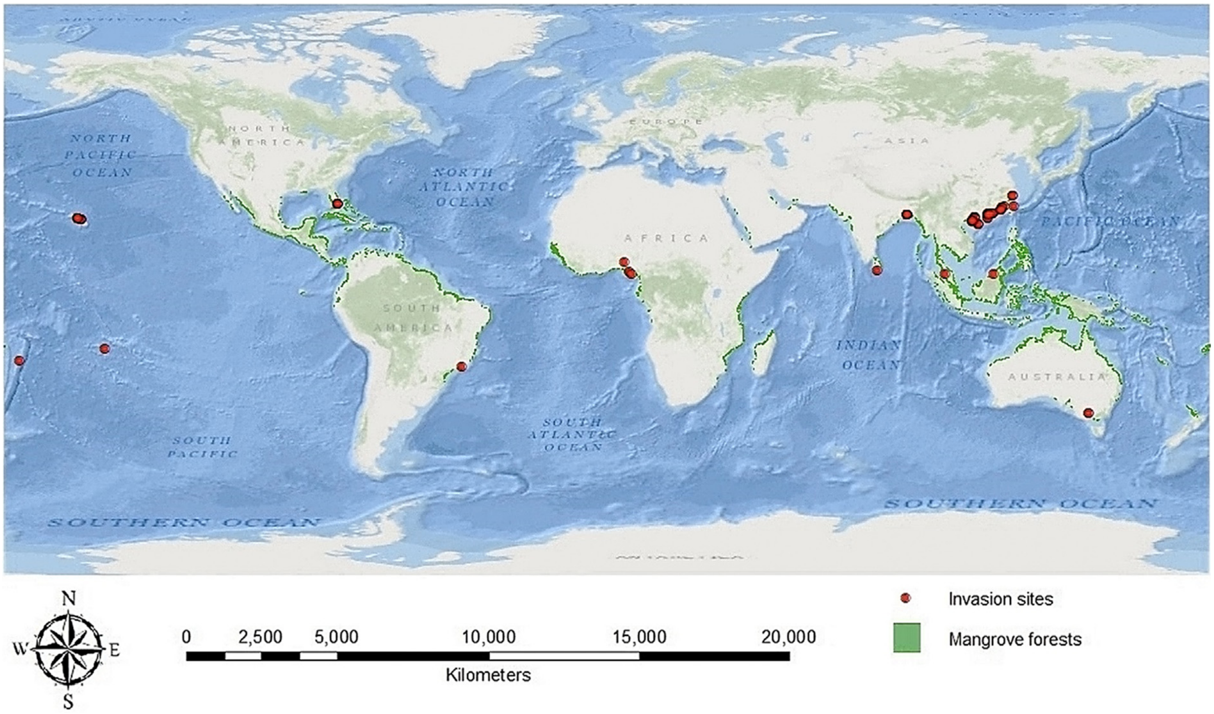


**Fig. 1.** Global distribution of studies on plant invasion in mangrove forests.

bank, vegetative spread ability, salinity tolerance, tolerance to anaerobic condition, shade tolerance and ability to form monotype as candidate traits for plant invaders in mangrove forests. Trait states were defined according to USDA plants database (USDA, 2018). For each invasive plant and for each trait, we collated detailed information from scattered literature, database, or from personal field observation.

(iii) *Disturbance and invasion pathways:* Lugo (1998) argued that habitat modification as a result of disturbance could facilitate plant invasion in mangrove forests. Therefore, we examined if the species-specific invasion event was associated with any form of habitat modification or disturbance. We considered natural disturbance such as cyclones, flooding and lighting strikes, and anthropogenic disturbance such as land clearing, forest clearing or construction of barrage that eventually modify the physical environment of a mangrove forest. On the other hand, we classified invasion pathways into intentional or accidental introduction. Species that were introduced into the mangrove system for restoration or coastal land stabilization were classified into the category of intentionally introduced species. All other species, whose specific introduction pathways could not be verified unambiguously, were put into the category of accidental introduction.

(iv) *Patterns of invasion:* Because invasive plants often reach a mangrove forest through hydrologic flow (Biswas et al., 2012), it is important to know whether they are primarily concentrating around the water channels or whether they are spreading inside the forests, and how long they last in the mangrove forests (Lugo, 1998). Thus, we identified species-specific spatial and temporal patterns of invasion. We distinguished the spatial pattern of invasion into forest edge and forest interior. Within each of two spatial locations, we further classified the types of microhabitat in which invasive plants occur into: intertidal mudflats (river banks; inundated by regular tidal inundation), raised lands (i.e., not inundated by regular tidal inundation), depressions (i.e., neither connected to rivers, nor to regular tidal inundation), and soft sandy microhabitats (i.e., connected to sea and inundated by regular tidal inundation). Note that, intertidal mudflats and soft sandy microhabitats considered here are located within the spatial extents a mangrove forest, and these microhabitats are either already colonized by early successional mangroves or to be colonized by mangroves under normal conditions (i.e., these microhabitats are suitable for mangrove development). On the other hand, temporal patterns of invasions were divided into transient (i.e. invasive species occurs only for a particular time of a year) and persistent invasion (i.e., invasive species occurs all year round).

(v) *Consequences of invasion:* We assessed the species-specific impact of plant invasion on habitat characteristics, plant assemblage and faunal community. For habitat characteristics, we considered the effects on physical template or environmental site conditions of a mangrove forest. For plant assemblage, we considered the effects on species composition, regeneration or successional pathways. For the fauna-level impact, we considered the direct or indirect effects of an invasive plant on the faunal community. The species-specific impacts were compiled from scattered literature as well as databases such as Global Invasive Species Database (Global Invasive Species Database, 2018), Invasive Species Compendium (CABI, 2018), USDA plants database (USDA, 2018), Plant directory of Center for Aquatic and Invasive Plants, University of Florida (UF-IFAS, 2018) and Hawaiian Ecosystem at Risk project (Hawaiian Ecosystems at Risk project, 2018).

