

REVIEW: PART OF A SPECIAL ISSUE ON COASTAL FLOODING AND STORM RISKS

The gathering storm: optimizing management of coastal ecosystems in the face of a climate-driven threat

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- **Background** The combination of rising sea levels and increased likelihood of extreme storm events poses a major threat to our coastlines and as a result, many ecosystems recognized and valued for their important contribution to coastal defence face increased damage from erosion and flooding. Nevertheless, only recently have we begun to examine how plant species and communities, respond to, and recover from, the many disturbances associated with storm events.
- **Scope** We review how the threats posed by a combination of sea level rise and storms affects coastal sub-, inter- and supra-tidal plant communities. We consider ecophysiological impacts at the level of the individual plant, but also how ecological interactions at the community level, and responses at landscape scale, inform our understanding of how and why an increasing frequency and intensity of storm damage are vital to effective coastal management. While noting how research is centred on the impact of hurricanes in the US Gulf region, we take a global perspective and consider how ecosystems worldwide (e.g. seagrass, kelp forests, sand dunes, saltmarsh and mangroves) respond to storm damage and contribute to coastal defence.
- **Conclusions** The threats posed by storms to coastal plant communities are undoubtedly severe, but, beyond this obvious conclusion, we highlight four research priority areas. These call for studies focusing on (1) how storm disturbance affects plant reproduction and recruitment; (2) plant response to the multiple stressors associated with anthropogenic climate change and storm events; (3) the role of ecosystem-level interactions in dictating post-disturbance recovery; and (4) models and long-term monitoring to better predict where and how storms and other climate change-driven phenomena impact coastal ecosystems and services. In so doing, we argue how plant scientists must work with geomorphologists and environmental agencies to protect the unique biodiversity and pivotal contribution to coastal defence delivered by maritime plant communities.

Key words: Coastal erosion, flooding, hurricanes, kelp, mangrove, pine savannah, salt marsh, sand dunes, seagrass, sea-level rise, storm surge, wave attenuation.

INTRODUCTION

The past, present and probable future impacts of anthropogenic climate change (ACC) on terrestrial plant species and communities are widely reported and reasonably well understood (Parmesan and Hanley, 2015). Most studies focus on long-term, chronic effects, but considerable environmental threat is likely to stem from an increased frequency and intensity of acute, extreme events (Vasseur *et al.*, 2014; Parmesan and Hanley, 2015). Although chronic stressors doubtless reduce ecosystem resilience, for many coastal plant communities the most important manifestation of ACC is likely to come from the acute disturbance, erosion and flooding associated with storm events.

In their most recent assessment of our changing climate, the Intergovernmental Panel on Climate Change (IPCC, 2019) asserted that anthropogenically driven sea level rise (SLR), in tandem with an increase in storm frequency and intensity, poses

a severe environmental threat to estuarine and coastal ecosystems (ECEs). Nonetheless, plant biologists have recognized this threat only recently, and, when combined with our inability to predict where and when storms might occur, it is perhaps no surprise that relatively few authors have systematically addressed the issue. In fact much of the initial relevant research was conducted in the south-eastern USA where low-lying freshwater wetlands regularly experience periodic seawater inundation as a result of isostatic movements and subsidence, and changes in channel flow regime. Studies by Haller *et al.* (1974), McKee and Mendelssohn (1989) and Flynn *et al.* (1995) reporting species-specific variation in Floridian and Louisianan freshwater marsh plants to ‘natural’ salinity pulses were nonetheless prescient of how these communities can be expected to respond to contemporary and predicted changes in frequency and intensity of ACC-linked extreme events. Subsequently, a

body of work conducted around the Gulf of Mexico has described the responses of wetland vegetation to the disturbance associated with recent hurricanes (Tate and Battaglia, 2013; Meixler, 2017; Imbert, 2018).

The realization that coastlines globally now face increasing erosion and flood risk provides the impetus for understanding how hurricanes, typhoons, cyclones and other extreme weather events affect coastal vegetation. Moreover, in many vulnerable locations, ECEs have ‘added value’ in that they offer natural coastal protection against erosion and flooding (Temmerman *et al.*, 2013; Morris *et al.*, 2018). This key ecosystem service has considerable socio-economic benefits, reducing flood risk and damage for a fraction of the costs associated with constructing so-called ‘hard defences’ such as concrete walls (Narayan *et al.*, 2016; Morris *et al.*, 2018). Nonetheless, society is only just beginning to appreciate this valuable service and how ECEs can be integrated into a dynamic flood defence strategy. Consequently, understanding the response of vegetation to shifts in storm regimes is critical to ensure effective risk management over the coming decades.

With this in mind, we offer here a synthesis of the response of ECE vegetation to extreme storm events, and signpost how an understanding of these responses aids management of ECEs for flood and erosion mitigation. We contextualize recent scientific studies by exploring the threats to, and response of, plants challenged by both SLR and increasing storm frequency and severity. This necessitates understanding ecophysiological responses from the level of the individual, up to geomorphological factors operating across the entire tidal range. We also highlight future research priorities, from laboratory experiments to large-scale modelling and mapping of post-disturbance vegetation responses, needed to provide an appreciation of the wider ecosystem services delivered by coastal habitats. By bringing together this diversity of topics, our aim is not only to signpost interdisciplinary research towards better management of ECEs, but also to promote their integration into strategic coastal defence.

THREATS TO COASTAL ECOSYSTEMS

Although, historically, land use change, pollution and invasive species have all impacted ECEs, and while these threats are certain to continue into the future, our focus is on ACC. Indeed, there seems little doubt that ACC will pose the greatest challenge to coastal habitats for the remainder of this century and beyond (Millennium Ecosystem Assessment, 2005). Although elevated atmospheric CO₂ (eCO₂), and associated shifts in temperature, and precipitation will have profound effects on all plant communities (Parmesan and Hanley, 2015), the combination of SLR, and increased sea surface temperatures (SST) and enhanced wave forcing is a particular pressing and unique issue for ECEs.

Rising sea levels have already affected many coastal regions. IPCC (2019) stated with ‘high confidence’ that the 0.32 m increase in global sea levels observed between 1970 and 2015 was attributable to ACC-driven thermal expansion of the seas and glacier mass loss. It seems clear that SLR will accelerate into the 21st century, although IPCC (2019) have ‘high confidence’ that variation in ocean dynamics and coastal land use will generate regional departures of about 30 % around global

averages. Not only does this place coastal regions and habitats at significant (but varying) flood risk, but also there is ‘high confidence’ that SLR will continue for centuries, even if global mean temperatures are stabilized (IPCC, 2019). The ramifications of these changes are severe. IPCC (2019) has ‘very high confidence’ that low-lying coastal areas will increasingly experience submergence, flooding and erosion throughout this century and beyond.

It is important, however, to distinguish between the impacts of long-term, chronic changes in Earth’s climate, and those imposed by acute ACC-linked events. Although a maximum predicted global SLR of 15 mm year⁻¹ (IPCC (2019) poses problems for coastal plants due to landward/upward displacement of the freshwater–saltwater aquifer interface (White and Kaplan, 2017), SLR and extreme weather together are likely to constitute the greatest environmental threat to our coastlines (IPCC, 2019). A combination of increased SST coupled with SLR is widely predicted to increase the frequency, severity and geographical distribution of tropical cyclones and storm surge events (IPCC, 2019). Consequently, present-day ‘one per century’ sea level extremes are expected on an annual basis for most coastlines by 2100 (IPCC, 2019). Not only will many supra-tidal ECEs face an increased risk of short duration, seawater inundation as a result, but the wave energies and sediment disturbance associated with intense storm activity will impact the many ECEs that help protect coastlines. In addition, most coastal habitats are strongly interconnected, such that acute erosion and sediment loss from one (e.g. a sub-tidal sand bar) has major repercussions for sediment transport to nearby supra-tidal habitat (e.g. sand dunes) (Hanley *et al.*, 2014).

