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

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

4
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22 **Running Head:** Coastal plants and extreme storm events
23

24

ABSTRACT

25 • **Background** The combination of rising sea levels and increased likelihood of extreme
26 storm events poses a major flood and erosion threat to our coastlines. As a result, many
27 ecosystems recognized and valued for their important contribution to coastal defence,
28 face increased damage from erosion and flooding. Nevertheless, only recently have we
29 begun to examine how plant species and communities, respond to, and recover from,
30 the many disturbances associated with storm events.

31 • **Scope** We review how the threats posed by a combination of sea level rise and storms
32 affects coastal sub-, inter-, and supra-tidal plant communities. We consider
33 ecophysiological impacts at the level of the individual plant, but also how ecological
34 interactions at community-level, and responses at landscape-scale, inform our
35 understanding of how and why an increasing frequency and intensity of storm damage
36 is vital to effective coastal management. While noting how research is centred on the
37 impact of hurricanes in the US Gulf region, we take a global perspective and consider
38 how ecosystems worldwide (e.g., seagrass, kelp forests, sand dunes, saltmarsh,
39 mangroves) respond to storm damage and contribute to coastal defence.

40 • **Conclusions** The threats posed by storms to coastal plant communities are undoubtedly
41 severe, but beyond this obvious conclusion, we highlight four research priority areas.
42 These call for studies focusing on (1) how storm disturbance affects plant reproduction
43 and recruitment; (2) plant response to the multiple-stressors associated with ACC and
44 storm events; (3) the role of ecosystem-level interactions in dictating post-disturbance
45 recovery; and (4) models and long-term monitoring to better predict where and how

46 storms and other climate change-driven phenomenon impact coastal ecosystems and
47 services. In so doing, we argue how plant scientists must work with geomorphologists
48 and environmental agencies to protect the unique biodiversity and pivotal contribution
49 to coastal defence delivered by plant communities.

50

51 **Key Words:** Coastal Erosion - Flooding – Hurricanes -Kelp – Mangrove – Pine savannah -
52 Salt Marsh – Sand Dunes – Seagrass - Sea-Level Rise - Storm Surge – Wave Attenuation

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INTRODUCTION

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

66 In their most recent assessment of our changing climate, the Intergovernmental Panel on
67 Climate Change (IPCC 2019) asserted that anthropogenically-driven Sea Level Rise (SLR),
68 in tandem with an increase in storm frequency and intensity, poses a severe environmental
69 threat to estuarine and coastal ecosystems (ECEs). Nonetheless, plant biologists have
70 recognized this threat only recently, and when combined with our inability to predict where
71 and when storms might occur, it is perhaps no surprise that relatively few authors have
72 systematically addressed the issue. In-fact much of the initial relevant research was
73 conducted in the SE United States where low-lying freshwater wetlands regularly
74 experience periodic seawater inundation as a result of isostatic movements and subsidence,
75 and changes in channel flow regime. Studies by Haller *et al.* (1974), McKee and
76 Mendelssohn (1989) and Flynn *et al.* (1995) reporting species-specific variation in
77 Floridian and Louisianan freshwater marsh plants to ‘natural’ salinity pulses, were

78 nonetheless prescient of how these communities can be expected to respond to
79 contemporary and predicted changes in frequency and intensity of ACC-linked extreme
80 events. Subsequently, a body of work conducted around the Gulf of Mexico has described
81 the responses of wetland vegetation to the disturbance associated with recent hurricanes
82 (Tate and Battaglia, 2013; Meixler, 2017; Imbert, 2018).

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

94 With this mind, we offer here a synthesis of the response of ECE vegetation to extreme
95 storm events, and signpost how an understanding of these responses aids management of
96 ECEs for flood and erosion mitigation. We contextualize recent scientific studies by
97 exploring the threats to, and response of, plants challenged by both SLR and increasing
98 storm frequency and severity. This necessitates understanding ecophysiological responses
99 from the level of the individual, up to geomorphological factors operating across the entire

100 tidal range. We highlight also future research priorities, from laboratory experiments to
101 large-scale modelling and mapping of post-disturbance vegetation responses, needed to
102 provide an appreciation of the wider ecosystem services delivered by coastal habitats. By
103 bringing together this diversity of topics, our aim is not only to signpost interdisciplinary
104 research towards better management of ECEs, but also promote their integration into
105 strategic coastal defence.

106 **THREATS TO COASTAL ECOSYSTEMS**

107 Although historically, land use change, pollution, and invasive species have all impacted
108 ECEs, and while these threats are certain to continue into the future, our focus is on ACC.
109 Indeed, there seems little doubt that ACC will pose the greatest challenge to coastal habitats
110 for the remainder of this century and beyond (Millennium Ecosystem Assessment, 2005).

111 Although elevated atmospheric CO₂ (eCO₂), and associated shifts in temperature, and
112 precipitation will have profound effects on all plant communities (Parmesan and Hanley,
113 2015), the combination of SLR, and increased sea surface temperatures (SST) and
114 enhanced wave forcing is a particular pressing and unique issue for ECEs.

115 Rising sea levels have already affected many coastal regions. IPCC (2019) stated with '*high*
116 *confidence*' that the 0.32m increase in global sea levels observed between 1970-2015 was
117 attributable to ACC-driven thermal expansion of the seas and glacier mass loss. It seems
118 clear that SLR will accelerate into the 21st century, although IPCC (2019) have '*high*
119 *confidence*' that variation in ocean dynamics and coastal land-use will generate regional
120 departures of about 30% around global averages. Not only does this place coastal regions

121 and habitats at significant (but varying) flood risk, there is ‘*high confidence*’ that SLR will
122 continue for centuries, even if global mean temperatures are stabilized (IPCC, 2019). The
123 ramifications of these changes are severe. IPCC (2019) has ‘*very high confidence*’ that low-
124 lying coastal areas will increasingly experience submergence, flooding and erosion
125 throughout this century and beyond.

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

142 Indeed, where sufficient ‘pre-event’ data are available, studies show major changes in
143 coastal geomorphology and vegetation for many years afterwards. Carter *et al.* (2018) for
144 example, used a time series of remotely sensed images to show major breaching, land-area
145 reduction, and vegetation loss throughout the Mississippi-Alabama barrier islands in the
146 first 10 months after Hurricane Katrina made landfall. These changes were however, site-
147 specific depending on sediment removal or accretion, underscoring the more general
148 problem that it is difficult to predict exactly how and when storms affect particular
149 coastlines. For example, in the unusually energetic series of winter storms that affected SW
150 England in 2013/4, the most severe impacts coincided with high spring tides and occurred
151 on west-facing beaches where subsequent dune erosion was extensive (Masselink *et al.*,
152 2015). Similarly, variation in wind directions meant a brackish marshland in Louisiana,
153 USA, apparently unaffected by Hurricane Katrina in August 2005, experienced major
154 seawater incursion following Hurricane Rita only a month later (Steyer *et al.*, 2007).

