MANGROVES IN CHANGING ENVIRONMENTS



The state of the world's mangroves in the 21st century under climate change

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Abstract Concerted mangrove research and rehabilitation efforts over the last several decades have prompted a better understanding of the important ecosystem attributes worthy of protection and a better conservation ethic toward mangrove wetlands globally. While mangroves continue to be degraded and lost in specific regions, conservation initiatives, rehabilitation efforts, natural regeneration, and climate range expansion have promoted gains in other areas, ultimately serving to curb the high mangrove habitat loss statistics from the doom and gloom of the 1980s. We highlight those trends in this article and introduce

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R. R. Lewis III Lewis Environmental Services, Inc., P.O. Box 5430, Salt Springs, FL 32134, USA Meeting. This collection of papers represents studies presented at the fourth such meeting (MMM4) held in St. Augustine, Florida, USA, on July 18–22, 2016. Our intent is to provide a balanced message about the global state of mangrove wetlands by describing recent reductions in net mangrove area losses and highlighting primary research studies presented at MMM4 through a collection of papers. These papers serve not only to highlight on-going global research advancements, but also provide an overview of the vast amount of data on mangrove ecosystem ecology, biology and rehabilitation that emphasizes the uniqueness of the mangrove community.

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Introduction

Tropical and sub-tropical mangrove forests are considered a particularly important ecosystem for human coastal communities due to their provision of ecosystem services, such as timber and fuelwood (Palacios & Cantera, 2017), fisheries (Benzeev et al., 2017; Goecke & Carstenn, 2017), sediment trapping (Kamal et al., 2017), coastal defense (Doughty et al., 2017;



Sheng & Zou, 2017), and carbon storage (Donato et al., 2011; Kelleway et al., 2016; Yando et al., 2016). Nevertheless, mangrove forests are considered one of the most threatened ecosystems across the tropics (Duke et al., 2007). This is due in large part to anthropogenic impacts on mangroves, including conversion to aquaculture and agriculture, urbanization, and pollution (UNEP, 2014). As a transitional intertidal ecosystem, mangrove forests are also considered to be particularly vulnerable to climate change stressors, such as sea-level rise (Lovelock et al., 2015) and drought (Duke et al., 2017), where changing environmental conditions push mangroves beyond speciesspecific thresholds of tolerance (Ball, 1988). Mangrove loss may not always be attributable to a single driver like agriculture; instead, many natural and anthropogenic stressors often interact additively or synergistically, leading to rapid and large-scale dieoffs in some locales, exemplified by recent (2016) events in Australia (Duke et al., 2017; Lovelock et al., 2017a).

Whereas the general trend for mangroves across the tropics and sub-tropics is one of decline, the broader picture of the true state of the world's mangroves is more nuanced and complex. Huge efforts are being put into mangrove rehabilitation and creation at landscape scales. While such large-scale efforts are generally unsuccessful due to poor species selection, inappropriate choice of rehabilitation locations, and local governance issues (Lewis, 2005; Primavera & Esteban, 2008; Elliott et al., 2016; Kodikara et al., 2017), some efforts are becoming more successful as elements of species biology and hydrological requirements are incorporated into the design and implementation of rehabilitation projects (e.g., Matsui et al., 2010; Oh et al., 2017). On a larger scale, climate change may promote some positive gains, especially at the northern and southern latitudinal limits of mangroves, as mangroves encroach on and replace saltmarsh species in some localities, which was a major theme of the 4th Mangrove and Macrobenthos Meeting (MMM4) held in St. Augustine, Florida in 2016.

The aim of this article is first to describe the MMM4 conference that was held in 2016 and its focus, and then to assess the true state of the world's mangroves early in the 21st century, including some of the potentially positive messages discussed during MMM4.



The MMM4 conference

The Mangrove and Macrobenthos Meeting series was first convened in 2000 in Mombasa, Kenya, with the primary goal of developing a community of practice surrounding the role that macrobenthic invertebrates had on the ecology of mangrove ecosystems globally. Through this dedicated focus on faunal and ecological processes occurring in mangroves, the mangrove community as a whole gained a wider stance among marine ecological systems in subsequent years. The MMM series eventually developed a broader focus, with subsequent meetings held in Australia (2006) and Sri Lanka (2012). This venue now amasses the largest collection of mangrove specialists working across disciplines, from benthic invertebrate ecology and soil biogeochemistry to macroclimatic drivers, latitudinal limits, and ecophysiological constraints to regional and local mangrove expansion.