## 3. Results

### 3.1. Which plant species commonly invade mangrove forests?

A total of 57 plants had been reported as invasive in the world's mangrove forests (Table 1). Of which, 40 species were invasive alien and 17 species were invasive native. *Soneratia apetala* was the most frequently encountered (also the most frequently studied) invasive plant, followed by *Spartina alterniflora*, *Rhizophora mangle* and *Mikania micartha*. The highest number of invasive plants belonged jointly to the families Asteraceae and Poaceae; each contributed 11 species. The family Fabaceae was the second largest contributor of invasive species (4 species), followed by the family Rhizophoraceae (3 species). The

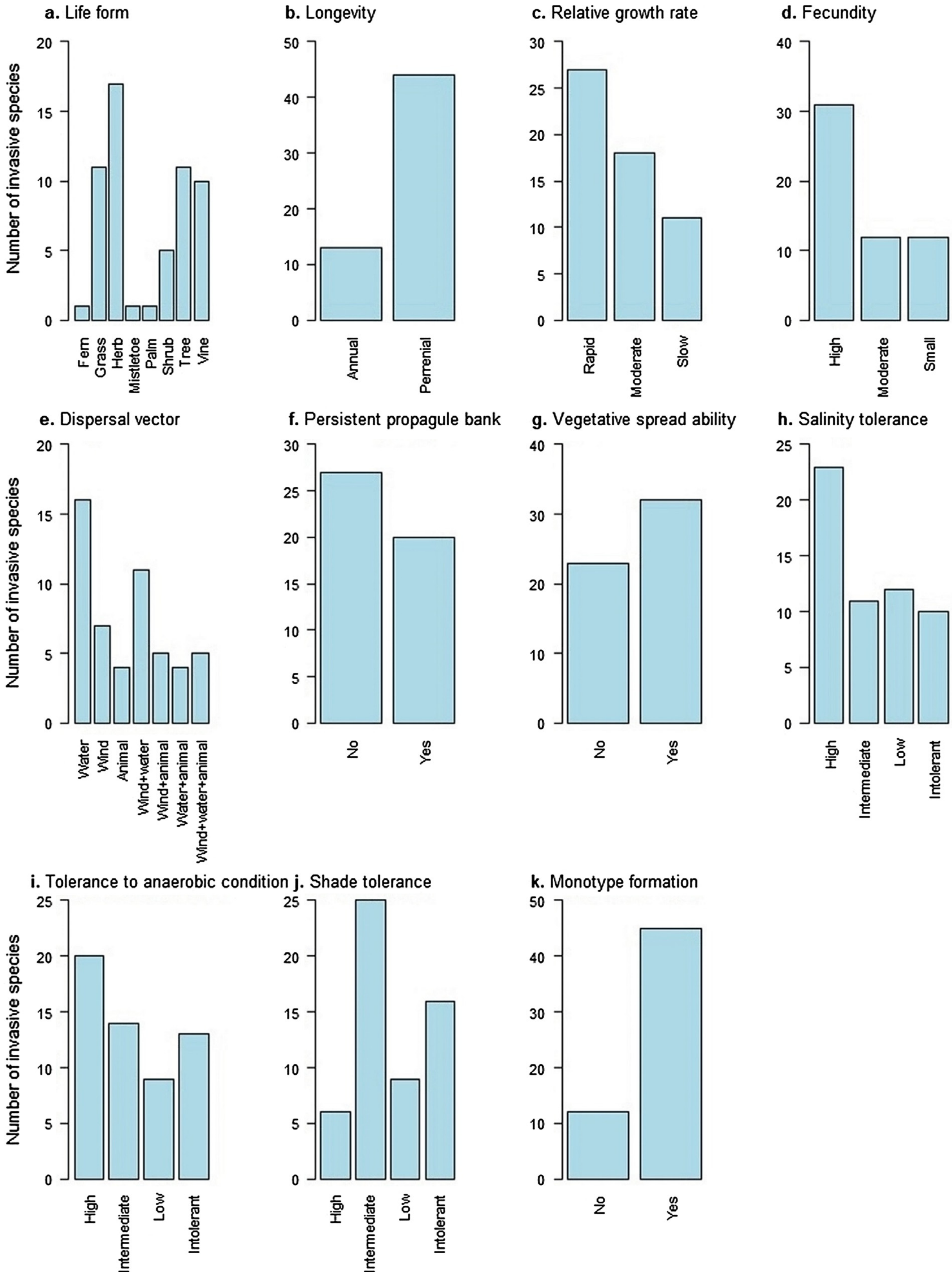


**Fig. 2.** Bar plots showing common traits of the recorded invasive plants.

invasive contributions of other families were minor, and limited to one or two species. About 36.2% of invasive plants were aquatic and 63.8% were terrestrial (Table 1).

### 3.2. What are the traits of a plant invader occupying mangrove forests?

The recorded invasive plants comprised a rich variety of life forms, including tree, shrub, herb, grass, vine, palm and mistletoes (Fig. 2a). The dominant invasive life form was herb (29.82%, 17 species), followed by trees (19.30%, 11species), grasses (19.30%, 11species) and vines (17.54%, 10 species). The shrub life form accounted only 8.77% (or 5 species). Of the recorded invasive plants, 77.19% (44 species) were perennial and 22.81% (13 species) were annual (Fig. 2b).