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

162

163 **IMPACTS ON COASTAL PLANT COMMUNITIES**

164 *Supra-tidal Plant Communities*

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

168 Due, in part, to our inability to predict where and when storm surges will occur, and even
169 less effectively, control and replicate natural flood events, few field studies deal with the
170 impact of storm disturbance on supra-tidal plant communities. Although remote sensing
171 offers a way to assess and monitor largescale changes in vegetation following storm events
172 (e.g. Carter *et al.*, 2018; Douglas *et al.*, 2018; Stagg *et al.*, 2020), elucidating how saltwater
173 flooding, mechanical damage, litter accumulation, and sediments affect the plant
174 community is challenging. There is however, a relatively large body of research describing
175 the (species-specific) effects of burial by sediments on sand dune species (Sykes and
176 Wilson, 1990; Harris *et al.*, 2017; Brown and Zinnert, 2018), while Tate and Battaglia,
177 (2013) and Platt *et al.*, (2015) report major negative effects of simulated post-hurricane
178 litter deposition on Floridian and Mississippian pine savannah. Surprisingly however, few
179 studies consider the immediate effects of physical damage on supra-littoral coastal
180 vegetation (see Platt *et al.*, 2000).

181 The most widely reported impact of ACC-linked extreme events on supra-littoral ECEs is
182 seawater flooding. Immersion in seawater brings additional problems for supra-littoral
183 plants compared to those experienced by species in inland riparian, or coastal inter-tidal

184 communities. Flooding of the former is exclusively freshwater, while plants in most inter-
185 tidal ECEs have an inherent ability to tolerate salinity associated with (twice-daily) tidal
186 immersion. Although by virtue of their association with the coast, sand dune, cliff edge, and
187 other supra-littoral plants may be tolerant of salt spray (Malloch *et al.*, 1985; Sykes and
188 Wilson 1988), the combination of anoxia and salt stress imposed by seawater flooding is
189 unique to these habitats.

190 In fact the ‘salt stress’ associated with coastal flooding seems to be much more important to
191 plant response and recovery than anoxia. In experiments where supra-littoral plants have
192 been simultaneously exposed to freshwater and seawater immersion, the former has never
193 resulted in any noticeable impact on plant ecophysiology compared with untreated (no
194 immersion) controls (Tolliver *et al.*, 2009; Hanley *et al.*, 2013, 2017, 2020a,b; White *et al.*,
195 2014). A full appraisal of how and why salinity stress affects plant ecophysiology is beyond
196 the scope of this review (see instead Flowers and Colmer, 2008; Munns and Tester, 2008;
197 Negrão *et al.*, 2017; the latter an excellent assessment of methods to evaluate plant
198 physiological responses to salinity stress). In short however, high seawater salinity (of
199 which chloride (55%) and sodium (31%) contribute most of the ‘salt’ content), causes both
200 osmotic (limiting the plant's ability to absorb water) and ionic (increased toxicity via Na⁺
201 and Cl⁻ accumulation) stresses (Munns and Tester, 2008). It is worth bearing in mind
202 though that our oceans have marked seasonal and regional salinity variation (Donguy and
203 Meyers, 1996) and that seawater is much more than ‘NaCl in solution’. Some ions such as
204 K⁺ and Ca²⁺ have direct negative toxicological or osmotic effects, but also the potential to
205 mitigate the impact of Na⁺ and Cl⁻ on plant metabolism (Flowers and Colmer, 2008; Munns

206 and Tester, 2008). It is likely that other ions have similar moderating influences over Na⁺
207 and Cl⁻ stress, and consequently, understanding how seawater affects plant
208 ecophysiological responses requires much more than a simplistic evaluation of the effects
209 of NaCl alone. This point was reinforced by **Hanley *et al.*, (2020a)**, who show how short-
210 duration immersion of *Trifolium repens* in NaCl solutions elicited almost total mortality
211 compared to plants subject to immersion in natural seawater or commercially available
212 marine aquarium salt solutions.

213 It is possible to monitor ECE recovery after a natural flood event (e.g. Flynn *et al.*, 1995;
214 Lantz *et al.*, 2015), but this requires the ability to allocate resources quickly to an affected
215 site in order to capture changes in vegetation as floodwaters recede. Moreover, to
216 appreciate fully post-inundation transitions, a thorough understanding of the pre-flood
217 ecosystem is also essential (Langston *et al.*, 2017; Masselink *et al.*, 2017). Some
218 manipulative field experiments have been attempted, but logistical and even ethical issues
219 mean these are uncommon (McKee and Mendelsohn, 1989; Tate and Battiglia, 2013;
220 Abbott and Battiglia, 2015). Consequently, many studies employ controlled ‘flooding’ in
221 greenhouse or ‘common garden’ experiments, although inevitably, experiments are
222 constrained to focus on a limited species or habitat pool (van Zandt *et al.*, 2003; Hanley *et*
223 *al.*, 2013, 2017, Li and Pennings, 2018). Many studies also impose long-term, or periodic,
224 chronic salinity, rather than replicating the short-duration, acute immersion experienced
225 immediately after a storm (Tolliver *et al.*, 1997; van Zandt and Mopper 2002; van Zandt *et*
226 *al.*, 2003; Mopper *et al.*, 2016; Li and Pennings, 2018). A further problem is that rather
227 than use natural seawater, experiments are often undertaken using commercially available

228 marine aquarium salt or even NaCl solutions (Sykes and Wilson 1988; Flynn *et al.*, 1995;
229 Tolliver *et al.*, 1997; Mopper *et al.*, 2016), with no assessment of their validity as
230 alternatives. In the second experiment described by **Hanley *et al.*, (2020a)** however, six
231 different European sand dune plant species showed remarkable uniformity in stress and
232 ecophysiological responses to marine aquarium salt versus locally collected seawater. This
233 consistency suggests that the chemistry of the former is indeed close enough to the latter to
234 use marine aquarium salt as a reliable experimental substitute.

235 Despite the various methodological problems, unsurprisingly perhaps, significant negative
236 repercussions for plant survival, growth, and reproduction are apparent for plants subjected
237 to seawater (or surrogate) immersion (van Zandt *et al.*, 2003; Mopper *et al.*, 2016; Hanley
238 *et al.*, 2017, 2020a,b; Li and Pennings, 2018; Lum and Barton, 2020). Mortality is
239 common, but even where plants survive short-pulses of seawater exposure subsequent
240 recovery is compromised. A typical response to the ionic and osmotic shock associated
241 with salinity is the accumulation of stress metabolites (e.g. proline) and ions (Ca^{2+} and K^{+})
242 to exclude or compartmentalize Na^{+} and Cl^{-} (Flowers and Colmer, 2008; Munns and Tester,
243 2008) (likely explaining why plant response to NaCl solution is more extreme than
244 seawater which contains 1.2% Ca^{2+} and 1% K^{+}). Even if achieved however, a cost on plant
245 fitness is probably inevitable (Munns and Tester, 2008; White *et al.*, 2014; Hanley *et al.*,
246 2020a,b).

