

Are all intertidal wetlands naturally created equal? Bottlenecks, thresholds and knowledge gaps to mangrove and saltmarsh ecosystems

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ABSTRACT

Intertidal wetlands such as saltmarshes and mangroves provide numerous important ecological functions, though they are in rapid and global decline. To better conserve and restore these wetland ecosystems, we need an understanding of the fundamental natural bottlenecks and thresholds to their establishment and long-term ecological maintenance. Despite inhabiting similar intertidal positions, the biological traits of these systems differ markedly in structure, phenology, life history, phylogeny and dispersal, suggesting large differences in biophysical interactions. By providing the first systematic comparison between saltmarshes and mangroves, we unravel how the interplay between species-specific life-history traits, biophysical interactions and biogeomorphological feedback processes determine where, when and what wetland can establish, the thresholds to long-term ecosystem stability, and constraints to genetic connectivity between intertidal wetland populations at the landscape level. To understand these process interactions, research into the constraints to wetland development, and biological adaptations to overcome these critical bottlenecks and thresholds requires a truly interdisciplinary approach.

Key words: colonization, dispersal, establishment, gene flow, life history, propagule, restoration, salt marsh, sea level rise.

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I. INTRODUCTION

Coastal wetlands, specifically arctic to temperate saltmarshes and subtropical/tropical mangroves, provide numerous ecosystem services (reviewed by Zedler & Kercher, 2005). However, coastal wetlands are suffering severe and long-term global degradation due to land conversion and altered hydrodynamic and sediment conditions, and will be further lost throughout the 21st Century (e.g. Duke *et al.*, 2007). Accelerated sea level rise (SLR) poses a serious threat of ‘ecological drowning’, as a rising tidal frame increases the physical parameters of inundation frequency and period above a threshold of species-specific vegetation tolerance. SLR is a particular threat for systems that are unable to keep their relative position in the tidal frame by landward migration to higher elevations due to topographical or physical barriers (such as sea defences), suffer reduced accretion due to sediment starvation, or are unable to adjust through other shallow-surface mechanisms to keep pace vertically with SLR (Cahoon *et al.*, 2006). In conjunction with anthropogenic pressures, a 1 m rise in relative sea level could threaten as much as 70% of the world’s coastal wetlands (Nicholls, 2004). To maintain, restore and create new coastal wetlands in the coming decades, it is essential to identify critical physical, biogeomorphological and ecological bottlenecks and thresholds that govern their establishment, development and long-term ecological functioning, and to understand how these constraints may be affected by future SLR.

Bottlenecks and thresholds are important features in ecological system dynamics. Bottlenecks are a constraint on system success due to a limited number of components, individuals or resources, such as poor propagule availability (Simberloff, 2009). By contrast, a threshold corresponds to a limit beyond which a state change is ensured. Examples of thresholds include overharvesting leading to fisheries collapse (Hutchings, 2000) and nutrient loading in lakes and reservoirs above which eutrophication occurs (Carpenter & Lathrop, 2008). Thresholds are fundamental to alternative stable-state theory, in which a threshold is surpassed for state changes to occur in order to establish a new steady state multiple times (see Scheffer *et al.*, 2001). Recent studies suggest that coastal vegetation may conform to alternative stable-state theory by surpassing seedling biomass or density thresholds to enhance seedling survival and facilitate later ecosystem success (Bos & van Katwijk, 2007, van Wesenbeeck *et al.*, 2008).