The fourth conference in the series, MMM4, was held July 18–22, 2016 in St. Augustine, Florida, USA, on the campus of Flagler College. MMM4 represented the very first of the MMM series held in the Americas. Approximately 270 scientists from 32 countries attended MMM4. This location along the Atlantic Coast of Florida was chosen because it represents the transition between temperate and tropical zones where the pressures of climate change on mangroves are very visible. This location provided numerous opportunities for conference attendees to witness the consequences of climate change at this dynamic ecotone, as well as a developing story of concurrent faunal shifts with mangrove expansion (Diskin & Smee, 2017; Hamilton et al., 2017; Langston et al., 2017). As a result of decreasingly cold winters and sea-level rise, the distribution of mangroves is expanding northward and landward along this part of the Florida peninsula into coastal wetlands that have historically been dominated by saltmarsh plants. The location also allowed attendees to participate in field trips to local sites of ecotone shifts and to see actual examples of construction of mangrove restoration projects and completed projects on very large scales as described in Rey et al. (2012).

The goals of MMM4 were: (1) to promote interdisciplinary research on mangroves and associated coastal ecosystems; (2) to build and strengthen further linkages and collaboration among mangrove specialists; (3) to advance education of students,

scientists, decision-makers, managers, the media, and the general public; and (4) to facilitate communications among all these groups on a global scale. Conference attendees presented original research on mangrove and associated ecosystems covering all elements of the system from the top of the canopy to the bottom of the sea, including the flora, fauna, biogeochemical cycles, climate change, human impacts, economics, and management. Papers published as part of this Special Issue of *Hydrobiologia*, entitled "Causes and Consequences of Mangrove Ecosystem Responses to an Ever-Changing Climate" highlight specific papers presented at MMM4.

Mangrove losses due to deforestation

Mangroves have been lost and disturbed due to human use for centuries, though most assessments of mangrove area and rates of change originate from estimates from the second half of the 20th century onwards. Though data quality is highly variable, it has been previously considered that 35% of original mangrove area was lost by the end of the 20th century (Valiela et al., 2001). Mangroves were also considered to be losing 1-3% of their area globally per year, with substantial regional variation (FAO, 2007). Mangrove loss in the early 21st century has declined from expected highs in the mid- to late 20th century (Spalding et al., 2010), with a global-scale remote sensing study showing that annual rates of mangrove deforestation averaged 0.2-0.7% between 2000 and 2012 (Hamilton & Casey, 2016). Some of this apparent reduction may be due to methodological differences between surveys and studies, though improved conservation successes can be an important factor as a number of countries have introduced conservation and sustainable forest-management laws and pursued community-based management (e.g., Chen et al., 2009; Friess et al., 2016), which may explain some of the reduction in deforestation rates.

While the average rate of mangrove loss is lower globally, this masks substantial variation in deforestation rates among regions and countries as well as the continual decline in general mangrove condition through degradation of existing habitats or replacement of mature diverse forests by monospecific plantations. Annual deforestation rates (Table 1; Hamilton & Casey, 2016) between 2000 and 2012 were perhaps not surprisingly highest in nations with small mangrove extent. However, a number of Southeast Asian countries also experienced high percentage rates of mangrove deforestation, particularly Myanmar (the second highest globally), Malaysia, and Cambodia. In terms of absolute loss, Southeast Asian countries are heavily affected, accounting for five of the top 10 countries (Table 2; Hamilton & Casey, 2016). Globally, Indonesia has the highest rate of mangrove loss annually due to its large mangrove area, although both Myanmar and Malaysia also lost approximately 20 km² of mangrove forest every year.