247 Most importantly perhaps, the ability of plants to tolerate, and recover from, seawater
248 flooding seems to be species-specific. Long-term observation of Arctic tundra following a
249 major storm surge in the Mackenzie Delta, Canada, shows that dwarf shrub tundra had a

250 much-reduced regenerative capacity than graminoids or upright shrubs (Lantz *et al.*, 2015 -
251 see also Middleton, 2009; Tate and Battaglia, 2013). Manipulative greenhouse experiments
252 (Hanley *et al.*, 2017, 2020a; Li and Pennings, 2018; Edge *et al.*, 2020) generally
253 corroborate field observations of species-specific variation. Working on two native
254 Hawaiian plants, **Lum and Barton (2020)** for example, report not only species-specific
255 variation in ecophysiological responses to increased salinity (imposed over 3-weeks), but
256 also that tolerance increased for both species as plants aged. These observations represent a
257 critical component of our understanding of plant response to the environmental pressures
258 associated with SLR and storm surges. Not only is species-specific variation important, but
259 it is essential to elucidate plant responses throughout ontogeny. Middleton (2009) for
260 example describes species-specific variation in post-hurricane germination and recruitment
261 ability of US Gulf Coast marshland species, a response ascribed principally to increased
262 salinity. At the other end of the plant life cycle, **Hanley *et al.*, (2020b)** report how
263 immersion of oilseed rape (*Brassica napus*) in seawater reduced seed yield, and perhaps
264 most importantly, that growth of the resulting seedlings was also greatly reduced in
265 comparison with progeny cultivated from non-flooded or even freshwater-flooded parent
266 plants.

267 Although work in this area is anything but ‘mature’, these studies signpost flooding as a
268 potential selective filter that could remove species from the post disturbance community.
269 The loss of key species or functional groups from any vegetation is likely to compromise
270 ecosystem processes and so limit the ability to supply essential ecosystem services. For
271 vegetation like sand dunes, these losses may be particularly profound. In Florida for

272 example, Miller (2015) identified reduced cover of the dune building grass, *Uniola*
273 *paniculata*, in low elevation areas subject to frequent flooding as a likely reason why dune
274 erosion was more common in these sites. The interplay of ACC-linked changes in storm
275 frequency and severity, with resulting shifts in plant community composition and thus
276 resilience against further storm damage, is pivotal for understanding how ECEs contribute
277 to coastal defence.

278 *Inter-tidal Plant Communities*

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

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

287 The physical damage caused by storms ranges from waves and strong currents dislodging
288 or breaking above-ground tissue (Möller *et al.*, 2014), to complete denudation of vegetation
289 (Morton and Barras, 2011). Fragmented or degraded marshes are generally more vulnerable
290 to disturbance than intact habitat (Stagg *et al.*, 2020) and so are less resilient to extreme
291 events. Responses also vary with vegetation height and stiffness (Vuik *et al.*, 2018). For
292 example, when exposed to simulated storm conditions, the tall, rigid grass *Elymus athericus*

293 experienced more breakage than the shorter, more flexible *Puccinellia maritima* (Rupprecht
294 *et al.*, 2017). Strong winds and water flows can tear the root mat from the marsh surface,
295 laterally folding it into ridges – described by Cahoon (2006) as like ‘pushing a rug up along
296 a wooden floor’. This alters marsh topography, lowering areas where turf was lost and
297 raising elevations (up to 2 m) on the folded ridges (Guntenspergen *et al.*, 1995). This can
298 affect long-term community recovery (Leonardi *et al.*, 2018; Mossman *et al.*, 2019).

299 In addition to direct damage, storms modify plant communities through changes to the
300 physical environment (see reviews by Cahoon, 2006; Leonardi *et al.*, 2018). Storm-driven
301 waves can cause lateral erosion of tidal flats and marshes (Callaghan *et al.*, 2010), with
302 erosion of fronting tidal flats increasing marsh loss by amplifying the consistent pressure
303 imposed by normal wind and wave action (Leonardi *et al.*, 2016). Saltmarshes are resistant
304 to storm-driven erosion of the marsh surface however, with vegetation playing a key role in
305 stabilizing the sediment (Spencer *et al.*, 2016). Importantly, significant amounts of
306 sediment (mobilised from sub-tidal, intertidal or upstream areas) are deposited on
307 saltmarshes during these events (de Groot *et al.*, 2011). For example, a single hurricane can
308 deposit the equivalent of over a century of sediment accumulated in ‘normal’ conditions,
309 and account for up to two thirds of long-term sedimentation (Williams and Flanagan,
310 2009). Burial under such rapid deposition can kill vegetation (Callaway and Zedler, 2004),
311 and reduce growth and seedling establishment (Langlois *et al.*, 2001; Cao *et al.*, 2018).
312 Marsh recovery following storm-driven sediment deposition can be rapid however,
313 (Guntenspergen *et al.*, 1995) and increases in elevation improve colonization, particularly
314 in subsiding marshes (Mendelssohn and Kuhn, 2003).

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

324 The impact of changes in soil salinity following storms is less clear. In some circumstances,
325 high rainfall can ameliorate conditions, allowing plants to colonize or grow faster. For
326 example, in the dry climate of California, Noe and Zedler (2001) found that heavy rainfall
327 provided a window for germination by reducing soil salinity and increasing soil moisture.

328 Storms can also alter the inundation regime of tidal marshes through changes to coastal
329 morphology that lead to closure of an estuary mouth or movements of tidal channels.

330 Zedler (2010) summarises how the storm-driven closure of the Tijuana estuary had
331 substantial negative impacts on tidal marsh vegetation when subsequent drought caused
332 moisture loss and hypersalinity in sediments.

333 More typical is the generally negative effect of seawater inundation; Janousek *et al.*, (2016)
334 report how experimental increases in inundation over one growing season reduced plant
335 productivity. It is also likely that even where tidal marsh plants survive storm disturbance,
336 they are so ecophysiologicaly compromised that interactions with other species change.

337 The study by **Edge *et al.*, (2020)** on three European saltmarsh species is an excellent
338 example. Following seawater immersion, the biomass of *Triglochin maritima* decreased
339 markedly in mixed assemblages with *Plantago maritima* and *Aster tripolium*, compared to
340 monoculture. Interestingly, *Plantago* performed markedly better in flooded, mixed
341 assemblages than in monoculture, appearing to ‘take advantage’ of a relative decline in the
342 growth of the other species (Hanley *et al.*, (2017) describe very similar shifts for supra-
343 littoral plants). Edge *et al.*, (2020) further note how that for 14 out of 18 trait-species
344 combinations examined (including height, SLA, and leaf number), flooding response in
345 mixed assemblages differed from monocultures, changing the direction, as well as
346 magnitude, of flood effects. Plant trait and species composition shifts within saltmarsh
347 communities are likely important to ecosystem stability and function (Ford *et al.*, 2016),
348 but if disturbance associated with storm events facilitates the spread of non-native species,
349 repercussions could be more severe. This is exactly what **Gallego-Tévar *et al.*, (2020)**
350 report when they found that an invasive *Spartina* hybrid was better able to tolerate stressful
351 post-flood salinity conditions than its parent species (see also Charbonneau *et al.*, 2017).
352 Together, these studies underscore the importance of species identity in dictating
353 community responses to storm disturbances, and thus the capacity of the saltmarsh
354 ecosystem to continue to deliver key services as ACC continues.

355 *Subtidal Plant Communities*

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

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

362 High wave energy and flow speeds can physically damage fronds and stipes (Denny *et al.*,
363 1989), uproot individuals (Preen *et al.*, 1995) or cause failure of holdfasts (Seymour *et al.*,
364 1989). While the biomechanics of storm effects are well understood (see Denny and
365 Gaylord, 2002), predicting the impact of storm events is more complex. Structural damage
366 and uprooting/ dislodgement can result in high mortality; for example, complete loss of
367 giant kelp occurs in storm-intense years but is not seen everywhere (Edwards, 2004). Large,
368 frequent and breaking waves exert the greatest forces and are most likely to result in
369 structural damage or dislodgement, particularly in shallow water when a storm coincides
370 with low tide (Preen *et al.*, 1995; Filbee-Dexter and Scheibling, 2012). Even moderate
371 waves can lead to entanglement of kelp fronds, increasing the potential for tissue damage
372 (Seymour *et al.*, 1989). Effects can vary according to substrate type, as wave-carried rocks
373 can dislodge individuals, while sand grains and small pebbles scour roots and holdfasts or
374 damage tissue (Shanks and Wright, 1986). Substrate type also affects the forces needed to
375 dislodge macroalgae (Thomsen *et al.*, 2004).