About 47.37% of invasive plants (27 species) possessed the trait of rapid growth, while 31.58% (18 species) and 19.30% (11 species) of invasive plants possessed the trait of moderate and slow growth, respectively (Fig. 2c). More than half of the recorded invasive plants (54.39%, 31 species) were highly fecund (i.e., produce more than 1000 seeds/propagules per individuals/per year), and the rest possessed moderate to small fecundity (Fig. 2d). Although invaders could be dispersed by a number of dispersal vectors, water and wind were the predominant vectors (Fig. 2e). Surprisingly, only 38.09% of invasive plants (20 species) could form persistent propagule bank (Fig. 2f), although the majority of invasive plants (56.14%, 32 species) could spread through vegetative means (Fig. 2g).

A large portion of invasive plants (81.70%, 46 species) possessed some degrees of salt tolerance: specifically, 40.35% (23 species), 19.30% (11 species) and 21.05% (12 species) of the recorded invasive plants possessed high, intermediate and low degrees of salinity tolerance, respectively (Fig. 2h). Only 17.55% of invasive plants were salinity intolerant. Similarly, 75.44% of invasive plants (43 species) had some degrees of tolerance to anaerobic conditions; more specifically, 40.35% (23 species), 19.30% (11 species) and 21.05% (12 species) of invasive plants possessed high, intermediate and low degrees of tolerance to anaerobic conditions, respectively (Fig. 2i). About 22.81% of invasive plants were intolerant to anaerobic conditions. About 71.93% of invasive plants (41 species) could tolerate shade to some extent: more specifically, 10.53% (6 species), 43.86% (25 species) and 15.79% (9 species) of invasive plants possessed high, intermediate and low degrees of shade tolerance, respectively (Fig. 2j). About 28.07% of invasive plants were shade intolerant. About 78.95% (45 species) of the recorded invasive plants possessed the ability to form monotype community (Fig. 2k).

### 3.3. Is plant invasion in mangrove forests related to the modified habitat condition?

The occurrence of about 70.18% (40 species) of invasive plants was related to the modified habitat conditions (Fig. 3). The typical mangrove habitat condition refers to the closed canopy settings. By contrast, the modified habitat conditions could be the result of natural disturbance such as canopy gap created by cyclones, lighting strikes or anthropogenic disturbances such as forest clearing. The occurrence of about 29.82% of invasive plants (17 species) was unrelated to disturbance.

### 3.4. What are the pathways of plant invasion in mangrove forests?

About 19.30% (11 species) of invasive plants were anthropogenically introduced, mainly for coastal land stabilization or restoration. By contrast, majority of invasive plants (80.70%, 46 species) were accidental introduction. Although not explicitly studied, the dispersal trait of the invaders (Fig. 2e) indicated that wind and water could be the predominant pathways of accidental introduction. We also found that 38.6% of our recorded invasive plants (22 species) were among the known weed in agricultural system.

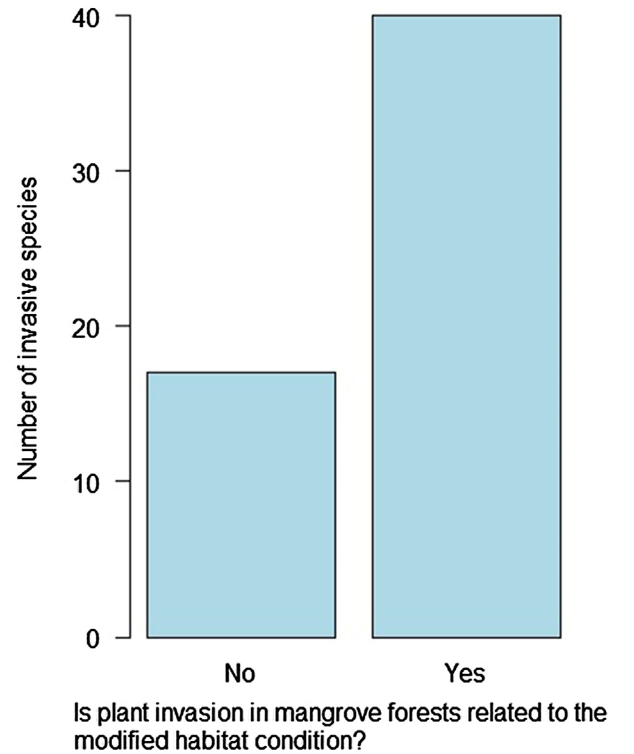


**Fig. 3.** Bar plot showing the frequency of invasive events associated with modified habitat conditions.

### 3.5. What are the patterns of plant invasion in mangrove forests?

The raised land within a mangrove forest was the dominant microhabitat type in which most invasive plants (64.9%, 37 species) colonized and persisted, while only 21% of invasive plants (12 species) colonized in the intertidal mudflats (Fig. 4). Few species also invaded the depressions (i.e., wetlands) and soft sandy microhabitats (3 species in each microhabitat). In terms of spatial location along a gradient of forest edge to interior, at least 45.6% of invasive plants (26 species) occurred both in the edge and in the forest interior interchangeably, while 43% and 10.5% of the invaders (25 and 6 species) occurred only in the interior and in the edges, respectively. About 87.72% of invasive plants (50 specie) were persistent, and 12.28% (7 species) were transient. Floating aquatics or some annuals were the transient invader, and the rest were persistent invader.