Anthropogenic mangrove loss has traditionally been due to aquaculture throughout much of the tropics, especially in Southeast Asia (e.g., Primavera, 2006). The scale of mangrove conversion to aquaculture has been historically dramatic, with an estimated 140,000 ha of mangrove lost to conversion in the 1950s-1980s (Primavera, 2000). A global-scale quantitative assessment of the proximate drivers of mangrove deforestation has only recently been produced (Thomas et al., 2017), and a qualitative survey of 10 mangrove experts by UNEP (2014) suggested that aquaculture is still one of the largest threats to mangroves globally, though other drivers such as overexploitation, pollution and coastal development are also important. All drivers are expected to increase in magnitude in the future (UNEP, 2014). At the regional scale, Richards & Friess (2016) systematically quantified proximate drivers of deforestation for the whole of Southeast Asia. Between 2000 and 2012, aquaculture was still the dominant driver of mangrove loss in the region (30%), although other agricultural commodities such as rice (22%) and oil palm (16%) were also substantial drivers (Richards & Friess, 2016). The latter has not previously been considered a driver of mangrove loss. Similar to the spatial distribution of loss rates, drivers are also spatially heterogeneous in Southeast Asia. National aquaculture and agriculture policies drive patterns of mangrove loss, with aquaculture being the main driver of mangrove loss in Indonesia (49%) due to food export policies. However, rice is the main driver of mangrove loss in Myanmar (88%) due to national-level plans for food security and food redistribution (Richards & Friess, 2016).



Table 1 Top 10 countries with the highest annual percentage rates of deforestation between 2000 and 2012 *Source* Hamilton & Casey (2016)

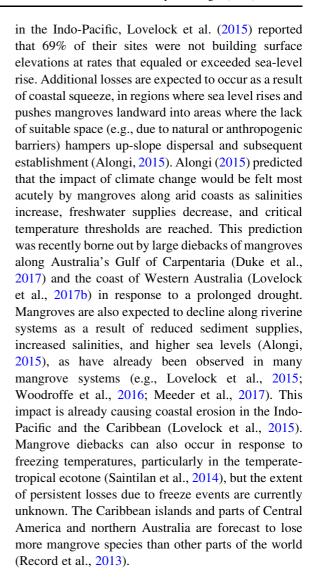
Country	Annual average deforestation rate: 2000 and 2012 (%)	Total mangrove area in 2012 (km²)
Saint Kitts and Nevis	1.67	0.12
Myanmar	0.70	2557.50
Aruba	0.64	0.12
Guatemala	0.53	257.10
Curacao	0.48	0.33
Malaysia	0.41	4725.80
Cambodia	0.37	323.22
Ghana	0.31	23.58
Taiwan	0.30	0.81
Grenada	0.29	1.10

Table 2 Top 10 countries with the highest annual total area of mangrove deforestation between 2000 and 2012 *Source* Hamilton & Casey (2016)

Country	Annual average mangrove loss per year: 2000 and 2012 (km²)	Total mangrove area in 2012 (km²)
Indonesia	62.4	23324.3
Malaysia	20.2	4725.8
Myanmar	19.6	2557.5
Thailand	3.9	1886.3
Brazil	3.9	7674.9
USA	3.6	1568.6
Mexico	2.4	2991.8
India	2.3	797.8
Cuba	2.2	1633.5
Philippines	2.2	2064.2

Potential mangrove losses due to climate change

Mangrove losses as a result of climate change are attributed mainly to increased rates of sea-level rise, high water events, storms, and precipitation as well as altered ocean circulation patterns, health of functionally linked ecosystems, and socio-economic activities (Field, 1995; Gilman et al., 2008). When mangroves are not able to build surface elevations commensurate with the rate of sea-level rise, they are submerged and subsequently lost (Krauss et al., 2014). For mangroves



Potential mangrove gains due to climate change

Although climate change is generally considered to pose a threat to mangroves across the tropics and subtropics, interactions with climate change processes may also lead to increases in mangrove area through at least two mechanisms. Firstly, mangroves may respond to sea-level rise in at least three ways: by submerging, by building vertically, and if vertical building is sufficient and corridors exist, by migrating into adjacent wetlands (Krauss et al., 2014). Transgression or loss among coastal wetlands with sea-level rise and fall has been described in numerous studies (Woodroffe & Davies, 2009; Meeder et al., 2017). As