376 Storm-driven waves do not affect every organism equally however. Vulnerability varies
377 with spatial arrangement and age; individuals in the centre of algal stands are less likely to
378 be removed by waves or strong currents, and small, young kelp are more easily dislodged
379 than older, larger individuals (Thomsen *et al.*, 2004). Nonetheless, the higher biomass of

380 very large kelp makes them more susceptible to high wave energies (Seymour *et al.*, 1989).
381 Consequently, severe storms can result in homogenization of age structure in kelp beds.
382 Ecotypes or morphological plasticity provide resistance to high wave action (e.g. in shallow
383 waters) (Fowler-Walker *et al.*, 2006), allowing some individuals or populations to better
384 cope with an extreme event. Storms are also generally most frequent at the point in the
385 annual cycle where organisms are most resistant (Burnett and Koehl, 2019); accordingly,
386 changes to storm seasonality may have significant consequences for these communities.

387 In addition to the effects of wave action and shear stress, storm-generated waves and
388 currents redistribute sediments, causing erosion in some areas and burial in others. Cabaco
389 *et al.*, (2008) identified significant species-specific variation in seagrass tolerance to both
390 burial with sediment and erosion. Recovery is generally rapid under shallow burial, but this
391 capacity decreases markedly when more sediment is deposited (Fourqurean and Rutten,
392 2004; Gera *et al.*, 2014). Consequently, burial by up to 45 cm of sediment, reported
393 following some severe storms (Kosciuch *et al.*, 2018; Browning *et al.*, 2019), is likely to
394 lead to localized loss of communities.

395 As well as the impacts of storms at sea, heavy rainfall can have major impacts on sub-tidal
396 ECEs via the discharge of nutrient-rich, sediment-laden freshwaters into coastal areas.
397 These enriched waters cause turbidity and stimulate algal blooms and epiphytic growth,
398 both of which lower light availability (Lapointe *et al.*, 2019). Seagrasses are especially
399 vulnerable (Cobaco *et al.*, 2008), and impacts of flood-induced light limitation can be more
400 severe than the physical impacts of storms (Carlson *et al.*, 2010). In addition, heavy rainfall
401 can reduce salinity, particularly in lagoons or estuaries, sometimes for several months

402 (Herbeck *et al.*, 2011; Kowalski *et al.*, 2018,). Some seagrasses are intolerant of hyposaline
403 conditions, leading to mortality and sub-lethal effects (Fernandez-Torquemada and
404 Sanchez-Lizaso, 2011). Ridler *et al.*, (2006) observed that while thinning and leaf loss
405 occurred immediately after hurricanes, further declines continued for many months likely
406 due to low and fluctuating salinity. Tolerance to hyposalinity is however, variable between
407 and within species, ecotype (Benjamin *et al.*, 1999) and season (Fernandez-Torquemada
408 and Sanchez-Lizaso, 2011) reducing the predictability of how seagrass communities
409 respond.

410 Storms are nonetheless important disturbance agents, and seagrasses can rapidly regrow
411 from roots or rhizomes, despite substantial above-ground loss (Valiela *et al.*, 1998). Other
412 macroalgae can reattach or regenerate when broken or dislodged (Thomsen and Wernberg,
413 2005). Furthermore, storms may actually facilitate medium and long distance dispersal of
414 seagrass and macroalgae propagules (Bell *et al.*, 2008; Waters *et al.*, 2018) and be
415 important in maintaining food web complexity, although increasing storm frequencies can
416 challenge the ability of kelps to regrow and simplify food web structure (Byrnes *et al.*,
417 2011). Damage to kelp fronds can for example, stimulate grazing activity, so increasing
418 potential tissue loss to an already stressed individual (O'Brien *et al.*, 2015). Reductions in
419 canopy-forming macroalgae and seagrasses through a combination of direct storm damage
420 and herbivory can lead to community shifts to opportunistic species, such as turf-forming
421 algae (O'Brien *et al.*, 2015, Filbee-Dexter and Wernberg, 2018). Gaps resulting from the
422 storm-driven loss of corals and other benthic animals can nevertheless facilitate macroalgal

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

425 The impacts of extreme storm events are not experienced in isolation. Long-term
426 environmental changes, such as SLR, eutrophication and overfishing, influence community
427 susceptibility, as does the legacy of previous storms (i.e. position in the ‘storm recovery
428 cycle’). For example, substantial seagrass losses in North Queensland, Australia, were the
429 cumulative result of a succession of intense storm and flood years, urbanization, and
430 agricultural run-off, rather than the consequence of a single storm (McKenna *et al.*, 2015).

431 Storm events are also stressing systems already impacted by ACC, a combination that
432 could lead to higher losses than imposed by either driver in isolation (Babcock *et al.*, 2019).
433 Smale and Vance, (2016) for example report that while the cold-water kelp *Laminaria*
434 *hyperborea* was relatively resistant to storms, mixed stands containing warm water species,
435 such as *L. ochrolueca*, were more vulnerable. Consequently, observed and projected shifts
436 in kelp community composition due to increasing temperatures (Pessarrodona *et al.*, 2018)
437 could lead to greater kelp community vulnerability.

438 Collectively, the processes described above underpin observations of highly variable storm
439 impact on sub-tidal plant communities (Edwards, 2004; Filbee-Dexter and Scheibling,
440 2012). Long term studies can help identify the relative impacts of storms and anthropogenic
441 factors (Cuvillier *et al.*, 2017), but our understanding of storms on subtidal ECEs is limited
442 by few long term studies outside of coral reefs (Duffy *et al.*, 2019). While there are many
443 estimates of the impacts of single storms, it is rarely possible to put the patch-scale losses in
444 the context of the dynamics of the system. Despite advances with remote-sensing

445 techniques, the depth and turbidity of these systems mean that ground based observation
446 will continue to be essential.

447 **PLANT COMMUNITIES AND COASTAL DEFENCE**

448 In addition to biodiversity loss, recent concern about the various threats to ECEs stems
449 from their role in protecting agricultural land and urban communities from storm damage.
450 Consequently, there is increasing focus on quantifying and valuing benefits associated with
451 the ecosystem services provided by ECEs (Barbier *et al.* 2011, 2015; Temmerman *et al.*,
452 2013; Morris *et al.*, 2018). Although the methods used to generate accurate, global,
453 economic estimates remain in their infancy (Barbier 2016), Costanza *et al.*, (2014)
454 estimated that for tidal marshes alone, the provision of nursery grounds for commercial
455 fisheries, carbon storage, recreation and flood protection provided US\$24.8 trillion to the
456 global economy.