### 3.6. What are the consequences of plant invasion in mangrove forests?

About 47.37% of invasive plants (27 species) could modify coastal hydrology and geomorphology by trapping sediments through their vegetative parts, by blocking coastal drainage system, by converting intertidal mangrove habitat to marsh lands, or by accelerating soil erosion (Table 2). About 26.32% of invasive plants (15 species) could alter soil fertility, nutrient and light regimes by modifying water table and nutrient balance, or by suppressing mangrove canopy. On the other hand, species like *Arundo donax* and *Lantana camara* could increase fire hazard by increasing fuel load. The habitat-level consequences of about 47.37% of invasive plants (27 species) remained unclear (Table 2).

About 33.33% of invasive plants (19 species) could impede natural regeneration by blocking propagule dispersal or by inhibiting seed germination through allelochemicals. About 47.37% of invasive plants (27 species) could modify native vegetation structure and composition by modifying successional pathways, by displacing mangrove species, or by dominating mangrove understory. About 54.39% of invasive plants could impede mangrove growth by suppressing canopy, by

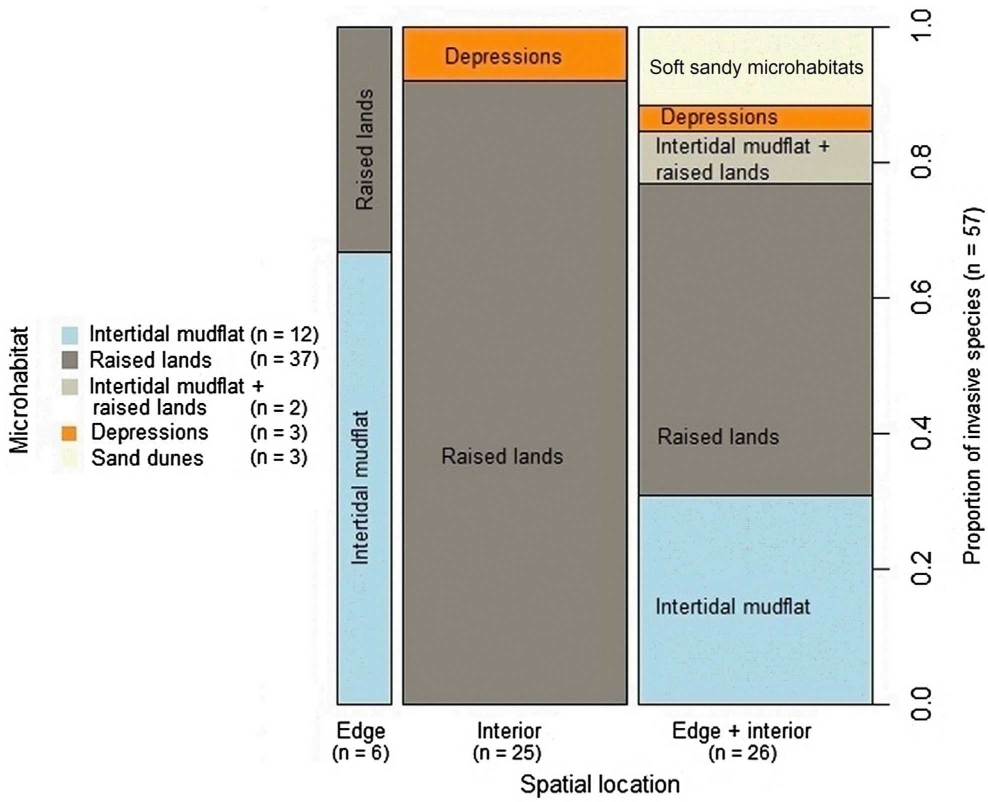


**Fig. 4.** Mosaic plot showing the relative frequency of microhabitat types for different spatial patterns of plant invasion in mangrove forests. Bar widths are proportional to the number of species per spatial location. The height of each bar segment corresponds to the proportional occurrence of invasive plant per microhabitat.

outcompeting native mangrove vegetation, or by crowding out mangrove vegetation. Few invasive plant, however, could reduce native biodiversity and productivity (12.28%, 7 species), or transmit insect and pathogens (2 species). The plant community-level consequences of about 12.28% of invasive plants (7 species) remained unclear (Table 2).

About 28.07% of invasive plants (16 species) could modify animal breeding and foraging habitat such as the nesting or breeding and foraging habitats of water/shore birds and turtles. About 12.28% of invasive plants (7 species) could contribute to the reduction of faunal diversity in terms of reduction of burrowing animals, bivalves, shore birds, arthropods and monkeys. The dense vegetation of *Acrostichum aureum* could also hinder the movement of large animals. The impact of about 68.42% of invasive plants (39 species) on faunal community remained unclear (Table 2).

## 4. Discussion

This paper, to our knowledge, is the first to provide a detailed assessment of invasive plants, their functional traits, invasion patterns and pathways and the ecological consequences of invasion in the world's mangrove forests.