Indeed, where sufficient ‘pre-event’ data are available, studies show major changes in coastal geomorphology and vegetation for many years afterwards. Carter *et al.* (2018), for example, used a time series of remotely sensed images to show major breaching, land area reduction, and vegetation loss throughout the Mississippi–Alabama barrier islands in the first 10 months after Hurricane Katrina made landfall. These changes were, however, site specific, depending on sediment removal or accretion, underscoring the more general problem that it is difficult to predict exactly how and when storms affect particular coastlines. For example, in the unusually energetic series of winter storms that affected south-west England in 2013–2014, the most severe impacts coincided with high spring tides and occurred on west-facing beaches where subsequent dune erosion was extensive (Masselink *et al.*, 2015). Similarly, variation in wind directions meant that a brackish marshland in Louisiana, USA, apparently unaffected by Hurricane Katrina in August 2005, experienced major seawater incursion following Hurricane Rita only a month later (Steyer *et al.*, 2007).

The spatio-temporal stochasticity associated with forecasting storm events presents a major limitation to our ability to predict where and when ECEs will be impacted. Nevertheless, it seems certain that ECEs globally can expect a significant increase in erosion and in flood frequency and duration over coming decades. In Table 1, we summarize how the threats associated with extreme storms are likely to affect coastal habitats across the tidal range, and, in the following sections, discuss how some of these key threats exert major ecological effects on sublittoral, inter-tidal and supra-littoral habitats.

TABLE 1. A summary of the principal acute threats and example responses reported for (semi-)natural coastal plant communities subject to extreme storm events

Habitat		Threat	Response	Example studies
Sub-tidal	Kelp forests	Physical damage and dislodgement	Storms cause widespread mortality, but age- and species-specific effects.	Thomsen <i>et al.</i> (2004); Smale and Vance (2016)
		Seagrass	Physical damage	Major losses of seagrass biomass following tropical cyclones.
		Sand deposition	High deposition causes (species-specific) mortality.	Cabaco <i>et al.</i> (2008)
		Turbidity	Sediment run-off had greater negative impact than storm damage.	Carlson <i>et al.</i> (2010)
Inter-tidal	Saltmarsh	Rapid salinity change	Long-term, post-storm impacts on community composition.	Benjamin <i>et al.</i> (1999); Ridler <i>et al.</i> (2006)
		Physical damage	Stem breakage likely, although response differs among species. Denudation of vegetation can also occur.	Cahoon (2006); Möller <i>et al.</i> (2014); Vuik <i>et al.</i> (2018)
		Erosion	Storm-induced erosion of the fronting tidal flat may induce marsh erosion and vegetation loss.	Callaghan <i>et al.</i> (2010); Bouma <i>et al.</i> (2016);)
		Sand, sediment or litter deposition	Burial under sediment or debris can kill vegetation (depending on timing, depth and species).	Callaway and Zedler (2004); Meixler (2017); Leonardi <i>et al.</i> , (2018)
	Mangrove	Changes in salinity or inundation	Heavy rainfall can create opportunities for germination, but salinity changes cause shifts in species and communities.	Zedler (2010); Meixler (2017); Edge <i>et al.</i> (2020)
		Physical damage/erosion	Species-specific variation in tree response (including mortality) to storm damage. Scour caused <i>Avicenna marina</i> mortality along South African shoreline fringe.	Doyle <i>et al.</i> (1995); Imbert (2018) Steinke and Ward (1989)
		Sand/litter deposition	Impact of litter largely unknown (see Krauss and Osland 2020), but increased decomposition influences carbon budgets. Phosphorus-rich sediments stimulate post-storm forest productivity. Sediments covered roots, causing anoxia and tree mortality	Barr <i>et al.</i> (2012) Castañeda-Moya <i>et al.</i> (2010); Adame <i>et al.</i> (2013) Paling <i>et al.</i> (2008)
		Supra-tidal	Sand dunes	Physical damage/ Erosion
Sand deposition	Sand accumulation induced (species-specific) morphological responses.			Harris <i>et al.</i> (2017); Brown and Zinnert (2018)
Saline Inundation	Reduced plant performance but species-specific variation in 'stress' responses.			Camprubi <i>et al.</i> , (2012); Hoggart <i>et al.</i> (2014); Hanley <i>et al.</i> (2020a)
Freshwater marshland	Erosion		Plant mortality facilitated subsequent sediment loss and erosion.	Howes <i>et al.</i> (2010); Hauser <i>et al.</i> (2015)
	Litter deposition		Experimental litter deposition reduced species diversity.	Tate and Battaglia (2013)
	Saline inundation		Widespread plant mortality observed.	Abbott and Battaglia (2015); Hauser <i>et al.</i> (2015)
Other habitats	Physical damage	Storm damage caused localized <i>Pinus elliotii</i> mortality in Florida everglades.	Platt <i>et al.</i> (2000)	
	Litter deposition	High litter density reduced species diversity in south-eastern USA pine savannah.	Tate and Battaglia (2013); Platt <i>et al.</i> (2015)	
	Saline inundation	Negative effects on recovery of Canadian tundra, but with species-specific variation. High mortality of Floridian 'freshwater forest' species.	Lantz <i>et al.</i> (2015) Langston <i>et al.</i> (2017)	

IMPACTS ON COASTAL PLANT COMMUNITIES

Supra-tidal plant communities

Vegetation subject to seawater immersion at exceptionally high tides or during storm surge events only. Affected habitats include sand dunes, and other (semi-)natural terrestrial and aquatic ecosystems (grasslands, pine savannah and freshwater wetlands).

Due, in part, to our inability to predict where and when storm surges will occur, and, even less effectively, control and replicate

natural flood events, few field studies deal with the impact of storm disturbance on supra-tidal plant communities. Although remote sensing offers a way to assess and monitor large-scale changes in vegetation following storm events (e.g. Carter *et al.*, 2018; Douglas *et al.*, 2018; Stagg *et al.*, 2020), elucidating how saltwater flooding, mechanical damage, litter accumulation and sediments affect the plant community is challenging. There is, however, a relatively large body of research describing the (species-specific) effects of burial by sediments on sand dune species (Sykes and Wilson, 1988; Harris *et al.*, 2017; Brown

and Zinnert, 2018), while Tate and Battaglia, (2013) and Platt *et al.*, (2015) report major negative effects of simulated post-hurricane litter deposition on Floridian and Mississippian pine savannah. Surprisingly, however, few studies consider the immediate effects of physical damage on supra-littoral coastal vegetation (see Platt *et al.*, 2000).

The most widely reported impact of ACC-linked extreme events on supra-littoral ECEs is seawater flooding. Immersion in seawater brings additional problems for supra-littoral plants compared with those experienced by species in inland riparian or coastal inter-tidal communities. Flooding of the former is exclusively freshwater, while plants in most inter-tidal ECEs have an inherent ability to tolerate salinity associated with (twice-daily) tidal immersion. Although by virtue of their association with the coast, sand dune, cliff edge and other supra-littoral plants may be tolerant of salt spray (Malloch *et al.*, 1985; Sykes and Wilson 1988), the combination of anoxia and salt stress imposed by seawater flooding is unique to these habitats.

In fact the 'salt stress' associated with coastal flooding seems to be much more important to plant response and recovery than anoxia. In experiments where supra-littoral plants have been simultaneously exposed to freshwater and seawater immersion, the former has never resulted in any noticeable impact on plant ecophysiology compared with untreated (no immersion) controls (Tolliver *et al.*, 1997; Hanley *et al.*, 2013, 2017, 2020a, b; White *et al.*, 2014). A full appraisal of how and why salinity stress affects plant ecophysiology is beyond the scope of this review (see instead Flowers and Colmer, 2008; Munns and Tester, 2008; Negrão *et al.*, 2017; the latter is an excellent assessment of methods to evaluate plant physiological responses to salinity stress). In short, however, high seawater salinity [of which chloride (55 %) and sodium (31 %) contribute most of the 'salt' content] causes both osmotic (limiting the plant's ability to absorb water) and ionic (increased toxicity via Na⁺ and Cl⁻ accumulation) stresses (Munns and Tester, 2008). It is worth bearing in mind though that our oceans have marked seasonal and regional salinity variation (Donguy and Meyers, 1996) and that seawater is much more than 'NaCl in solution'. Some ions such as K⁺ and Ca²⁺ have direct negative toxicological or osmotic effects, but also the potential to mitigate the impact of Na⁺ and Cl⁻ on plant metabolism (Flowers and Colmer, 2008; Munns and Tester, 2008). It is likely that other ions have similar moderating influences over Na⁺ and Cl⁻ stress, and, consequently, understanding how seawater affects plant ecophysiological responses requires much more than a simplistic evaluation of the effects of NaCl alone. This point was reinforced by Hanley *et al.* (2020a), who show how short-duration immersion of *Trifolium repens* in NaCl solutions elicited almost total mortality compared with plants subject to immersion in natural seawater or commercially available marine aquarium salt solutions.