457 ECEs provide storm protection principally through the stabilization of substrates, and
458 therefore the prevention of erosion, and attenuation of wave energy, and thus flood risk
459 (Barbier 2015). Unlike hard (engineered) defences they are also dynamic; indeed the IPCC
460 (2019) recognized how saltmarshes and mangroves can keep pace with fast rates of SLR (>
461 10mm yr⁻¹), depending on local variation in wave exposure, tidal range, sediment
462 dynamics, and coastal land-use. Moreover, it is even possible that the extent of coastal
463 wetlands (saltmarsh, freshwater marsh and mangrove) could increase by up to 60% because
464 of SLR (Schuerch *et al.*, 2018). With appropriate management, supra-littoral sand dunes are
465 also capable of adapting to shifts in sea levels and storm frequencies (Hanley *et al.*, 2014).

466 The growing evidence that ECEs reduce storm damage underpins their recognition as
467 nature-based flood protection (Temmerman *et al.*, 2013; Narayan *et al.*, 2016; Van
468 Coppenolle & Temmerman, 2019). The traditional approach to coastal defence has been to
469 counter flood risk with ‘hard’ engineering, but measures like seawalls are expensive (up to
470 £5,000 per m [Hudson *et al.*, 2015]), inflexible, and often deliver unexpected
471 environmental outcomes (Firth *et al.*, 2014). Vegetated shorelines by contrast, are a natural
472 defence and offer adaptability, flexibility and cost-effectiveness (e.g. £20 per m for dune
473 stabilization (Hudson *et al.*, 2015)), with the additional benefit of the other ecosystem
474 services they provide (Costanza *et al.*, 2014; Barbier 2015).

475 *Protective role played by different ECEs*

476 The protective value differs not only between ECEs, but also with regional and local
477 geographical context. The principal defensive role played by dunes for example, stems
478 from being a physical barrier to marine flooding, but their importance in this regard
479 depends on local coastal geomorphology (e.g. sediment supply, land relief) and on the use
480 and asset value of the land they protect (Hanley *et al.*, 2014). Dune vegetation stabilises
481 substrates and reduces wave-driven erosion, with plant shoots reducing wave swash and
482 roots increasing mechanical strength of the sediment (Feagin *et al.*, 2019), but even the
483 identity of component species can be important. **de Battisti and Griffin (2020)** for
484 example examined how three common European foredune species (*Ammophila arenaria*,
485 *Cakile maritima*, and *Salsola kali*) varied in their ability to withstand simulated wave
486 swash. Although *Ammophilla* was by far the most robust, by virtue of the protection
487 provided by their roots, rhizomes and below ground shoots, all three species had a

488 remarkable capacity to tolerate wave action, underscoring how different plant species can
489 contribute to sand dune stability. (See also Charbonneau *et al.*, (2017) who report how
490 North American dunes stabilized by the invasive *Carex kobomugi* were less affected by
491 storm damage than those colonized by native *Ammophila breviligulata*). Nonetheless, de
492 Battisti and Griffin (2020) also show that despite an exceptionally well-developed
493 belowground shoot system, *Ammophila* resistance varies depending on sand particle size;
494 the coarser sediments associated with restored habitats increasing erosion potential
495 compared to finer sediment of natural regeneration sites. This finding is important since it
496 underscores why elucidation of biological and environmental factors is crucial to the
497 integration of natural habitats like sand dunes into coastal protection schemes. For other
498 supra-littoral habitats however, we understand little about their putative role in coastal
499 defence. Nonetheless, there is little doubt that coastal forests and freshwater wetlands
500 provide other vital ecosystem services like carbon sequestration and storage (see Stagg *et*
501 *al.*, 2020; Ury *et al.*, 2020).

502 The ability to track SLR (Kirwan *et al.*, 2016; IPCC, 2019) along with their well-known
503 capacity for wave attenuation (Möller *et al.*, 2014; Rupprecht *et al.*, 2017), has put
504 saltmarshes at the centre of current interest in ‘nature-based’ coastal defence solutions.
505 How effective wave attenuation is, depends strongly on topography (even to the extent of
506 friction imposed by the biogeomorphic landscape created by the plants) and (ontogenetic,
507 seasonal or species-specific) plant traits like shoot stiffness and density (Bouma *et al.*,
508 2010, 2014; Möller *et al.*, 2014). As a result, studies such as **Zhu *et al.* (2020)**, describing
509 variation in stem flexibility and breakability for a variety of European saltmarsh species,

510 are vital to understanding how communities will respond to increased storminess. Plant
511 response can vary with wave conditions however. **Shao et al. (2020)** exposed *Spartina*
512 *alterniflora* to different wave environments for 8 weeks and showed that key physiological
513 and biochemical plant parameters varied accordingly; i.e. higher and more frequent waves
514 imposed more stress. Nonetheless, wave-exposed plants tended to allocate more biomass to
515 their roots, a response that may facilitate anchorage against wave impact. These
516 biomechanical and morphological properties are likely to vary with plant age. **Cao et al.,**
517 **(2020)** for instance describe how after seven weeks of simulated wave exposure, seedling
518 survival and growth declined for all three common marshland species examined (*Spartina*
519 *anglica*, *Scirpus maritimus* and *Phragmites australis*). Taken together these studies
520 increase our understanding and prediction of spatio-temporal variation in saltmarsh
521 community response to wave exposure, an essential pre-requisite in the design and
522 implementation of nature-based flood protection.

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

532 coastal management approach, but long-term salt marsh persistence depends on continual
533 recruitment of new plants.

534 For saltmarshes, propagule establishment often occurs on leading edges when sediment
535 accretes on the adjacent ‘tidal flat’ (Bouma *et al.*, 2016). Even an apparently minor change
536 in sediment levels may be sufficient to facilitate seedling establishment; an effect
537 demonstrated by **Fivash *et al.*, (2020)** in their mesocosm experiment with the pioneer
538 *Salicornia procumbens*. They show that elevation of sediment micro-topography by just 2
539 cm was the overwhelming driver of seedling growth (i.e. an average 25 % increase). They
540 ascribed this response primarily to the effects of the ‘tidally driven oxygen pump’, i.e.
541 increased emersion time allows more aeration of the raised sediment (see also Mossman *et*
542 *al.*, 2019). Once pioneers like *Salicornia* have established, the environment they create
543 (wave attenuation, sediment trapping and enhanced drainage) facilitates subsequent
544 colonisation by later successional species and so the marsh can expand seaward
545 (Temmerman *et al.*, 2007). Storms also have the potential to increase the landward marsh
546 area if the habitat can retreat and displace terrestrial habitats. In these circumstances,
547 **Kotter and Gedan (2020)** demonstrate that saltmarsh is pre-primed to take advantage of
548 this opportunity, reporting how seeds of halophytic species can disperse up to 15 m into
549 northeast American coastal pine forest. They argue that although saltwater intrusion will
550 limit forest regeneration, the soil seed bank can thus support continued landward migration
551 of saltmarsh species.

552 Much of the recent interest in mangroves stems from their perceived mitigation of the 2004
553 Indian Ocean Tsunami on coastal settlements. While their actual contribution remains

554 questionable (Barbier 2015), nonetheless, a number of studies report that mangroves can
555 lower wave heights and reduce water levels during storm surges (Das and Vincent, 2009;
556 Armitage *et al.*, 2019) and that their removal leads to increased coastal erosion and damage
557 (Granek and Ruttenger 2007; Barbier 2015). Like saltmarsh therefore, mangroves are at
558 the forefront of contemporary research into how ECEs help defend our coastlines (see
559 Krauss and Osland, 2020). It is also noteworthy, that Alongi (2008) highlights how much
560 mangroves offer protection against extreme events is strongly linked to intrinsic habitat
561 characteristics (these include forest location and width, tree density and size, soil texture),
562 but also the presence of other ECEs, such as coral reefs, seagrass beds, and dunes.