the rate of global average sea-level rise decreased progressively during the late Holocene (Lambeck et al., 2014), the capacity of mangroves to build vertically by trapping sediments and increasing root biomass in situ overcame the need for inland migration in some Caribbean wetlands (McKee, 2011). For example, it was once thought that sea-level rise involved gains associated with inland encroachment of mangroves in the Everglades region of Florida that balanced appreciably by losses along the seaward fringe from submergence (Egler, 1952). Rather, mangroves moved inland and adjusted vertically along the fringes, resulting in a 35% increase in total mangrove coverage in some portions of the Ten Thousand Islands region of Florida (Krauss et al., 2011). Such sea-level-rise induced expansion has also been documented along the coasts of the Gulf of Mexico, southeast Australia, and the Pacific coast of Mexico (Rogers et al., 2006; Saintilan et al., 2009; López-Medellín et al., 2011). While it is true that mangroves have the ability in some cases to migrate landward and invade adjacent wetlands in response to sea-level rise, net loss or gain of mangrove area has been shown to vary by region as a function of the local rates of sealevel rise and coastal subsidence (Ellison & Strickland, 2015), landform slope and tidal forcing (Doyle et al., 2010), vertical accretion (Lovelock et al., 2015), sedimentation rates (Krauss et al., 2010), and the absence or presence of actual migration corridors (Enwright et al., 2016).

Secondly, evidence is mounting that climate change is affecting the latitudinal range of mangroves, including recent observations of mangrove expansion at or near their poleward range limits on at least five continents (Saintilan et al., 2014). Based on 28 years of Landsat imagery coupled with gridded climate data, Cavanaugh et al. (2014) showed that a doubling in mangrove abundance in northeastern Florida was closely tied to a decrease in the number of freeze events, but not to changes in sea-level rise, precipitation, or other hypothesized drivers. Based on species-specific cold tolerances coupled with climate models, Cavanaugh et al. (2015) predicted that this increase would continue and result in a dramatic expansion of mangroves up the east coast of the USA over the next 50 years. However, in an analysis of historical aerial photographs and recent satellite imagery of the coastal marshes near the range edge of mangroves in northeast Florida from 1942 to 2014, Rodriguez et al. (2016) determined that mangroves have both expanded and contracted over the past 70 years, resulting in recurrent shifts from saltmarsh to mangrove and back again multiple times. Such changes in habitat composition were related to large infrequent disturbances, including hurricanes and severe freeze events (Rodriguez et al., 2016), both of which have been linked to regime shifts from one ecosystem state into another (e.g., Michener et al., 1997). In Florida, rare severe freeze events have led to large-scale contractions of the mangrove range edge and killed mangroves as far south as the Everglades (Bidlingmayer & McCoy, 1978; Wade et al., 1980). Mangrove species, seedling age, salinity, and the presence/absence of marsh grass can influence mangrove survival outcomes to such events (Coldren & Proffitt, 2017). Mangroves are also expanding into coastal saltmarshes along the Gulf of Mexico (Comeaux et al., 2012; Osland et al., 2013; Guo et al., 2017; Yando et al., 2016) and throughout the Americas with historical evidence of similar largescale contractions in the past as a result of severe freeze events (Sherrod & McMillan, 1985; Everitt & Judd, 1989).

In addition to sea-level rise, climate change is expected to result in increased frequency and intensity of rainfall and associated flooding that can discharge massive amounts of sediment into nearshore environments, which then provide favorable new substrate for rapid seaward expansion of mangroves, as has been observed in Northern Australia along the Gulf of Carpentaria (Ashbridge et al., 2016). However, this expansion of mangrove area may be short-lived if it is followed by a large-scale drought, as has more recently occurred along the Gulf of Carpentaria (Duke et al., 2017). The rapid mangrove expansion and growth documented by Ashbridge et al. (2016) following the sedimentation event may have made the mangroves along that coast more sensitive to the drought conditions that followed (Lovelock et al., 2009). Although several studies have documented poleward range expansion by mangroves at their latitudinal limits in response to global warming, more evidence is needed to show whether mangrove forests in the tropics may experience range contraction in response to increasing temperatures and drought. The climate-driven expansion of mangroves has been hypothesized to reduce gene diversity and cause founder effects or a genetic bottleneck at the range



edge (Triest, 2008; Pil et al., 2011; Sandoval-Castro et al., 2012). Genetic studies are becoming much more common in mangrove ecology to elucidate processes that promote or inhibit mangrove dispersal (Ngeve et al., 2017). Yet, contrary to expectations, dramatic increases in the genetic diversity of mangrove trees colonizing the northeast coast of Florida have been observed as a result of increased long-distance dispersal of propagules by strong poleward-flowing ocean currents (Kennedy et al., 2016). This pattern is contrasted with mangroves from Florida's west coast where low genetic diversity was caused by the lack of strong ocean currents and limited local propagule dispersal and migration rates, resulting in founder effects (Kennedy et al., 2016).