### 4.1. Invasion stages and the invasibility of mangrove forests

The rich variety of invasive plants, their widespread occurrences and recognizable negative impacts indicate that plant invasion is indeed a major threat to the world's mangrove forests. The total number of recorded invasive plants in mangrove forest may seem low compared to the number of invasive plants in freshwater wetlands (UF-IFAS (2018) listed a total of 439 species in saline and freshwater wetlands versus 57 invasive species in this study); however, compared to the total number of mangrove species in the world (about 60 species of trees and shrubs; Tomlinson (1986)), the number is still high. Our results can help reconstruct the stage-specific invasion processes (Colautti and MacIsaac, 2004; Inderjit et al., 2005) to understand the invasibility of mangrove forests. The stage-0 of invasion is the source pool of invasive species (Fig. 5). The source pool is relatively large for mangrove forests as evidenced from the presence of floating and emergent aquatics and terrestrial plants. However, how the invasive plants are transported from nearby sources to mangrove forests (stage -I) remains somewhat unclear, although wind and water appeared to be the dominant dispersal vectors. Importantly, only 19.30% of invasive plants (e.g. *R. mangle, B. gymnorhiza, S. apetala* and *Spartina* spp) are introduced (stage-II) deliberately, mainly for restoration or coastal land stabilization. Invasion spillover constituted a significant part of invasive plants in the mangrove forests, as evidenced from the presence of large number of agricultural weeds in the list of invasive plants (Table 1). Hurst and Boon (2016) also reported large-scale invasion of agricultural weeds in Australian salt marshes. A recent meta-analysis suggests that mangroves increasingly coexist within highly anthropogenic landscapes along urbanized coasts (Branoff, 2017). Therefore, human settlement in the periphery of mangrove forests and their forest-dependent livelihood activities may play an important role to the spread of agricultural weeds into the mangrove forests (Cao et al., 2007).

The stage III of invasion is the establishment of transported species in mangrove forests (Inderjit et al., 2005). Theory suggests that soil and water salinity, tidal flooding, prolonged anaerobic conditions and closed mangrove canopy may limit the establishment of non-halophytic plants in the mangrove environment (Lugo, 1998). By contrast, our findings suggest that 90% of invasive plants are non-halophytic. Non-halophytic plants seem to evade the constraints of salinity and tidal inundation by colonizing the raised lands. The diversity of microhabitat within a mangrove forest might be a key factor contributing to the establishment of a rich variety of halophytic and non-halophytic invasive plants and, in turn, contributing to the invasibility of mangrove forests (Junk et al., 2006).

**Table 2**
Impacts of invasive plants on habitat, mangrove flora and mangrove fauna. The species-specific impacts were compiled from scattered literature as well as established databases.

| Impacts on | Impact type | Associated species |
|---|---|---|
| Habitat | Modify coastal geomorphology and hydrology | *Acrostichum aureum, Arundo donax, Bruguiera gymnorhiza, Bruguiera sexangula, Casuarina equisetifolia, Eichhornia crassipes, Eupatorium catarium, Eupatorium odoratum, Helianthus tuberosu, Ipoemea fistulosa, Ipomoea cairica, Ipomoea purpurea, Nypa fruticans, Panicum repens, Rhizophora stylosa, Rhizophora mangle, Sonneratia apetala, Spartina anglica, Spartina townsendii, Spartina alterniflora, Typha angustata* |
| | Modify soil fertility, nutrient and light | *Casuarina equisetifolia, Crassocephalum crepidioides, Dendropthoe falcate, Derris trifoliata, Eichhornia crassipes, Eupatorium catarium, Eupatorium odoratum, Excoecaria indica, Imperata cylindrical, Mikania micrantha, Mimosa pudica, Spartina anglica, Spartina townsendii, Spartina alterniflora, Syzygium fruticosum* |
| | Increase fire hazard | *Arundo donax, Lantana camara* |
| | Unknown | *Ageratum conyzoides, Amaranthus tricolor, Axonopus compressus, Bidens frondosa, Bidens pilosa, Clerodendrum inerme, Conyza bonariensis, Cryptocoryne ciliate, Eleusine indica, Entada rheedii, Euphorbia hirta, Flagillaria indica, Hibiscus tilliaceus, Hoya parasitica, Lumnitzera racemosa, Micania scandens, Paspalum dilatatum, Passiflora foetida, Plantago virginica, Pongamia pinnata, Saccahrum spontaneum, Salacia prinoides, Sarcolobus globosus, Schinus terebinthifolius, Scoparia dulcis, Tamarix indica, Wedelia trilobata* |
| Mangrove flora | Impede natural regeneration | *Acrostichum aureum, Ageratum conyzoides, Arundo donax, Bruguiera gymnorhiza, Bruguiera sexangula, Derris trifoliata, Eichhornia crassipes, Eleusine indica, Euphorbia hirta, Helianthus tuberosu, Micania scandens, Mikania micrantha, Nypa fruticans, Rhizophora stylosa, Rhizophora mangle, Sonneratia apetala, Syzygium fruticosum, Tamarix indica, Typha angustata* |
| | Modify native vegetation structure and composition | *Amaranthus tricolor, Arundo donax, Axonopus compressus, Bruguiera gymnorhiza, Bruguiera sexangula, Casuarina equisetifolia, Crassocephalum crepidioides, Derris trifoliata, Eichhornia crassipes, Eupatorium catarium, Eupatorium odoratum, Ipoemea fistulosa, Ipomoea cairica, Ipomoea purpurea, Lantana camara, Rhizophora stylosa, Rhizophora mangle, Schinus terebinthifolius, Schinus terebinthifolius, Sonneratia apetala, Spartina anglica, Spartina townsendii, Spartina alterniflora, Syzygium fruticosum, Tamarix indica* |
| | Impede mangrove growth and development | *Ageratum conyzoides, Casuarina equisetifolia, Clerodendrum inerme, Dendropthoe falcate, Derris trifoliata, Eupatorium catarium, Eupatorium odoratum, Flagillaria indica, Helianthus tuberosu, Hibiscus tilliaceus, Hoya parasitica, Imperata cylindrical, Lantana camara, Mikania micrantha, Mimosa pudica, Mimosa pudica, Nypa fruticans, Paspalum dilatatum, Passiflora foetida, Plantago virginica, Pongamia pinnata, Scoparia dulcis, Sonneratia apetala, Syzygium fruticosum, Tamarix indica, Wedelia trilobata* |
| | Reduce native biodiversity and productivity | *Axonopus compressus, Bidens frondosa, Bidens pilosa, Casuarina equisetifolia, Conyza bonariensis, Eleusine indica, Excoecaria indica* |
| | Transmit insect and pathogen | *Ageratum conyzoides, Hibiscus tilliaceus* |
| | Unknown | *Cryptocoryne ciliate, Entada rheedii, Lumnitzera racemosa, Panicum repens, Saccahrum spontaneum, Salacia prinoides, Sarcolobus globosus* |
| Mangrove fauna | Reduces animal breeding and foraging habitat | *Arundo donax, Bruguiera gymnorhiza, Bruguiera sexangula, Casuarina equisetifolia, Derris trifoliata, Eleusine indica, Excoecaria indica, Excoecaria indica, Imperata cylindrical, Rhizophora stylosa, Rhizophora mangle, Saccahrum spontaneum, Schinus terebinthifolius, Spartina anglica, Spartina townsendii, Spartina alterniflora* |
| | Reduces faunal diversity (e.g. burrowing animals, monkeys, bivalves, shore bird, arthropod etc.) | *Arundo donax, Helianthus tuberosu, Imperata cylindrical, Mikania micrantha, Spartina anglica, Spartina townsendii, Spartina alterniflora* |
| | Hinder animal movement | *Acrostichum aureum* |
| | Unknown | *Ageratum conyzoides, Amaranthus tricolor, Axonopus compressus, Bidens frondosa, Bidens pilosa, Clerodendrum inerme, Conyza bonariensis, Crassocephalum crepidioides, Cryptocoryne ciliate, Dendropthoe falcate, Eichhornia crassipes, Entada rheedii, Eupatorium catarium, Eupatorium odoratum, Euphorbia hirta, Flagillaria indica, Hibiscus tilliaceus, Hoya parasitica, Ipoemea fistulosa, Ipomoea cairica, Ipomoea purpurea, Lantana camara, Lumnitzera racemosa, Micania scandens, Mimosa pudica, Nypa fruticans, Panicum repens, Paspalum dilatatum, Passiflora foetida, Plantago virginica, Pongamia pinnata, Salacia prinoides, Sarcolobus globosus, Scoparia dulcis, Sonneratia apetala, Syzygium fruticosum, Tamarix indica, Typha angustata, Wedelia trilobata* |