563 The case for a substantial protective role of sub-tidal ECEs remains less clear (although
564 coral reefs are well studied and widely believed to play a major role – see Barbier 2015). It
565 is known however, that seagrasses attenuate wave energy (Christianen *et al.*, 2013;
566 Reidenbach and Thomas, 2018), and thus likely offer some coastal defence (Barbier *et al.*,
567 2011; Ondiviela *et al.*, 2014). Furthermore, the reduction in wave energy seagrasses
568 provide can reduce the erosion experienced by adjacent tidal marsh systems (Carr *et al.*,
569 2018) and stabilise or even facilitate beach expansion (James *et al.*, 2019). Consequently,
570 the dramatic global decline of seagrass habitat is of great concern and underscores recent
571 calls for wider habitat protection (Cullen-Unsworth and Unsworth 2018). It is less clear
572 whether sub-tidal macroalgal communities play any role in wave attenuation and therefore
573 coastal protection, but a full review is provided in this special issue (see **Morris *et al.*,**
574 **2020**). In short, Morris *et al.*, (2020) note how only a limited number of studies have
575 investigated coastal protection, and in their own study in Australia found that wave

576 attenuation by the kelp *Ecklonia radiata* was restricted to a small subset of the
577 environmental conditions sampled.

578 *Using ECEs in integrated coastal defence*

579 The implementation of ‘soft’ or natural flood defences depends on landscape context
580 (including the economic value of the land threatened by SLR, erosion, and storm damage)
581 and whether it is actually feasible and cost-effective to maintain or move defences (Hoggart
582 *et al.*, 2014). The ‘hold the line’ option has been traditionally met by the construction of
583 ‘hard’ defences (engineered solutions utilising concrete walls, rocky breakwaters, steel
584 piling, or stone gabions) but these are extremely expensive and have limited ecological
585 value. There is nonetheless considerable interest in how we might ‘soften’ structures using
586 design alterations (e.g. modification of surface topography) to increase biodiversity value
587 (Firth *et al.*, 2014). It is also recognised that vegetated foreshores reduce wave impact on
588 sea walls, such that a fronting saltmarsh provides sufficient additional defence to allow sea
589 wall height to be lowered, with substantial savings to capital and maintenance costs (Vuik
590 *et al.*, 2016). Where natural habitat is absent, it may be possible to create it using
591 management actions to stabilize or accrete sediment. For example, the combination of
592 beach nourishment, sand traps and planting can establish sand dunes to provide storm
593 protection to landward hard defences (Feagin *et al.*, 2015). At the landscape scale, the
594 strategic integration of hard engineered and soft natural defences may provide the only
595 realistic, cost-effective way to protect large sections of coastline.

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

606 The most common example is the breaching of sea walls or dykes to allow tidal flooding
607 with the expectation that newly inundated land will develop into saltmarsh. These schemes
608 have met with mixed success however, many studies showing that the plant communities
609 developing in MR sites differ from those in adjacent natural marshes (Mossman *et al.*,
610 2012; Masselink *et al.*, 2017). Environmental conditions, such as elevation in the tidal
611 frame or geomorphic setting (Mossman *et al.*, 2012; Masselink *et al.*, 2017) are critical to
612 successful restoration, but these alone are insufficient to explain all observed differences
613 (Sullivan *et al.*, 2018). Propagule dispersal is often limited and limiting (Mossman *et al.*,
614 2012) and species-specific differences in dispersal ability could mean that early colonisers
615 inhibit the establishment of later arriving species (Sullivan *et al.*, 2018). Planting species
616 with low recruitment potential into newly established marshes could resolve this (Mossman
617 *et al.*, 2019). A relative lack of topographic heterogeneity in MR sites may also limit

618 transition to saltmarsh (Masselink *et al.*, 2017; Lawrence *et al.*, 2018). As we have seen
619 (Mossman *et al.*, 2019; Fivash *et al.*, 2020), even minor changes in surface elevation can
620 have a substantial impact on seedling recruitment in saltmarsh. These studies highlight that,
621 while MR often fails to deliver ‘natural’ saltmarshes, there is considerable potential for
622 research-led management to improve restoration success.

623 **SYNTHESIS AND FUTURE STUDIES**

624 Although considerable research effort is focused on the response of ECEs to disturbance
625 events, there remains both a geographical bias towards the US Gulf and Atlantic seaboard
626 states, and limited understanding of how the multiple stressors associated with SLR,
627 extreme storms, and other anthropogenic activities affect even a fraction of ECE species or
628 habitats. Beyond a simplistic call for ‘more research with additional species and regions’,
629 we discuss how illumination of plant species and community responses to flooding,
630 sediment movement, mechanical damage and landscape-scale processes is needed to better
631 inform our ability to manage the biodiversity of ECEs and ensure their continued
632 contribution to coastal defence (Fig 1).

633 **Research Priority I – *Effects of storm damage and flooding on plant reproductive*** 634 ***performance and recruitment***

635 Parmesan and Hanley (2015) highlighted how despite a wealth of information detailing
636 plant species and community response to the warming, drought and elevated atmospheric
637 CO₂ (eCO₂) associated with ACC, remarkably little is known about how any of these factors
638 influence plant regeneration biology. The same failing is true of ECE response to SLR and

639 storms, even though recruitment success is manifestly pivotal to understanding how
640 environmental stress and perturbation influence plant community recovery. Indeed, it is at
641 this point worth stressing that the disturbance associated with storms is an important,
642 positive, factor in ECE dynamics. It is for example, well understood that tropical cyclones
643 stimulate reproduction and open regeneration opportunities (Zimmerman *et al.*, 2018;
644 Krauss and Osland 2020), while disturbance of sand dune vegetation is a key driver of plant
645 biodiversity in these most dynamic of ecosystems (Green and Miller, 2019). What is less
646 clear however, is how ACC-linked shifts in storm intensity and return times disrupt
647 recruitment processes that have evolved in response to environmental dynamics typical of
648 pre-industrial times (Hanley *et al.*, 2014; Imbert 2018).

649 Some experiments have focused on the effect of elevated salinity on flowering and
650 reproduction, but all too often consider only long-term, chronic effects (e.g. Van Zandt and
651 Mopper, 2002; Pathikonda *et al.*, 2010; Rajaniemi and Barrett, 2018). Nonetheless, these
652 studies are important as they show; (a) responses may only become apparent long after
653 exposure (Van Zandt and Mopper, 2002), (b) reduced sexual reproduction was not
654 compensated by vegetative reproduction (Pathikonda *et al.*, 2010), and (c) germination
655 potential is species-specific (Rajaniemi and Barrett, 2018). Many fewer authors report the
656 impact of acute seawater flooding on the reproductive potential of coastal plants, but those
657 that do evidence reduced flowering (White *et al.*, 2014; Hanley *et al.*, 2020a), and
658 reproductive output (Hanley *et al.*, 2020b). A critical element of the latter study was that
659 the growth of seedlings cultivated from parent plants subject to acute seawater immersion
660 declined; i.e. while the parent plant might survive long enough to reproduce, longer-term

661 regeneration potential is compromised. The importance of changes in wave action on the
662 dynamic sediment environment in saltmarsh regeneration may be better understood
663 (Boauma *et al.*, 2016; Cao *et al.*, 2018), but there is a need to elucidate the effects of all
664 manifestations of storm damage and flooding on plant reproductive and recruitment
665 potential, including storm-driven dispersal.