It is possible to monitor ECE recovery after a natural flood event (e.g. Flynn *et al.*, 1995; Lantz *et al.*, 2015), but this requires the ability to allocate resources quickly to an affected site in order to capture changes in vegetation as floodwaters recede. Moreover, to appreciate fully post-inundation transitions, a thorough understanding of the pre-flood ecosystem is also essential (Langston *et al.*, 2017; Masselink *et al.*, 2017). Some manipulative field experiments have been attempted, but logistical and even ethical issues mean that these are uncommon

(McKee and Mendelssohn, 1989; Tate and Battaglia, 2013; Abbott and Battaglia, 2015). Consequently, many studies employ controlled 'flooding' in greenhouse or 'common garden' experiments, although, inevitably, experiments are constrained to focus on a limited species or habitat pool (van Zandt *et al.*, 2003; Hanley *et al.*, 2013, 2017, Li and Pennings, 2018). Many studies also impose long-term, or periodic, chronic salinity, rather than replicating the short-duration, acute immersion experienced immediately after a storm (Tolliver *et al.*, 1997; van Zandt and Mopper 2002; van Zandt *et al.*, 2003; Mopper *et al.*, 2016; Li and Pennings, 2018). A further problem is that rather than use natural seawater, experiments are often undertaken using commercially available marine aquarium salt or even NaCl solutions (Sykes and Wilson, 1988; Flynn *et al.*, 1995; Tolliver *et al.*, 1997; Mopper *et al.*, 2016), with no assessment of their validity as alternatives. In the second experiment described by Hanley *et al.*, (2020a) however, six different European sand dune plant species showed remarkable uniformity in stress and ecophysiological responses to marine aquarium salt vs. locally collected seawater. This consistency suggests that the chemistry of the former is indeed close enough to the latter to use marine aquarium salt as a reliable experimental substitute.

Despite the various methodological problems, unsurprisingly perhaps, significant negative repercussions for plant survival, growth and reproduction are apparent for plants subjected to seawater (or surrogate) immersion (van Zandt *et al.*, 2003; Mopper *et al.*, 2016; Hanley *et al.*, 2017, 2020a, b; Li and Pennings, 2018; Lum and Barton, 2020). Mortality is common, but, even where plants survive short pulses of seawater exposure, subsequent recovery is compromised. A typical response to the ionic and osmotic shock associated with salinity is the accumulation of stress metabolites (e.g. proline) and ions (Ca²⁺ and K⁺) to exclude or compartmentalize Na⁺ and Cl⁻ (Flowers and Colmer, 2008; Munns and Tester, 2008) (probably explaining why plant response to NaCl solution is more extreme than seawater which contains 1.2 % Ca²⁺ and 1 % K⁺). Even if achieved, however, a cost on plant fitness is probably inevitable (Munns and Tester, 2008; White *et al.*, 2014; Hanley *et al.*, 2020a, b).

Most importantly perhaps, the ability of plants to tolerate, and recover from, seawater flooding seems to be species specific. Long-term observation of Arctic tundra following a major storm surge in the Mackenzie Delta, Canada, shows that dwarf shrub tundra had a much reduced regenerative capacity compared with graminoids or upright shrubs (Lantz *et al.*, 2015; see also Middleton, 2009; Tate and Battaglia, 2013). Manipulative greenhouse experiments (Hanley *et al.*, 2017, 2020a; Li and Pennings, 2018; Edge *et al.*, 2020) generally corroborate field observations of species-specific variation. Working on two native Hawaiian plants, Lum and Barton (2020), for example, report not only species-specific variation in ecophysiological responses to increased salinity (imposed over 3 weeks), but also that tolerance increased for both species as plants aged. These observations represent a critical component of our understanding of plant response to the environmental pressures associated with SLR and storm surges. Not only is species-specific variation important, but it is essential to elucidate plant responses throughout ontogeny. Middleton (2009), for example, describes species-specific variation in post-hurricane germination and

recruitment ability of US Gulf Coast marshland species, a response ascribed principally to increased salinity. At the other end of the plant life cycle, Hanley et al. (2020b) report how immersion of oilseed rape (*Brassica napus*) in seawater reduced seed yield and, perhaps most importantly, that growth of the resulting seedlings was also greatly reduced in comparison with progeny cultivated from non-flooded or even freshwater-flooded parent plants.

Although work in this area is anything but ‘mature’, these studies signpost flooding as a potential selective filter that could remove species from the post-disturbance community. The loss of key species or functional groups from any vegetation is likely to compromise ecosystem processes and so limit the ability to supply essential ecosystem services. For vegetation such as sand dunes, these losses may be particularly profound. In Florida, for example, Miller (2015) identified reduced cover of the dune-building grass, *Uniola paniculata*, in low-elevation areas subject to frequent flooding as a likely reason why dune erosion was more common in these sites. The interplay of ACC-linked changes in storm frequency and severity, with resulting shifts in plant community composition and thus resilience against further storm damage, is pivotal for understanding how ECEs contribute to coastal defence.

Inter-tidal plant communities

Communities subject to periodic, but predictable (twice daily), tidal submersion and exposure to air – mangroves, saltmarshes and some algal communities.

Although mangrove forests are both a globally widespread and exceptionally important habitat for biodiversity and coastal defence provision in (sub-)tropical regions, we focus here on the saltmarsh ecosystems more typically associated with temperate coastlines. This is simply because in this special issue, Krauss and Ostler (2020) provide a comprehensive review of how storms influence mangrove ecosystems and the vital ecosystem services they provide.

The physical damage caused by storms ranges from waves and strong currents dislodging or breaking above-ground tissue (Möller et al., 2014), to complete denudation of vegetation (Morton and Barras, 2011). Fragmented or degraded marshes are generally more vulnerable to disturbance than intact habitat (Stagg et al., 2020) and so are less resilient to extreme events. Responses also vary with vegetation height and stiffness (Vuik et al., 2018). For example, when exposed to simulated storm conditions, the tall, rigid grass *Elymus athericus* experienced more breakage than the shorter, more flexible *Puccinellia maritima* (Rupprecht et al., 2017). Strong winds and water flows can tear the root mat from the marsh surface, laterally folding it into ridges – described by Cahoon (2006) as like ‘pushing a rug up along a wooden floor’. This alters marsh topography, lowering areas where turf was lost and raising elevations (up to 2 m) on the folded ridges (Guntenspergen et al., 1995). This can affect long-term community recovery (Leonardi et al., 2018; Mossman et al., 2019).

In addition to direct damage, storms modify plant communities through changes to the physical environment (see reviews by Cahoon, 2006; Leonardi et al., 2018). Storm-driven waves

can cause lateral erosion of tidal flats and marshes (Callaghan et al., 2010), with erosion of fronting tidal flats increasing marsh loss by amplifying the consistent pressure imposed by normal wind and wave action (Leonardi et al., 2016). Saltmarshes are resistant to storm-driven erosion of the marsh surface, however with vegetation playing a key role in stabilizing the sediment (Spencer et al., 2016). Importantly, significant amounts of sediment (mobilized from sub-tidal, inter-tidal or upstream areas) are deposited on saltmarshes during these events (de Groot et al., 2011). For example, a single hurricane can deposit the equivalent of over a century of sediment accumulated in ‘normal’ conditions, and account for up to two-thirds of long-term sedimentation (Williams and Flanagan, 2009). Burial under such rapid deposition can kill vegetation (Callaway and Zedler, 2004), and reduce growth and seedling establishment (Langlois et al., 2001; Cao et al., 2018). Marsh recovery following storm-driven sediment deposition can be rapid however (Guntenspergen et al., 1995), and increases in elevation improve colonization, particularly in subsiding marshes (Mendelssohn and Kuhn, 2003).