Consistent with Lugo (1998) and Simberloff et al. (2012), our results indicate that the modified habitat conditions associated with natural or anthropogenic disturbances could facilitate the establishment of invasive plants. The combination of large cyclone, which creates canopy gaps, and tidal flooding, which brings propagules, can create favorable conditions for the establishment of invasive plants as observed in *Eichhornia crassipes* and *Derris trifoliata* invasion in the Sundarbans mangrove forest (Biswas et al., 2012). In Brazilian, Sri Lankan and Malaysian mangroves, anthropogenic hydrologic flow regulation in the upstream or clear-cutting facilitated plant invasion in the downstream mangrove forest (Soares, 1999; Dahdouh-Guebas et al., 2005).

Nonetheless, invasive plants often establish in the form of a few individual with small population size or in few localities. Only a fraction of the established invasive species becomes widespread and abundant to become real nuisance (Colautti and MacIsaac, 2004). Our analysis indicate that traits that allow invasive plants to become widespread and abundant may include salinity tolerance, high fecundity, rapid growth, vegetative spread ability and effective dispersal mechanisms (Zedler and Kercher, 2004; Pyšek and Richardson, 2007).

Invasibility of a habitat may change over time (Davis et al., 2005). It has been suggested that the modified habitat conditions that facilitates invasion in the mangrove forest may not last long (Lugo, 1998), so that invasive species in the mangrove forest may not persist for long. Although there is a lack of long-term study to support or refute this assentation, we found many opportunist invaders are perennial (83%) and some of them are transformer species. A transformer species could modify the habitat condition either through sediment trapping or through formation of dense thickets in such a way that the habitat could become unsuitable for the successive colonization of desired mangrove species (Richardson et al., 2000). ***Eichhornia crassipes, A. aureum, S. apetala, Spartina*** spp, ***R. mangle, A. donax*** are examples of transformer invasive species. Once these species invade and persist, they could

