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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