Storms can generate significant debris, through either breakage of local coastal vegetation or the remobilization of existing natural and artificial debris (Meixler, 2017). Like sediment, debris can kill or damage the vegetation beneath (Uhrin and Schellinger, 2011), modify environmental conditions such as sediment redox potential (Abbas et al., 2014) and lead to reductions in species richness (Tate and Battaglia, 2013). The amount of damage depends on the type of debris deposited (Uhrin and Schellinger, 2011), the size of the mat and how long it persists (Valiela and Rietsma, 1995), so, in some circumstances, recovery can be quick (Ehl et al., 2017). Plant debris can also be important for propagule dispersal, but can act as a pathway for invasive species (Minchinton, 2006).

The impact of changes in soil salinity following storms is less clear. In some circumstances, high rainfall can ameliorate conditions, allowing plants to colonize or grow faster. For example, in the dry climate of California, Noe and Zedler (2001) found that heavy rainfall provided a window for germination by reducing soil salinity and increasing soil moisture. Storms can also alter the inundation regime of tidal marshes through changes to coastal morphology that lead to closure of an estuary mouth or movements of tidal channels. Zedler (2010) summarizes how the storm-driven closure of the Tijuana estuary had substantial negative impacts on tidal marsh vegetation when subsequent drought caused moisture loss and hypersalinity in sediments.

More typical is the generally negative effect of seawater inundation; Janousek et al., (2016) report how experimental increases in inundation over one growing season reduced plant productivity. It is also likely that even where tidal marsh plants survive storm disturbance, they are so ecophysiologicaly compromised that interactions with other species change. The study by Edge et al. (2020) on three European saltmarsh species is an excellent example. Following seawater immersion, the biomass of *Triglochin maritima* decreased markedly in mixed assemblages with *Plantago maritima* and *Aster tripolium*, compared with monoculture. Interestingly, *Plantago* performed markedly better in flooded, mixed assemblages than in monoculture, appearing to ‘take advantage’ of a relative decline in the growth of the other species (Hanley et al., 2017 describe very similar

shifts for supra-littoral plants). [Edge et al. \(2020\)](#) further note how that for 14 out of 18 trait–species combinations examined (including height, specific leaf area and leaf number), flooding response in mixed assemblages differed from that in monocultures, changing the direction, as well as the magnitude, of flood effects. Plant trait and species composition shifts within saltmarsh communities are likely to be important to ecosystem stability and function ([Ford et al., 2016](#)), but, if disturbance associated with storm events facilitates the spread of non-native species, repercussions could be more severe. This is exactly what [Gallego-Tévar et al. \(2020\)](#) report when they found that an invasive *Spartina* hybrid was better able to tolerate stressful post-flood salinity conditions than its parent species (see also [Charbonneau et al., 2017](#)). Together, these studies underscore the importance of species identity in dictating community responses to storm disturbances, and thus the capacity of the saltmarsh ecosystem to continue to deliver key services as ACC continues.

Sub-tidal plant communities

Ecosystems continually submerged below sea-level – primarily seagrass beds, but includes marine macro-algal communities, most commonly kelp ‘forests’

Storm events can have substantial impacts on seagrass and macroalgal communities, from changes in the relative abundance of species within a community to total habitat loss. These impacts occur through physical disturbance from violent storms, burial by displaced sediment and even subsequent ‘knock-on’ effects from pluvial flooding.

High wave energy and flow speeds can physically damage fronds and stipes ([Denny et al., 1989](#)), uproot individuals ([Preen et al., 1995](#)) or cause failure of holdfasts ([Seymour et al., 1989](#)). While the biomechanics of storm effects are well understood (see [Denny and Gaylord, 2002](#)), predicting the impact of storm events is more complex. Structural damage and uprooting/dislodgement can result in high mortality; for example, complete loss of giant kelp occurs in storm-intense years but is not seen everywhere ([Edwards, 2004](#)). Large, frequent and breaking waves exert the greatest forces and are most likely to result in structural damage or dislodgement, particularly in shallow water when a storm coincides with low tide ([Preen et al., 1995](#); [Filbee-Dexter and Scheibling, 2012](#)). Even moderate waves can lead to entanglement of kelp fronds, increasing the potential for tissue damage ([Seymour et al., 1989](#)). Effects can vary according to substrate type, as wave-carried rocks can dislodge individuals, while sand grains and small pebbles scour roots and holdfasts or damage tissue ([Shanks and Wright, 1986](#)). Substrate type also affects the forces needed to dislodge macroalgae ([Thomsen et al., 2004](#)).

Storm-driven waves do not affect every organism equally however. Vulnerability varies with spatial arrangement and age; individuals in the centre of algal stands are less likely to be removed by waves or strong currents, and small, young kelp are more easily dislodged than older, larger individuals ([Thomsen et al., 2004](#)). Nonetheless, the higher biomass of very large kelp makes them more susceptible to high wave energies ([Seymour et al., 1989](#)). Consequently, severe storms can result

in homogenization of age structure in kelp beds. Ecotypes or morphological plasticity provide resistance to high wave action (e.g. in shallow waters) ([Fowler-Walker et al., 2006](#)), allowing some individuals or populations to better cope with an extreme event. Storms are also generally most frequent at the point in the annual cycle where organisms are most resistant ([Burnett and Koehl, 2019](#)); accordingly, changes to storm seasonality may have significant consequences for these communities.

In addition to the effects of wave action and shear stress, storm-generated waves and currents redistribute sediments, causing erosion in some areas and burial in others. [Cabaco et al. \(2008\)](#) identified significant species-specific variation in seagrass tolerance to both burial with sediment and erosion. Recovery is generally rapid under shallow burial, but this capacity decreases markedly when more sediment is deposited ([Fourqurean and Rutten, 2004](#); [Gera et al., 2014](#)). Consequently, burial by up to 45 cm of sediment, reported following some severe storms ([Kosciuch et al., 2018](#); [Browning et al., 2019](#)), is likely to lead to localized loss of communities.

As well as the impacts of storms at sea, heavy rainfall can have major impacts on sub-tidal ECEs via the discharge of nutrient-rich, sediment-laden freshwaters into coastal areas. These enriched waters cause turbidity and stimulate algal blooms and epiphytic growth, both of which lower light availability ([Lapointe et al., 2019](#)). Seagrasses are especially vulnerable ([Cabaco et al., 2008](#)), and impacts of flood-induced light limitation can be more severe than the physical impacts of storms ([Carlson et al., 2010](#)). In addition, heavy rainfall can reduce salinity, particularly in lagoons or estuaries, sometimes for several months ([Herbeck et al., 2011](#); [Kowalski et al., 2018](#)). Some seagrasses are intolerant of hyposaline conditions, leading to mortality and sub-lethal effects ([Fernandez-Torquemada and Sanchez-Lizaso, 2011](#)). [Ridler et al. \(2006\)](#) observed that while thinning and leaf loss occurred immediately after hurricanes, further declines continued for many months probably due to low and fluctuating salinity. Tolerance to hyposalinity is, however, variable between and within species, ecotype ([Benjamin et al., 1999](#)) and season ([Fernandez-Torquemada and Sanchez-Lizaso, 2011](#)), reducing the predictability of how seagrass communities respond.

Storms are nonetheless important disturbance agents, and seagrasses can rapidly regrow from roots or rhizomes, despite substantial above-ground loss ([Valiela et al., 1998](#)). Other macroalgae can reattach or regenerate when broken or dislodged ([Thomsen and Wernberg, 2005](#)). Furthermore, storms may actually facilitate medium- and long-distance dispersal of seagrass and macroalgae propagules ([Bell et al., 2008](#); [Waters et al., 2018](#)) and be important in maintaining food web complexity, although increasing storm frequencies can challenge the ability of kelps to regrow and simplify food web structure ([Byrnes et al., 2011](#)). Damage to kelp fronds can, for example, stimulate grazing activity, so increasing potential tissue loss to an already stressed individual ([O’Brien et al., 2015](#)). Reductions in canopy-forming macroalgae and seagrasses through a combination of direct storm damage and herbivory can lead to community shifts to opportunistic species, such as turf-forming algae ([O’Brien et al., 2015](#); [Filbee-Dexter and Wernberg, 2018](#)). Gaps resulting from the storm-driven loss of corals and other benthic animals can, nevertheless, facilitate

macroalgal colonization, particularly in the absence or reduction of herbivory (Edmunds, 2019; Steneck et al., 2019).