666 **Research Priority II –*Coastal plant responses to multiple-stressors associated with SLR***
667 ***and storm damage***

668 Teasing apart the interactive effects of saltwater flooding, mechanical damage, litter
669 accumulation, and sediment shift on the plant community is challenging, a problem made
670 all the more difficult simply because so few studies (outside the SE USA at least) have
671 systematically examined how these different factors affect and shape plant community
672 responses in isolation, let alone combination. Using remote imaging, Hauser *et al.*, (2015)
673 report how saline inundation following Hurricane Sandy caused widespread wetland
674 degradation in New Jersey, first by marsh dieback, and as a consequence, subsequent
675 sediment erosion and retreat of the marsh inland. They also note the importance of plant
676 community composition in this interaction; woody plants being more tolerant than
677 herbaceous vegetation. Using an experimental approach, Tate and Battaglia (2013)
678 considered the combined effects of seawater flooding and litter deposition. The application
679 of locally sourced litter (degraded stems of black needlerush - *Juncus roemerianus*) to four
680 plant communities along a Floridian estuarine gradient (brackish marsh, freshwater marsh,
681 wetland forest, and pine savanna) had a profound negative effect on plant survival and
682 species richness in all communities. In tandem with controlled seawater flooding however,

683 litter had a major impact on species composition in pine savannah, as salt-tolerant species
684 capable of vegetative regrowth through dense detritus were the only species to persist. Tate
685 and Battaglia (2013) also noted how vegetation in habitats with higher ambient sediment
686 salinity was more resilient to the combined effects of flooding and litter deposition.

687 These studies (see also Imbert, 2018; Kendrick *et al.*, 2019) signpost the importance of
688 interactive factors on the recovery of ECEs following storm and other ACC-linked
689 disturbance events. Given the logistical issues associated with simultaneous replication or
690 observation of multiple-stressors, it is unreasonable to expect a flurry of research focused
691 on the interactive impacts of various storm disturbances on ECEs. Moreover, one could
692 also argue that a true picture of coastal plant response needs also to consider eCO₂ and
693 shifts in temperature and precipitation (Parmesan and Hanley, 2015). Indeed, Huang *et al.*,
694 (2018) argued that an increase in night-time temperatures had facilitated the expansion of
695 the shrub *Morella cerifera* into Virginian coastal grasslands with likely concomitant
696 impacts on erosion regimes. Although by definition, unpicking the simultaneous interplay
697 of several ACC-linked stressors is complex, as a first step studies could examine the
698 responses of the same species to different stressors in isolation, and elucidate how at least
699 two factors conspire to affect plant performance.

700 **Research Priority III –*Plant community interactions and post-disturbance recovery***

701 Although it is well known that environmental perturbations (e.g. fire, herbivory, etc.),
702 mediate plant community interactions, beyond a reasonable understanding of the role of
703 tropical cyclones in forest dynamics (Hogan *et al.*, 2016; but see Pruitt *et al.*, 2019), the

704 impact of storms and SLR on plant-plant, plant-animal, and plant-microbial interactions in
705 ECEs is poorly resolved. We have discussed already how species-specific variation in plant
706 response to storms might act as a selective filter, removing susceptible species from the
707 recovering plant community. This is why field and multi-species (microcosm) greenhouse
708 experiments are invaluable; as shown by Hanley *et al.*, (2017) and Edge *et al.*, (2020), it is
709 by no means certain that plant species responses in monoculture are replicated in mixed
710 assemblages. Nonetheless, these kinds of study are rare and yet required to disentangle how
711 plant-plant interactions vary in response to a variety of storm-related impacts.

712 It is also worth stressing, that community interactions go beyond shifts in plant competitive
713 hierarchies. For example, although Camprubi *et al.*, (2012) report how three of six
714 Mediterranean sand dune species suffered complete mortality within a week of exposure to
715 seawater, the remainder had delayed or greatly reduced mortality when grown in
716 association with the mycorrhizal fungi, *Glomus intradices*. Symbiotic mycorrhizal fungi are
717 well known for their importance to plant health and vigour (Smith and Read, 2008), but in
718 coastal vegetation like sand dunes, the association may be essential for survival (Koske *et*
719 *al.*, 2004). Unfortunately, the vast majority of work on how the plant-mycorrhizal
720 association affects plant response to salinity comes from agricultural systems (Evelin *et al.*,
721 2019) and consequently we know little about how microbial symbionts respond to storm-
722 linked disturbances in ECEs, or how they moderate plant responses in the post-event
723 community.

724 Seawater inundation is also likely to have major effects on the soil physico-chemical
725 environment upon which all organisms depend. A detailed assessment of soil structure and

726 chemistry is beyond the scope of this review, but in addition to reduced aeration, increasing
727 ionic concentrations and exchange capacity likely affect the bioavailability of key mineral
728 nutrients (Kadiri *et al.*, 2012). Saline flooding will affect also soil microbial and
729 invertebrate communities, and consequently, the decomposition and nutrient-cycling
730 services they provide (Sjøgaard *et al.*, 2018; Stagg *et al.*, 2018). Remarkably few studies
731 however, consider the impact of acute flooding on soil biogeochemistry, nor how additional
732 stresses like sediment movement and litter accumulation affect soil dwelling animal and
733 microbial communities and the processes they deliver.

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

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

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

758 The concept and application of coastal flood risk frameworks (CRAF) in coastal
759 management is relatively well developed, but the focus has tended to be on how
760 vulnerability to flooding affects human society rather than ECEs (Hallegatte *et al.*, 2013;
761 Reimann *et al.*, 2018; Viavattene *et al.*, 2018). Nonetheless, there is developing
762 appreciation that CRAF can be used to identify ‘at risk’ ecosystems (especially those that
763 offer some measure of flood protection), or parts of the coastline where flood risk might be
764 mitigated by virtue of the protection afforded by natural vegetation. In one such example,
765 Christie *et al.* (2018) use the CRAF approach to pinpoint ‘hot spot’ sections of the North
766 Norfolk (England) coast at greatest flood risk, and identify likely direct and indirect
767 impacts based on an understanding of local geomorphology and hydrodynamic forcing
768 during floods. Of particular note in this study is the finding that flood impact could be

769 reduced by saltmarsh; i.e. CRAF allows us to identify one of the key ecosystem services
770 provided by coastal vegetation (see also Torresan *et al.*, 2012).

771 Another modelling approach, more familiar to plant biologists and ecologists, are species
772 distribution models (SDMs). These have been widely used to predict how the geographical
773 distribution of plant populations will respond to ACC-linked changes in precipitation and
774 temperature (see Mairal *et al.*, 2018; Rodríguez-Rodríguez *et al.*, 2019). As noted already
775 however, the combination of SLR with additional climate-change drivers is a unique, but
776 largely ignored, issue for ECEs. Nonetheless, Garner *et al.* (2015) attempt some
777 comparative synthesis, using SDM for Californian coastal plant species. They predict that
778 by the end of this century, SLR alone threatens 60 of the 88 species considered and that 10
779 could completely lose their existing habitat range (due to flooding and erosion) within the
780 (24,000km²) study region. This compares with only four species where shifts in
781 temperature and precipitation alone eliminate all currently suitable habitats. Indeed, unlike
782 plants threatened by SLR, some species may even gain suitable habitat space under likely
783 temperature and precipitation scenarios. Garner *et al.* (2015) stress however, that in order to
784 develop robust predictive models for coastal species, a much better mechanistic
785 understanding of vegetation responses to SLR, flooding and climate scenarios is needed.