As climate change is driving the encroachment of mangroves into saltmarsh habitat around the world, the ability of mangroves to displace saltmarsh is likely due to a combination of biotic and abiotic factors in addition to increases in temperature (Coldren & Proffitt, 2017). For example, recent studies have reported an increase in the occurrence of precocious reproduction by mangrove seedlings and saplings at the leading edge of their ranges, which can accelerate population growth and hasten the expansion of mangroves into saltmarshes (Dangremond & Feller, 2016). For Avicennia germinans along the northern Gulf of Mexico, Langston et al. (2017) found that propagules and seedlings experienced mild to fatal herbivory, which suggested that biotic interaction may also play an important role in the ability of mangroves to expand into saltmarshes. Simpson et al. (2013) documented that greater phenotypic plasticity in mangroves compared to saltmarsh in response to increased nutrient availability allowed mangroves to outcompete co-occurring saltmarsh plants in the mangrove-saltmarsh ecotone. In addition, the ability of mangroves to encroach on saltmarshes depends on their ability to successfully disperse and establish, which depend on hydrologic forces and speciesspecific tolerances to light levels and floatation times (Alleman & Hester, 2011; Simpson et al., 2016). Using models that incorporated both coastal hydrodynamics and mangrove species characteristics, Hamilton et al. (2017) predicted that the rates of spread for mangroves were $<1 \text{ km y}^{-1}$ for the >200 km-longIndian River Lagoon (IRL) along Florida's east coast, which were less than half the expansion rate predicted by general circulation models that incorporated climate and species-specific freeze tolerances (Cavanaugh et al., 2015). However, the rate of spread varied significantly among the five inlets to the IRL as a function of hydrodynamics, habitat distributions, and species-specific traits (Hamilton et al., 2017).

Climate change and the temperature-driven displacement of saltmarsh plants by mangrove trees in the mangrove-saltmarsh ecotone are predicted to increase carbon sequestration in coastal wetlands (Megonigal et al., 2016), though results vary. Near the southern edge of the current mangrove-saltmarsh ecotone along the east coast of Florida, a 69% increase in mangrove cover in seven years resulted in a 25% increase in aboveground carbon storage but no difference in belowground storage (Doughty et al., 2016). Based on results from the Gulf of Mexico, Yando et al. (2016) found that mangrove encroachment into saltmarshes caused an increase in belowground carbon sequestration that varied with precipitation, with the greatest impact observed in hypersaline, arid systems. This influence was strongly related to forest structure; it was not until trees matured and built appreciable forest biomass that carbon storage shifted in some regions. In Australia's Botany Bay, both above- and belowground biomass increased dramatically with mangrove encroachment into saltmarsh over 70 years, with the highest rates of increase in a mesohaline riverine location (Kelleway et al., 2016).

It is currently unknown how ecosystem processes will differ when saltmarshes are replaced by mangroves under a changing climate, which is now a welldocumented global phenomenon (Saintilan et al., 2014). Both mangroves and saltmarshes are foundational habitats that are independently valued for their contributions to coastal productivity, buffering capacity, and carbon storage (e.g., Mazumder & Saintilan, 2003; McKee & Rooth, 2008; Nagelkerken et al., 2008; Feller et al., 2010; Lee et al., 2014). Recent expansion of mangroves into saltmarshes is likely to have large impacts on the structure, function and service provisioning of coastal wetlands (Kelleway et al., 2017). Although mangrove encroachment may increase nutrient storage and improve storm protection (Sheng & Zou, 2017), Kelleway et al. (2017) hypothesized that declines will occur in habitat availability for fauna requiring open vegetation structure, as well as in the recreational and cultural activities associated with this fauna. They further project that the impact on provisional services such as fisheries productivity and



cultural services will be site-specific and dependent on the species involved (Kelleway et al., 2017).