The impacts of extreme storm events are not experienced in isolation. Long-term environmental changes, such as SLR, eutrophication and overfishing, influence community susceptibility, as does the legacy of previous storms (i.e. position in the ‘storm recovery cycle’). For example, substantial seagrass losses in North Queensland, Australia, were the cumulative result of a succession of intense storm and flood years, urbanization and agricultural run-off, rather than the consequence of a single storm (McKenna et al., 2015). Storm events are also stressing systems already impacted by ACC, a combination that could lead to higher losses than imposed by either driver in isolation (Babcock et al., 2019). Smale and Vance (2016), for example, report that while the cold water kelp *Laminaria hyperborea* was relatively resistant to storms, mixed stands containing warm water species, such as *L. ochroleuca*, were more vulnerable. Consequently, observed and projected shifts in kelp community composition due to increasing temperatures (Pessarrodona et al., 2018) could lead to greater kelp community vulnerability.

Collectively, the processes described above underpin observations of highly variable storm impact on sub-tidal plant communities (Edwards, 2004; Filbee-Dexter and Scheibling, 2012). Long-term studies can help identify the relative impacts of storms and anthropogenic factors (Cuivillier et al., 2017), but our understanding of storms on sub-tidal ECEs is limited by few long-term studies outside of coral reefs (Duffy et al., 2019). While there are many estimates of the impacts of single storms, it is rarely possible to put the patch-scale losses in the context of the dynamics of the system. Despite advances with remote-sensing techniques, the depth and turbidity of these systems mean that ground-based observation will continue to be essential.

PLANT COMMUNITIES AND COASTAL DEFENCE

In addition to biodiversity loss, recent concern about the various threats to ECEs stems from their role in protecting agricultural land and urban communities from storm damage. Consequently, there is increasing focus on quantifying and valuing benefits associated with the ecosystem services provided by ECEs (Barbier et al., 2011, 2015; Temmerman et al., 2013; Morris et al., 2018). Although the methods used to generate accurate, global, economic estimates remain in their infancy (Barbier, 2016), Costanza et al. (2014) estimated that for tidal marshes alone, the provision of nursery grounds for commercial fisheries, carbon storage, recreation and flood protection provided US\$24.8 trillion to the global economy.

ECEs provide storm protection principally through the stabilization of substrates, and therefore the prevention of erosion, and attenuation of wave energy, and thus flood risk (Barbier, 2015). Unlike hard (engineered) defences, they are also dynamic; indeed the IPCC (2019) recognized how saltmarshes and mangroves can keep pace with fast rates of SLR (>10 mm year⁻¹), depending on local variation in wave exposure, tidal range, sediment dynamics and coastal land use. Moreover, it is even possible that the extent of coastal wetlands (saltmarsh, freshwater marsh and mangrove) could increase by up to 60 %

because of SLR (Schuerch et al., 2018). With appropriate management, supra-littoral sand dunes are also capable of adapting to shifts in sea levels and storm frequencies (Hanley et al., 2014).

The growing evidence that ECEs reduce storm damage underpins their recognition as nature-based flood protection (Temmerman et al., 2013; Narayan et al., 2016; Van Coppenolle and Temmerman, 2019). The traditional approach to coastal defence has been to counter flood risk with ‘hard’ engineering, but measures such as seawalls are expensive [up to £5000 m⁻¹ (Hudson et al., 2015)] and inflexible, and often deliver unexpected environmental outcomes (Firth et al., 2014). Vegetated shorelines, in contrast, are a natural defence and offer adaptability, flexibility and cost-effectiveness [e.g. £20 m⁻¹ for dune stabilization (Hudson et al., 2015)], with the additional benefit of the other ecosystem services they provide (Costanza et al., 2014; Barbier 2015).

Protective role played by different ECEs

The protective value differs not only between ECEs, but also with regional and local geographical context. The principal defensive role played by dunes, for example, stems from being a physical barrier to marine flooding, but their importance in this regard depends on local coastal geomorphology (e.g. sediment supply and land relief) and on the use and asset value of the land they protect (Hanley et al., 2014). Dune vegetation stabilizes substrates and reduces wave-driven erosion, with plant shoots reducing wave swash and roots increasing mechanical strength of the sediment (Feagin et al., 2019), but even the identity of component species can be important. de Battisti and Griffin (2020), for example, examined how three common European foredune species (*Ammophila arenaria*, *Cakile maritima* and *Salsola kali*) varied in their ability to withstand simulated wave swash. Although *Ammophilla* was by far the most robust, by virtue of the protection provided by its roots, rhizomes and below-ground shoots, all three species had a remarkable capacity to tolerate wave action, underscoring how different plant species can contribute to sand dune stability. [See also Charbonneau et al. (2017) who report how North American dunes stabilized by the invasive *Carex kobomugi* were less affected by storm damage than those colonized by native *Ammophila breviligulata*.] Nonetheless, de Battisti and Griffin (2020) also show that despite an exceptionally well-developed below-ground shoot system, *Ammophila* resistance varies depending on sand particle size, with the coarser sediments associated with restored habitats increasing erosion potential compared with finer sediment of natural regeneration sites. This finding is important since it underscores why elucidation of biological and environmental factors is crucial to the integration of natural habitats such as sand dunes into coastal protection schemes. For other supra-littoral habitats however, we understand little about their putative role in coastal defence. Nonetheless, there is little doubt that coastal forests and freshwater wetlands provide other vital ecosystem services such as carbon sequestration and storage (see Stagg et al., 2020; Ury et al., 2020).

The ability to track SLR (Kirwan *et al.*, 2016; IPCC, 2019) along with their well-known capacity for wave attenuation (Möller *et al.*, 2014; Rupprecht *et al.*, 2017), has put saltmarshes at the centre of current interest in ‘nature-based’ coastal defence solutions. How effective wave attenuation is depends strongly on topography (even to the extent of friction imposed by the biogeomorphic landscape created by the plants) and (ontogenetic, seasonal or species-specific) plant traits such as shoot stiffness and density (Bouma *et al.*, 2010, 2014; Möller *et al.*, 2014). As a result, studies such as that by Zhu *et al.* (2020), describing variation in stem flexibility and breakability for a variety of European saltmarsh species, are vital to understanding how communities will respond to increased storminess. Plant response can vary with wave conditions however, Shao *et al.* (2020) exposed *Spartina alterniflora* to different wave environments for 8 weeks and showed that key physiological and biochemical plant parameters varied accordingly, i.e. higher and more frequent waves imposed more stress. Nonetheless, wave-exposed plants tended to allocate more biomass to their roots, a response that may facilitate anchorage against wave impact. These biomechanical and morphological properties are likely to vary with plant age. Cao *et al.* (2020), for instance, describe how after 7 weeks of simulated wave exposure, seedling survival and growth declined for all three common marshland species examined (*Spartina anglica*, *Scirpus maritimus* and *Phragmites australis*). Taken together, these studies increase our understanding and prediction of spatio-temporal variation in saltmarsh community response to wave exposure, an essential prerequisite in the design and implementation of nature-based flood protection.

In addition to species identity, age and seasonality, other marsh-specific characteristics are important determinants of wave attenuation. One of the key attributes is habitat size (Shepard *et al.*, 2011). Indeed, in a recent analysis of the long-term marsh persistence around the UK, Ladd *et al.* (2019) revealed that marsh width was positively associated with higher sediment supply, although they noted also that current global declines in sediment flux are likely to diminish saltmarsh resilience to SLR. Although challenging, understanding the shifting dynamics of these regional-scale coastal processes is crucial to our ability to integrate marshes into coastal defence schemes (Bouma *et al.*, 2014, 2016). Not only is that because we need to know where and how ECEs fit into an integrated coastal management approach, but also because long-term salt marsh persistence depends on continual recruitment of new plants.