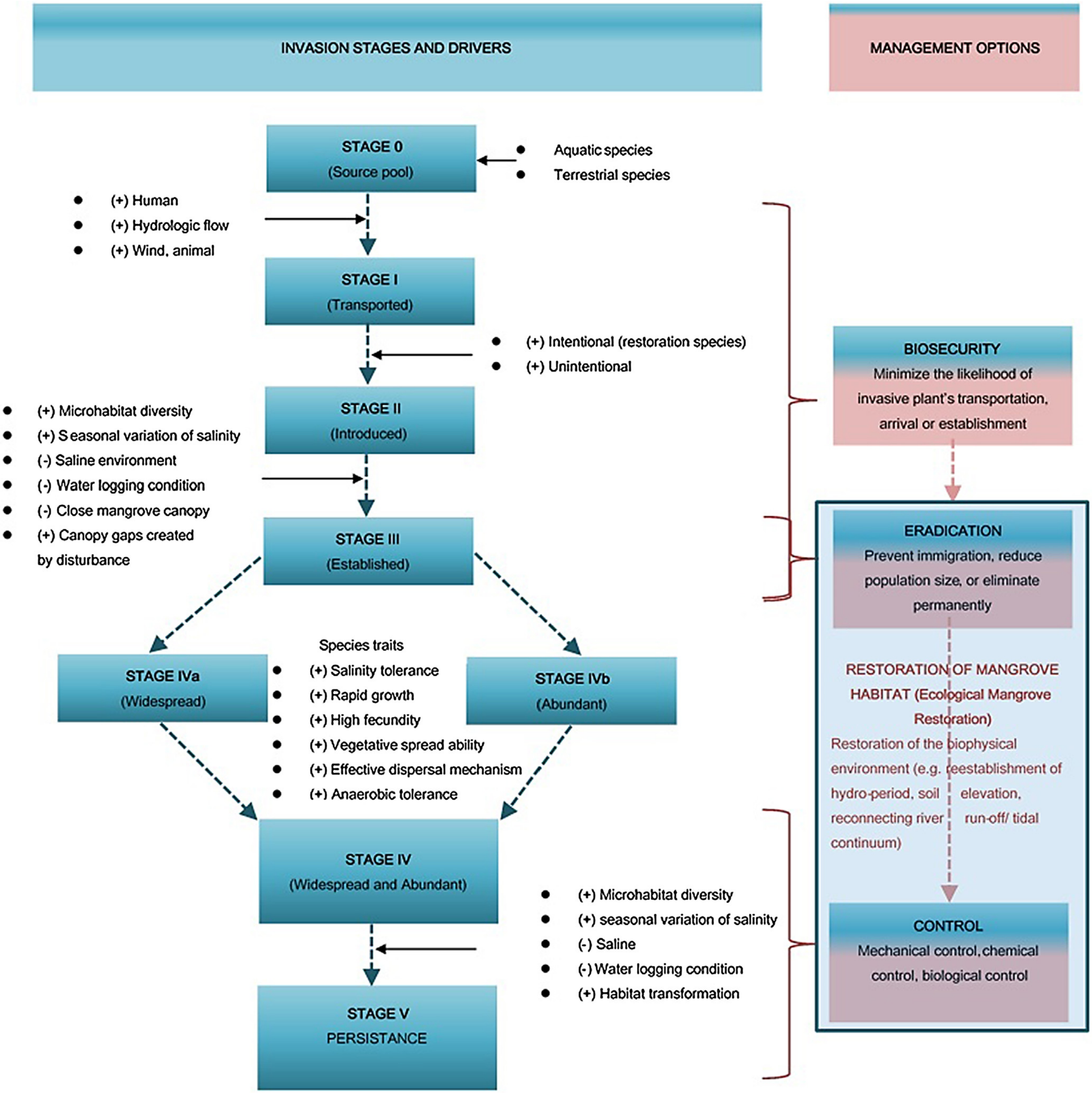


**Fig. 5.** A conceptual diagram with results from this review highlighting invasion stages and invasive species management options.

inflict irreversible damage to mangrove forests, e.g. formation of non-commercial cover in Sundarbans mangrove forests (Harun-or-Rashid et al., 2009), in Brazilian mangrove (Soares, 1999) or in Malaysian mangrove (Srivastava and Shaffie, 1979; Jawa and Srivastava, 1989).

### 4.2. Native invasion in mangrove forests

Historically, invasion ecology had been focusing mainly on alien/exotic species. In contrast, native plant invasions are typically considered small scale and primarily driven by habitat disturbance or anthropogenic land use change (Simberloff et al., 2012; Nackley et al., 2018). However, global change can redistribute species in such a way that native species expand or contract its ranges alarmingly (Alongi, 2015; Biswas et al., 2017); and such compositional shifts can emulate the functional and structural change of community associated with alien plant invasion (Nackley et al., 2018). In our study we found 20 species as invasive native in the world's mangrove forests, suggesting that native invasion is no longer an isolated case but a widespread phenomenon in mangrove forests. Therefore, inclusion of invasive native species into the framework of invasion ecology is important (Nackley et al., 2018).

We found that native species turn into invasive as a result of habitat modification, either through natural or anthropogenic disturbance (Simberloff et al., 2012). From a mangrove ecologist point of view, it is a philosophical dilemma to consider mangrove species (e.g., *S. apetala, R. mangle, B. gymnorhiza*) or mangrove associate species (e.g., *A. aureum, D. trifoliata*) as an invasive in mangrove forests (Lugo, 1998). However, the nuisance of *A. aureum* has been reported by several earlier studies (Soares, 1999; Dahdouh-Guebas et al., 2005; Harun-or-Rashid et al., 2009). *Acrostichum aureum* is also found to behave differently under different environmental condition (Srivastava and Shaffie, 1979); and this species can tolerate salinity up to 50 ppt (Medina et al., 1990). *Derris trifoliata,* on the other hand, is found to grow in the newly accreted mudflats, as opposed to its typical habitat of forest edge/river banks. This species shows shrub like traits and alter mangrove succession (Biswas et al., 2012). Altogether, if we consider the negative impacts of the native invaders to mangroves as discussed in previous section it is probably justified to designate them as such.