Mangrove gains due to rehabilitation and natural regeneration

Generally, the success of mangrove rehabilitation is considered to be very low (Primavera, 2000; Lewis, 2005, 2009; Brown & Lewis, 2006; Samson & Rollon, 2008) due to a variety of physical-ecological factors being ignored, such as planting inappropriate species in sub-tidal locations where the physical environment is less suitable for mangroves to colonize and grow (Sharma et al., 2017). This is compounded by a number of socio-political issues, such as land tenure arrangements constraining where mangrove rehabilitation can or cannot be conducted. However, largescale successes have occurred and are now increasingly documented in the published and grey literature (Rey et al., 2012; Brown et al., 2014a, b). Rey et al. (2012), for example, report successful restoration of 12,000 ha of mangroves and tidal marshes in the IRL, Florida, USA, over 25 years. In the Tampa Bay estuary of South Florida, mangrove creation has been widely successful, with most techniques using a combination of heavy equipment to grade the intertidal platform to an acceptable sea-level datum, followed by planting of nurse species (Lewis et al., 2005; Begam et al., 2017). Similar successes in Indonesia have been reported by Brown et al. (2014b). In both examples, mangrove planting was a secondary concern; instead, these schemes focused on hydrologic restoration methods (Lewis, 2009; Lewis & Brown, 2014; Lewis et al., 2017) using the Ecological Mangrove Rehabilitation (EMR) model first outlined by Lewis (2005) and later modified as a Community Based Ecological Mangrove Rehabilitation (CBEMR) model by Brown et al. (2014a, b) and Lewis & Brown (2014). The future success of restoration attempts over hundreds of thousands of hectares of abandoned fish and shrimp aquaculture ponds around the world may be possible if the basic principles outlined in Brown & Lewis (2006), Brown et al. (2014a), Lewis & Brown (2014), and Lewis et al. (2017) are followed. Cautionary notes are, however, outlined in Lewis et al. (2017) and Oh et al. (2017) regarding the importance of good engineering to achieve these successes.

Much opportunity exists in the natural resource community to facilitate mangrove habitat protection and rehabilitation through various techniques (Begam et al., 2017; Donnelly et al., 2017; Sharma et al., 2017), at potentially even larger scales. In Southeast Asia, 15.4% of mangroves that were deforested between 2000 and 2012 ultimately returned back to mangrove, either through natural regeneration or artificial rehabilitation (Richards & Friess, 2016), and some studies have suggested that India and Bangladesh have increased their overall mangrove area due to natural regeneration and artificial rehabilitation (Giri et al., 2008). In Puerto Rico, mangrove area has successively decreased and increased since the 1800s, but has expanded since 1972 as legal protections were given to mangroves (Martinuzzi et al., 2009).

With the advancement of remote sensing technologies (sensu Rogers et al., 2017), it is now also possible to identify large mangrove areas undergoing chronic stress before widespread mortality becomes an acute indicator. Altered river flows, regional water extraction, dykes and berms, and road construction are among the most prominent of such influences, documented the world over. In the future, management might transition to preemptive rehabilitation efforts to contribute to avoided losses (Lewis et al., 2016). However, such techniques would not be responsible for substantial mangrove area gains just yet, but a combination of better protections and rehabilitation efforts have demonstrated some positive gains globally, and greater potential in the future.

Conclusions and future research directions

Mangrove forests require urgent research, management, public attention, and rehabilitation; although when estimating the true state of the world's mangroves, it is important that scientists present a balanced viewpoint of mangrove loss that includes solutions to these global problems. On the whole, mangroves are still highly threatened in many locations, but rates of deforestation are lower than they once were in many locations (with substantial variation among countries). As a counter-balance, some successful large-scale rehabilitation initiatives are apparent, as well as natural regeneration from up-slope migration and climate range expansion. While these potential gains do not nearly balance out continued anthropogenic losses, they tell us that the true state of the world's mangroves



is more nuanced than scientists, managers, and policy makers sometimes communicate. Continued research on the basic biology and hydrology of mangroves is critical (Contreras et al., 2017; Lovelock et al., 2017b; Pérez et al., 2017), as well as the provisioning (Benzeev et al., 2017; Palacios & Cantera, 2017) and regulating ecosystem services (Doughty et al., 2017; Kamal et al., 2017; Sheng & Zou, 2017) they provide, because the interplay between mangrove expansion and biological requirements can manifest at very small spatial scales. There is a particularly active research community focusing on the role of mangrove invertebrates and their biology (Bakkar et al., 2017; Castellanos-Galindo et al., 2017; Fusi et al., 2017; Hendy & Cragg, 2017; Pestana et al., 2017; Raw et al., 2017; Saintilan & Mazumder, 2017). Modeling theoretical expansion and discerning drivers on a large scale are important, but local site adaptability is ultimately dictated by many other attributes (e.g., hydrology, biogeochemical condition, substrate, migration barriers, salinity). No doubt, future MMM themes will continue to tackle human and climate-change influences on mangroves through well-grounded biological studies.

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