For saltmarshes, propagule establishment often occurs on leading edges when sediment accretes on the adjacent ‘tidal flat’ (Bouma *et al.*, 2016). Even an apparently minor change in sediment levels may be sufficient to facilitate seedling establishment, an effect demonstrated by Fivash *et al.* (2020) in their mesocosm experiment with the pioneer *Salicornia procumbens*. They show that elevation of sediment microtopography by just 2 cm was the overwhelming driver of seedling growth (i.e. an average 25 % increase). They ascribed this response primarily to the effects of the ‘tidally driven oxygen pump’, i.e. increased emersion time allows more aeration of the raised sediment (see also Mossman *et al.*, 2019). Once pioneers such as *Salicornia* have established, the environment they create (wave attenuation, sediment trapping and enhanced drainage) facilitates

subsequent colonization by later successional species and so the marsh can expand seaward (Temmerman *et al.*, 2007). Storms also have the potential to increase the landward marsh area if the habitat can retreat and displace terrestrial habitats. In these circumstances, Kotter and Gedan (2020) demonstrate that saltmarsh is pre-primed to take advantage of this opportunity, reporting how seeds of halophytic species can disperse up to 15 m into north-east American coastal pine forest. They argue that although saltwater intrusion will limit forest regeneration, the soil seed bank can thus support continued landward migration of saltmarsh species.

Much of the recent interest in mangroves stems from their perceived mitigation of the 2004 Indian Ocean Tsunami on coastal settlements. While their actual contribution remains questionable (Barbier, 2015), nonetheless, a number of studies report that mangroves can lower wave heights and reduce water levels during storm surges (Das and Vincent, 2009; Armitage *et al.*, 2019) and that their removal leads to increased coastal erosion and damage (Granek and Ruttenberg 2007; Barbier 2015). Like saltmarsh therefore, mangroves are at the forefront of contemporary research into how ECEs help defend our coastlines (see Krauss and Osland, 2020). It is also noteworthy that Alongi (2008) highlights that how much protection mangroves offer against extreme events is strongly linked to intrinsic habitat characteristics (these include forest location and width, tree density and size, and soil texture), but also the presence of other ECEs, such as coral reefs, seagrass beds and dunes.

The case for a substantial protective role of sub-tidal ECEs remains less clear (although coral reefs are well studied and widely believed to play a major role – see Barbier 2015). It is known, however, that seagrasses attenuate wave energy (Christianen *et al.*, 2013; Reidenbach and Thomas, 2018), and thus probably offer some coastal defence (Barbier *et al.*, 2011; Ondiviela *et al.*, 2014). Furthermore, the reduction in wave energy seagrasses provide can reduce the erosion experienced by adjacent tidal marsh systems (Carr *et al.*, 2018) and stabilize or even facilitate beach expansion (James *et al.*, 2019). Consequently, the dramatic global decline of seagrass habitat is of great concern and underscores recent calls for wider habitat protection (Cullen-Unsworth and Unsworth, 2018). It is less clear whether sub-tidal macroalgal communities play any role in wave attenuation, and therefore coastal protection, but a full review is provided in this special issue (see Morris *et al.*, 2020). In short, Morris *et al.* (2020) note how only a limited number of studies have investigated coastal protection, and in their own study in Australia found that wave attenuation by the kelp *Ecklonia radiata* was restricted to a small sub-set of the environmental conditions sampled.

Using ECEs in integrated coastal defence

The implementation of ‘soft’ or natural flood defences depends on landscape context (including the economic value of the land threatened by SLR, erosion and storm damage) and whether it is actually feasible and cost-effective to maintain or move defences (Hoggart *et al.*, 2014). The ‘hold the line’ option has been traditionally met by the construction of ‘hard’ defences (engineered solutions utilizing concrete walls, rocky

breakwaters, steel piling or stone gabions), but these are extremely expensive and have limited ecological value. There is nonetheless considerable interest in how we might ‘soften’ structures using design alterations (e.g. modification of surface topography) to increase biodiversity value (Firth *et al.*, 2014). It is also recognized that vegetated foreshores reduce wave impact on sea walls, such that a fronting saltmarsh provides sufficient additional defence to allow sea wall height to be lowered, with substantial savings to capital and maintenance costs (Vuik *et al.*, 2016). Where natural habitat is absent, it may be possible to create it using management actions to stabilize or accrete sediment. For example, the combination of beach nourishment, sand traps and planting can establish sand dunes to provide storm protection to landward hard defences (Feagin *et al.*, 2015). At the landscape scale, the strategic integration of hard engineered and soft natural defences may provide the only realistic, cost-effective way to protect large sections of coastline.

It is imperative, however, to ensure that where integrated management is planned, an engineered intervention does not detrimentally affect nearby ECEs. For example, hard defences can disrupt natural coastal processes and sediment supply (Hanley *et al.*, 2014), while the problem of ‘coastal squeeze’ means that existing (or planned) ECEs fronting hard-engineered defences cannot always track SLR (Schuerch *et al.*, 2018). In these situations, the long-term sustainability of natural flood protection may be greater if there is the potential to move the line of defence landward. This can simply involve ensuring a capacity for an existing ECE to ‘roll back’ (see Kottler and Gedan, 2020) but, increasingly, ECEs are created in former terrestrial habitats; a process often termed ‘managed retreat’ or ‘managed realignment’ (MR).

The most common example is the breaching of sea walls or dykes to allow tidal flooding with the expectation that newly inundated land will develop into saltmarsh. These schemes have met with mixed success however, with many studies showing that the plant communities developing in MR sites differ from those in adjacent natural marshes (Mossman *et al.*, 2012; Masselink *et al.*, 2017). Environmental conditions, such as elevation in the tidal frame or geomorphic setting (Mossman *et al.*, 2012; Masselink *et al.*, 2017), are critical to successful restoration, but these alone are insufficient to explain all observed differences (Sullivan *et al.*, 2018). Propagule dispersal is often limited and limiting (Mossman *et al.*, 2012), and species-specific differences in dispersal ability could mean that early colonizers inhibit the establishment of later arriving species (Sullivan *et al.*, 2018). Planting species with low recruitment potential into newly established marshes could resolve this (Mossman *et al.*, 2019). A relative lack of topographic heterogeneity in MR sites may also limit transition to saltmarsh (Masselink *et al.*, 2017; Lawrence *et al.*, 2018). As we have seen (Mossman *et al.*, 2019; Fivash *et al.*, 2020), even minor changes in surface elevation can have a substantial impact on seedling recruitment in saltmarsh. These studies highlight that, while MR often fails to deliver ‘natural’ saltmarshes, there is considerable potential for research-led management to improve restoration success.

SYNTHESIS AND FUTURE STUDIES

Although considerable research effort is focused on the response of ECEs to disturbance events, there remains both a

geographical bias towards the US Gulf and Atlantic seaboard states, and limited understanding of how the multiple stressors associated with SLR, extreme storms and other anthropogenic activities affect even a fraction of ECE species or habitats. Beyond a simplistic call for ‘more research with additional species and regions’, we discuss how illumination of plant species and community responses to flooding, sediment movement, mechanical damage and landscape-scale processes is needed to better inform our ability to manage the biodiversity of ECEs and ensure their continued contribution to coastal defence (Fig. 1).

Research priority 1. Effects of storm damage and flooding on plant reproductive performance and recruitment

Parmesan and Hanley (2015) highlighted how despite a wealth of information detailing plant species and community response to the warming, drought and elevated atmospheric CO₂ (eCO₂) associated with ACC, remarkably little is known about how any of these factors influence plant regeneration biology. The same failing is true of ECE response to SLR and storms, even though recruitment success is manifestly pivotal to understanding how environmental stress and perturbation influence plant community recovery. Indeed, it is at this point worth stressing that the disturbance associated with storms is an important, positive, factor in ECE dynamics. It is, for example, well understood that tropical cyclones stimulate reproduction and open regeneration opportunities (Zimmerman *et al.*, 2018; Krauss and Osland 2020), while disturbance of sand dune vegetation is a key driver of plant biodiversity in these most dynamic of ecosystems (Green and Miller, 2019). What is less clear, however, is how ACC-linked shifts in storm intensity and return times disrupt recruitment processes that have evolved in response to environmental dynamics typical of pre-industrial times (Hanley *et al.*, 2014; Imbert 2018).