786 One way to achieve that aim is by undertaking long-term monitoring of threatened ECEs.
787 This allows us to ‘ground truth’ predictive models by ‘back casting’ how recent
788 environmental changes have actually influenced plant communities. By virtue of access to
789 the Carolina Vegetation Survey, Ury *et al.*, (2020) were able to monitor changes in coastal
790 forest communities over the past two decades. They report how the growth of tree species

791 like *Acer rubrum*, *Juniperus virginiana*, *Pinus serotina*, *Taxodium distichum* and various
792 *Quercus* species was considerably reduced in low elevation sites where high soil salt
793 content evidenced recent increased seawater seepage. In so doing, it is then possible to
794 track how chronic saltwater intrusion has influenced tree growth and shifts in community
795 composition over a 7-13 year time scale, exactly the kind of data needed to validate
796 predictive models and understand how vulnerable ECEs respond to SLR, and changing
797 storm frequencies and intensities. Long-term ecological surveys are time consuming and
798 labour intensive, and for large coastlines therefore, impractical over the decadal timeframes
799 in which we expect significant geomorphological and ecological changes to occur.
800 Nonetheless, the use of remote sensing techniques in combination with localised ‘ground-
801 truthing’ (see Stagg *et al.*, 2020) offers an effective combination to monitor and predict
802 coastal change. The fact that both Stagg *et al.*, (2020) and Ury *et al.* (2020) highlight how
803 the ability of coastal forests to deliver key ecosystem services is likely compromised by
804 seawater inundation presents the most compelling reason to undertake long-term
805 monitoring and predictive modelling studies into the future.

806 *Conclusions - ECEs in Perspective*

807 The threats posed by the myriad factors associated with ACC and changing storm patterns
808 are worthy of considerable attention, not only from the many geomorphologists,
809 environmental agencies and land managers already concerned with coastal defence, but also
810 from biologists with any interest in plant ecophysiology or community ecology. Beyond
811 any esoteric concern, as sea levels rise and the risk and impact of extreme storms increases,
812 the associated economic repercussions will escalate. Hallegatte *et al.*, (2013) for example,

813 estimated that the costs associated with flooding for the 136 largest coastal cities would
814 increase from US\$6 billion in 2005, to US\$52 billion in 2050. Even under these extreme
815 circumstances, it seems unlikely that taxpayers will willingly subsidize the high cost of
816 protecting every vulnerable urban centre, transport link, or farm, with hard-engineered
817 defences. Given that coastal cities and food production globally are exposed to increasing
818 ACC-driven flood risk, nature-based risk mitigation, employing the conservation,
819 management, or even creation of ECEs with the capacity to track SLR and mitigate storm
820 surges seems ever more desirable. Indeed, the fact that Van Coppenolle & Temmerman
821 (2019) suggest how a cost-effective and dynamic answer (i.e. wetland creation) to the
822 problem of coastal defence can potentially be applied to over a third of the global land area
823 within the influence zone of storm surges, it would seem foolish to ignore the possibility.

824 A better understanding of the response of ECEs to seawater flooding, physical damage,
825 litter accumulation etc., at the levels of individual plant species (ecophysiological),
826 ecosystem (interactions), and landscape (distributions), can be delivered by plant scientists
827 from across our various disciplines. In turn, conservation biologists and ecologists can set
828 to work protecting and enhancing those habitats that deliver coastal defence. Only by so
829 doing can society hope to protect the unique biodiversity of our coastal habitats and the
830 essential ecosystem services they offer us in return.

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- 1343

1344 **Figure Legend**

1345 Figure 1. A summary of the principal research priorities (I – IV) and avenues for future
1346 study needed to understand the response of estuarine and coastal plant communities to the
1347 disturbances associated with extreme storm events. The proposed level and overlap of study
1348 (Individual plant, Ecosystem, and Landscape) for each priority is shown. CRAF - Coastal
1349 Flood Risk Frameworks; SDM – Species Distribution Model

1350

1351

1352 **Table 1** A summary of the principal acute threats and example responses reported for (semi-)natural coastal plant communities
 1353 subject to extreme storm events.

Habitat		Threat	Response	Example studies
Sub-tidal	Kelp-forests	Physical damage & dislodgment	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.	Sachithanandam <i>et al.</i> (2014); Culliver <i>et al.</i> (2017)
		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)
		Rapid salinity change	Long-term, post-storm impacts on community composition.	Ridler <i>et al.</i> (2006); Benjamin <i>et al.</i> (1999)
Inter-tidal	Saltmarsh	Physical damage	Stem breakage likely, although response differs among species. Denudation of vegetation can also occur.	Möller <i>et al.</i> (2014); Vuik <i>et al.</i> (2018); Cahoon (2006)
		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); Leonardi <i>et al.</i> , (2016, 2018)
		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)
		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)

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	Mangrove	Physical damage/ Erosion	Species-specific variation in tree response (including mortality) to storm damage.	Doyle <i>et al.</i> (1995); Imbert (2018)
			Scour caused <i>Avicenna marina</i> mortality along South African shoreline fringe.	Steinke and Ward (1989)
		Sand/ Litter deposition	Impact of litter largely unknown (see Krauss and Osland 2020), but increased decomposition influences carbon-budgets.	Barr <i>et al.</i> (2012)
			Phosphorus-rich sediments stimulate post-storm forest productivity.	Castañeda-Moya <i>et al.</i> (2010); Adame <i>et al.</i> (2013)
			Sediments covered roots, causing anoxia and tree mortality	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 localised <i>Pinus elliotii</i> mortality in Florida everglades.	Platt <i>et al.</i> (2000)
	Litter deposition		High litter density reduced species	Tate and Battaglia, (2013);

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			diversity in SE USA pine savannah.	Platt <i>et al.</i> (2015)
		Saline Inundation	Negative effects on recovery of Canadian tundra, but with species-specific variation.	Lantz <i>et al.</i> (2015)
			High mortality of Floridian 'freshwater forest' species.	Langston <i>et al.</i> (2017)

1354

I. Reproduction and recruitment

Manipulative experiments to determine impacts of erosion, litter, sedimentation, inundation, flow & waves on;

- Fecundity
- Germination
- Seedling establishment
- Vegetative spread

II. Multiple stressors

Manipulative experiments to determine ecophysiological responses to ACC-linked stressors

- Temperature (averages & extremes)
- Precipitation
- Flooding
- Litter
- Elevated CO₂

III. Community Interactions

Manipulative experiments to elucidate how storms influence post-disturbance;

- Plant competition & facilitation
- Plant-animal interactions
- Plant-microbial interactions
- Soil biogeochemistry

IV. Storm prediction and ecosystem services

Long-term ecological (including remote sensing) monitoring to generate predictive models underpinned by priorities I-III.

- Geomorphological processes
- CRAF
- SDMs

Individual plant

Landscape

Ecosystem