### 4.3. Challenges and opportunities to manage the invasion

Plant invasion occurs through a series of stages, and management intervention at each stage is expected to be different (Fig. 5). Typically, early control/biosecurity, habitat restoration, mechanical removal and biological control are among the dominant approaches to invasive plant management (Hulme, 2009; Russell et al., 2017). Early control or biosecurity, which aims to prevent invasion, is suitable for the early stages of invasion (i.e., stage I-III). However, once invaders are established and their population size is low, it is necessary to eradicate them or to control their geographic spread. The most difficult task is to control the established invasive population. In this context, habitat restoration can be a useful and a cost-effective strategy, given that 70% invasion events are associated with disturbance-mediated habitat alteration (Fig. 3). In many regions, disturbances or stresses in mangroves are not limited to forest clearing or dredging but also includes the modification of the biophysical environment such as hydroperiods, soil elevation, soil salinity, river/run-off/tidal continuum (Lugo, 1978; Lugo et al., 1981). In such conditions, mangrove forests are often stressed beyond their limit of survival (Lewis et al., 2016), and hardly any mangroves can grow back naturally (Dale et al., 2014). Unless the stressors are eliminated and mangrove biophysical environment is restored to a condition that is suitable for mangrove development, it is unlikely that traditional approaches such as mechanical removal or biological control of invasive species would be successful. Habitat restoration is an integral component of ecological mangrove restoration (Lewis, 2000, 2005), so that ecological mangrove restoration can eliminate the stressors likely responsible for facilitating invasions (Lugo, 1998). Therefore, habitat restoration (sensu ecological mangrove restoration of Lewis, 2005) must precede all other management options (e.g., mechanical removal, biological control) to ensure self-sustained long term ecosystem health (Lewis, 2000; McKee and Faulkner, 2000; Proffitt and Devlin, 2005; Dale et al., 2014). However, when invasion become a real nuisance, mechanical removal, chemical control or biological control (Russell et al., 2017) may be integrated with habitat restoration (Fig. 5). Artificially induced water logging condition to control photosynthesis of invasive species is also used in Chinese salt marsh ecosystems (Chen and Ma, 2015).

Nonetheless, for effective invasive plant management, one needs to know how the invaders arrive in mangrove forests, how and where they establish, and how they become abundant. Only then measures can be taken to prevent or minimize the spread or occurrence of invasive plants. Unfortunately, there is a large knowledge gap regarding arrival or invasion pathways of about 80% of the invaders. Given the gravity of the invasion problem, it is necessary to initiate early control or biosecurity approach to prevent invasion.

Another issue is that several invasive species such as *Rhizophora* spp., *Bruguiera* spp., *Spartina* spp. and *S. apetala* were initially introduced as restoration species, which later turned into invasive. Restoration ecologists need to keep in mind about invasive potential of these species, so that they can plan to check the spread of these species. A further complicating issue is the presence of invasive native species, which usually become invasive following disturbances (Simberloff et al., 2012). While anthropogenic disturbances can be managed to some extent, natural disturbances are difficult to manage. It is important to integrate invasive plant eradication and management strategy as and when deemed necessary. Our results indicate that a large proportion of invasive plants in the mangrove forests are known agricultural weed, which may have been spilled over through human activities. It is thus important to initiate community awareness program to prevent accidental introduction of invasive plants along the urban mangroves.

Finally, many of the world's mangrove forests are located in tropical developing countries (FAO, 2007) with limited scientific or financial ability to address the issue of plant invasion individually. Increasing large disturbance (e.g. cyclones, tidal surges and flooding) and sea level rise due to climate change will bring additional challenge for mangrove forests in the future (Alongi, 2015; Lovelock et al., 2015). International collaboration would be helpful in attacking this problem together, since all mangrove forests are connected with oceans of the world. International conservation agencies like United National Environmental Programme (UNEP), International Union for the Conservation of Nature (IUCN) or others can initiate cross-country coordinated efforts to formulate new research or management plan for the protection of global mangrove forests.

### 4.4. Knowledge gaps and future research

First, most of our data on plant invasion came from only a few mangrove forests (Fig. 2), and there is a lack of information on invasive plants from many other mangrove forests. No doubt there will be addition of invasive species in the future as more mangrove forests are studied. Second, most of the reviewed study sites are with high riverine or groundwater inputs, i.e. relatively low salinity. The average salinity of our studied invasion sites ranged from 30 to 36 PSU, with > 95% of the sites are within the salinity range of 30–32 PSU (Supplementary material, Fig. S1). It would be interesting to study the patterns of plant invasion in mangrove forests of arid or semiarid regions, where salinity is relatively high. Third, with the exception of a few species, species-specific invasion pathways and invasion histories are often discussed somewhat casually without systematic investigation. As such, we are still unsure about how do invasive plants arrive in mangrove forests. It would be worthwhile to conduct expert survey studies involving mangrove forests around the world in the future to update the list of invasive plants and their invasion pathways. Fourth, while several hypothesis have been proposed to explain how populations of small size or in few localities become abundant and widespread (Inderjit et al., 2005), not a single hypothesis has been rigorously tested in mangrove ecosystems. Therefore, mechanistic understanding regarding how populations of a small size or in few localities become abundant and widespread is urgently required. Finally, the ecological consequences of many invasive plants on habitat, flora or fauna are still unclear (Table 2), and thus deserve immediate research attention on this issue.

## 5. Conclusions

Plant invasion in mangrove forest is much more widespread and problematic than commonly perceived. Both halophytic and non-halophytic plants could invade mangrove forests, although non-halophytic plants mostly colonize raised lands. Only 19.30% of invasive plants were anthropogenically introduced for coastal land stabilization, and the remaining due to accidental introduction. These invasive plants occurred in forest edges as well as in forest interior; and majority of the invaders were perennial, which means that they could persist long time in mangrove forests, and could alter mangrove habitat quality, impede natural regeneration, or disrupt mangrove fauna. That is, there are compelling reasons to worry about plant invasion in the mangrove forests. Considering that majority of invasions (> 70%) result from habitat alteration, ecological mangrove restoration (i.e., habitat restoration) should be the primary management practice to deal with mangrove invaders worldwide. We also encourage a more concerted effort to include the dimension of invasive plant management strategy in mangrove forest management and conservation worldwide.

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