Some experiments have focused on the effect of elevated salinity on flowering and reproduction, but all too often consider only long-term, chronic effects (e.g. Van Zandt and Mopper, 2002; Pathikonda *et al.*, 2010; Rajaniemi and Barrett, 2018). Nonetheless, these studies are important as they show that: (1) responses may only become apparent long after exposure (Van Zandt and Mopper, 2002); (2) reduced sexual reproduction was not compensated by vegetative reproduction (Pathikonda *et al.*, 2010); and (3) germination potential is species specific (Rajaniemi and Barrett, 2018). Many fewer authors report the impact of acute seawater flooding on the reproductive potential of coastal plants, but those that do evidence reduced flowering (White *et al.*, 2014; Hanley *et al.*, 2020a) and reproductive output (Hanley *et al.*, 2020b). A critical element of the latter study was that the growth of seedlings cultivated from parent plants subject to acute seawater immersion declined, i.e. while the parent plant might survive long enough to reproduce, longer term regeneration potential is compromised. The importance of changes in wave action on the dynamic sediment environment in saltmarsh regeneration may be better understood (Bouma *et al.*, 2016; Cao *et al.*, 2018), but there is a need to elucidate the effects of all manifestations of storm damage and flooding on plant reproductive and recruitment potential, including storm-driven dispersal.

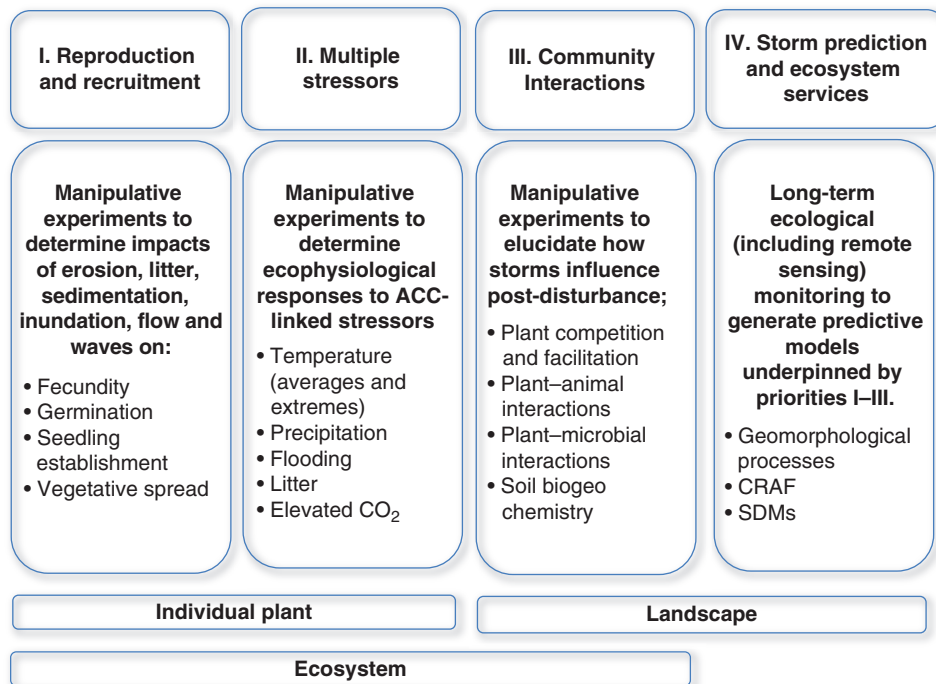


FIG. 1. A SUMMARY OF THE PRINCIPAL RESEARCH PRIORITIES (I–IV) AND AVENUES FOR FUTURE STUDY NEEDED TO UNDERSTAND THE RESPONSE OF ESTUARINE AND COASTAL PLANT COMMUNITIES TO THE DISTURBANCES ASSOCIATED WITH EXTREME STORM EVENTS. THE PROPOSED LEVEL AND OVERLAP OF STUDY (INDIVIDUAL PLANT, ECOSYSTEM AND LANDSCAPE) FOR EACH PRIORITY IS SHOWN. CRAF, COASTAL FLOOD RISK FRAMEWORK; SDM, SPECIES DISTRIBUTION MODEL.

Research Priority II. Coastal plant responses to multiple stressors associated with SLR and storm damage

Teasing apart the interactive effects of saltwater flooding, mechanical damage, litter accumulation and sediment shift on the plant community is challenging, a problem made all the more difficult simply because so few studies (outside the south-eastern USA at least) have systematically examined how these different factors affect and shape plant community responses in isolation, let alone in combination. Using remote imaging, Hauser *et al.* (2015) report how saline inundation following Hurricane Sandy caused widespread wetland degradation in New Jersey, first by marsh dieback and, as a consequence, subsequent sediment erosion and retreat of the marsh inland. They also note the importance of plant community composition in this interaction, woody plants being more tolerant than herbaceous vegetation. Using an experimental approach, Tate and Battaglia (2013) considered the combined effects of seawater flooding and litter deposition. The application of locally sourced litter [degraded stems of black needlerush (*Juncus roemerianus*)] to four plant communities along a Floridian estuarine gradient (brackish marsh, freshwater marsh, wetland forest and pine savanna) had a profound negative effect on plant survival and species richness in all communities. In tandem with controlled seawater flooding, however, litter had a major impact on species composition in pine savannah, as salt-tolerant species capable of vegetative regrowth through dense detritus were the only species to persist. Tate and Battaglia (2013) also noted how vegetation in habitats with higher ambient sediment salinity was more resilient to the combined effects of flooding and litter deposition.

These studies (see also Imbert, 2018; Kendrick *et al.*, 2019) signpost the importance of interactive factors for the recovery of ECEs following storm and other ACC-linked disturbance events. Given the logistical issues associated with simultaneous replication or observation of multiple stressors, it is unreasonable to expect a flurry of research focused on the interactive impacts of various storm disturbances on ECEs. Moreover, one could also argue that a true picture of coastal plant response needs also to consider eCO₂ and shifts in temperature and precipitation (Parmesan and Hanley, 2015). Indeed, Huang *et al.* (2018) argued that an increase in night-time temperatures had facilitated the expansion of the shrub *Morella cerifera* into Virginian coastal grasslands with probably concomitant impacts on erosion regimes. Although, by definition, unpicking the simultaneous interplay of several ACC-linked stressors is complex, as a first step studies could examine the responses of the same species to different stressors in isolation, and elucidate how at least two factors conspire to affect plant performance.

Research Priority III. Plant community interactions and post-disturbance recovery

Although it is well known that environmental perturbations (e.g. fire, herbivory, etc.) mediate plant community interactions, beyond a reasonable understanding of the role of tropical cyclones in forest dynamics (Hogan *et al.*, 2016; but see Pruiitt *et al.*, 2019), the impact of storms and SLR on plant–plant, plant–animal and plant–microbial interactions in ECEs is poorly

resolved. We have discussed already how species-specific variation in plant response to storms might act as a selective filter, removing susceptible species from the recovering plant community. This is why field and multispecies (microcosm) greenhouse experiments are invaluable; as shown by [Hanley et al., \(2017\)](#) and [Edge et al., \(2020\)](#), it is by no means certain that plant species responses in monoculture are replicated in mixed assemblages. Nonetheless, these kinds of study are rare and yet required to disentangle how plant–plant interactions vary in response to a variety of storm-related impacts.

It is also worth stressing that community interactions go beyond shifts in plant competitive hierarchies. For example, although [Camprubi et al. \(2012\)](#) report how three of six Mediterranean sand dune species suffered complete mortality within a week of exposure to seawater, the remainder had delayed or greatly reduced mortality when grown in association with the mycorrhizal fungi, *Glomus intradices*. Symbiotic mycorrhizal fungi are well known for their importance to plant health and vigour ([Smith and Read, 2008](#)), but, in coastal vegetation such as sand dunes, the association may be essential for survival ([Koske et al., 2004](#)). Unfortunately, the vast majority of work on how the plant–mycorrhizal association affects plant response to salinity comes from agricultural systems ([Evelin et al., 2019](#)) and consequently we know little about how microbial symbionts respond to storm-linked disturbances in ECEs, or how they moderate plant responses in the post-event community.

Seawater inundation is also likely to have major effects on the soil physicochemical environment upon which all organisms depend. A detailed assessment of soil structure and chemistry is beyond the scope of this review, but, in addition to reduced aeration, increasing ionic concentrations and exchange capacity probably affect the bioavailability of key mineral nutrients ([Kadiri et al., 2012](#)). Saline flooding will also affect soil microbial and invertebrate communities, and consequently the decomposition and nutrient-cycling services they provide ([Sjøgaard et al., 2018](#); [Stagg et al., 2018](#)). Remarkably few studies, however, consider the impact of acute flooding on soil biogeochemistry, or how additional stresses such as sediment movement and litter accumulation affect soil-dwelling animal and microbial communities and the processes they deliver.

Above-ground interactions are no less important. In an elegant experiment where sods of Louisianan marshland vegetation were exposed over 2 years to saline flood treatments, with and without herbivory, [Gough and Grace \(1999\)](#) reported that species loss was fastest in seawater treatments when mammal herbivores were also present. Although the flooding treatment was designed to mimic SLR rather than acute flooding, this study nonetheless emphasizes how, even if species can tolerate one stress (flooding), the imposition of a second (herbivory) may filter species from the ecosystem (see also [Mopper et al., 2004](#); [Schile and Mopper, 2006](#)). Taken together, these studies underscore how post-storm conditions can affect plant morphology and the expression of defence metabolites, change herbivore performance and selection preferences, and how, in combination, some plants may be excluded from the post-disturbance community. We cannot hope to understand how extreme storm events influence ECEs without a much greater understanding of these interactions.

Research Priority IV. Better prediction of where and how storm events and SLR impact ECEs and the delivery of essential ecosystem services

Although we know that storms are more likely to happen with greater frequency and greater intensity, a major challenge in predicting and understanding how ECEs will respond is to be able to forecast and define the range of storm surge and SLR scenarios for any given location. To achieve this, plant biologists must collaborate with geomorphologists who, with their understanding of bathymetry, wave dynamics, sediment supply, landform and the biomechanical properties of vegetation, can offer vital insight into which ECEs are most susceptible and how they are likely to be affected (see also [Krauss and Osland, 2020](#)). It is also true that, in order to deliver accurate flood risk predictions and mitigation scenarios, geomorphologists must consider the contribution of plant communities to coastal processes.

The concept and application of coastal flood risk frameworks (CRAFs) in coastal management is relatively well developed, but the focus has tended to be on how vulnerability to flooding affects human society rather than ECEs ([Hallegatte et al., 2013](#); [Reimann et al., 2018](#); [Viavattene et al., 2018](#)). Nonetheless, there is developing appreciation that CRAFs can be used to identify ‘at risk’ ecosystems (especially those that offer some measure of flood protection), or parts of the coastline where flood risk might be mitigated by virtue of the protection afforded by natural vegetation. In one such example, [Christie et al. \(2018\)](#) use the CRAF approach to pinpoint ‘hot spot’ sections of the North Norfolk (UK) coast at greatest flood risk, and identify likely direct and indirect impacts based on an understanding of local geomorphology and hydrodynamic forcing during floods. Of particular note in this study is the finding that flood impact could be reduced by saltmarsh, i.e. CRAF allows us to identify one of the key ecosystem services provided by coastal vegetation (see also [Torresan et al., 2012](#)).

Another modelling approach, more familiar to plant biologists and ecologists, are species distribution models (SDMs). These have been widely used to predict how the geographical distribution of plant populations will respond to ACC-linked changes in precipitation and temperature (see [Mairal et al., 2018](#); [Rodríguez-Rodríguez et al., 2019](#)). As noted already however, the combination of SLR with additional climate change drivers is a unique, but largely ignored, issue for ECEs. Nonetheless, [Garner et al. \(2015\)](#) attempt some comparative synthesis, using SDM for Californian coastal plant species. They predict that by the end of this century, SLR alone threatens 60 of the 88 species considered and that ten could completely lose their existing habitat range (due to flooding and erosion) within the (24 000 km²) study region. This compares with only four species where shifts in temperature and precipitation alone eliminate all currently suitable habitats. Indeed, unlike plants threatened by SLR, some species may even gain suitable habitat space under likely temperature and precipitation scenarios. [Garner et al. \(2015\)](#) stress, however, that in order to develop robust predictive models for coastal species, a much better mechanistic understanding of vegetation responses to SLR, flooding and climate scenarios is needed.

One way to achieve that aim is by undertaking long-term monitoring of threatened ECEs. This allows us to ‘ground truth’ predictive models by ‘back casting’ how recent environmental changes have actually influenced plant communities. By virtue of access to the Carolina Vegetation Survey, [Ury et al., \(2020\)](#) were able to monitor changes in coastal forest communities over the past two decades. They report how the growth of tree species such as *Acer rubrum*, *Juniperus virginiana*, *Pinus serotina*, *Taxodium distichum* and various *Quercus* species was considerably reduced in low elevation sites where high soil salt content evidenced recent increased seawater seepage. In so doing, it is then possible to track how chronic saltwater intrusion has influenced tree growth and shifts in community composition over a 7–13 year time scale, exactly the kind of data needed to validate predictive models and understand how vulnerable ECEs respond to SLR, and changing storm frequencies and intensities. Long-term ecological surveys are time consuming and labour intensive, and, for large coastlines therefore, impractical over the decadal time frames in which we expect significant geomorphological and ecological changes to occur. Nonetheless, the use of remote-sensing techniques in combination with localized ‘ground-truthing’ (see [Stagg et al., 2020](#)) offers an effective combination to monitor and predict coastal change. The fact that both [Stagg et al. \(2020\)](#) and [Ury et al. \(2020\)](#) highlight how the ability of coastal forests to deliver key ecosystem services is probably compromised by seawater inundation presents the most compelling reason to undertake long-term monitoring and predictive modelling studies into the future.

CONCLUSIONS: ECES IN PERSPECTIVE

The threats posed by the myriad factors associated with ACC and changing storm patterns are worthy of considerable attention, not only from the many geomorphologists, environmental agencies and land managers already concerned with coastal defence, but also from biologists with any interest in plant ecophysiology or community ecology. Beyond any esoteric concern, as sea levels rise and the risk and impact of extreme storms increases, the associated economic repercussions will escalate. [Hallegatte et al. \(2013\)](#), for example, estimated that the costs associated with flooding for the 136 largest coastal cities would increase from US\$6 billion in 2005 to US\$52 billion in 2050. Even under these extreme circumstances, it seems unlikely that taxpayers will willingly subsidize the high cost of protecting every vulnerable urban centre, transport link or farm with hard-engineered defences. Given that coastal cities and food production globally are exposed to increasing ACC-driven flood risk, nature-based risk mitigation, employing the conservation, management or even creation of ECEs with the capacity to track SLR and mitigate storm surges seems ever more desirable. Indeed, the fact that [Van Coppenolle and Temmerman \(2019\)](#) suggest how a cost-effective and dynamic answer (i.e. wetland creation) to the problem of coastal defence can potentially be applied to over a third of the global land area within the influence zone of storm surges, it would seem foolish to ignore the possibility.

A better understanding of the response of ECEs to seawater flooding, physical damage, litter accumulation, etc. at the levels of individual plant species (ecophysiological), ecosystem

(interactions) and landscape (distributions) can be delivered by plant scientists from across our various disciplines. In turn, conservation biologists and ecologists can set to work protecting and enhancing those habitats that deliver coastal defence. Only by so doing can society hope to protect the unique biodiversity of our coastal habitats and the essential ecosystem services they offer us in return.

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