As saltmarsh and mangroves both inhabit dynamic intertidal environments, our understanding of bottlenecks and thresholds is complicated by the many biophysical interactions between water and vegetation, and

biogeomorphological feedback processes *via* surface elevation movement, sediment accretion and erosion. The two ecosystems have widely differing plant growth forms; saltmarshes are dominated by herbaceous vegetation such as forbs and clonally growing graminoids (Allen, 2000), while the mangrove ecosystem is characterised by trees with a limited herbaceous understorey in undisturbed systems (Snedaker & Lahmann, 1988; Ellison & Farnsworth, 2001). However, both ecosystems exist in comparable physical settings (low-energy intertidal areas), despite such vegetative differences. To what extent are critical bottlenecks and thresholds similar in saltmarshes and mangroves? Have similar vegetative mechanisms evolved to overcome the physical and ecological constraints imposed by their comparably physically harsh coastal locations? Furthermore, what are the facilitative relationships between saltmarsh and mangrove vegetation in regions where both ecosystems adjoin and interact in the intertidal zone? These questions apply to all stages of wetland system evolution, from early establishment to long-term ecosystem maintenance.

Ecological interactions, facilitation by fauna, ecosystem services, growth optima and physical processes have been discussed extensively in previous reviews of the saltmarsh (ecosystem processes: Odum, 1988; marsh ecology: Adam, 1990; Saintilan, 2009*b*; morphodynamics: Allen, 2000) and mangrove literature (botany: Tomlinson, 1986; seedling establishment: Krauss *et al.*, 2008; faunal disturbance: Lindquist *et al.*, 2009; energetics: Alongi, 2009; morphodynamics: Woodroffe & Davies, 2009). However, there has been surprisingly little comparative review of the key points in mudflat colonization and later ecosystem development of saltmarshes and mangroves. Such a review requires an interdisciplinary view of both physical and ecological bottlenecks and thresholds to wetland success.

In this review we pursue four objectives: (i) identify the dominant biological bottlenecks and physical thresholds that govern vegetation establishment, development and long-term ecological maintenance of saltmarshes and mangroves; (ii) explore to what extent bottlenecks and thresholds are defined by differences in organism traits of both wetland ecosystems; (iii) highlight the role of hydrodynamics in governing similar or differential ecosystem success between these systems; and (iv) discuss how ecosystem-specific adaptations to bottlenecks and thresholds play a role in facilitation between saltmarsh and mangrove ecosystems, at latitudes where both coastal wetland ecosystems overlap. This review allows us to identify the critical questions that need to be resolved in order to progress management and restoration of these valuable coastal ecosystems.

II. THE CURRENT DISTRIBUTION OF MANGROVES AND SALTMARSHES

When considering constraints to intertidal wetland establishment and stability, it is pertinent first to consider the constraints that delimit the global distribution of such ecosystems. It is also important to highlight regions where these ecosystems overlap, and where subsequent inter-system facilitation or competition may affect adaptation to a bottleneck or threshold.

Mangrove distribution is constrained primarily by latitude, temperature, and to a lesser extent, aridity (Patterson, McKee & Mendelsohn, 1997; Saintilan, Rogers & McKee, 2009; Spalding, Kainuma & Collins, 2010). Mangroves are found in tropical and subtropical regions; Duke, Ball & Ellison (1998a) described the relationship between the 20°C winter seawater isotherm and the biogeographical limit of mangrove distribution (with the exception of mangroves in Australia and the east coast of South America due to localised warm-water currents). Whilst there is great uncertainty inherent in figures of large-scale mangrove extent (Friess & Webb, 2011), recent figures report global mangrove cover up to 137 000–150 000 km² (Spalding *et al.*, 2010; Giri *et al.*, 2011).

By contrast, saltmarshes occur predominantly in arctic through to temperate regions [see Adam (1990) for a latitudinal classification of saltmarsh communities]. Saltmarshes appear to be less constrained by climate compared to mangroves, being also found in the subtropics and tropics in localised areas where mangrove development is precluded, or as a component of a saltmarsh-mangrove ecotone (Adam, 1990). Information regarding the global distribution and extent of saltmarsh is poor (Saintilan *et al.*, 2009), especially outside temperate regions. Extensive, species-poor saltmarsh exists in tropical Northern Australia (Bridgewater & Cresswell, 1999; Saintilan, 2009a), dominated by species such as the grass *Sporobolus virginicus*, and members of the genus *Tecticornia* (Salicornioideae), a succulent plant related to the saltmarsh colonizer genus *Salicornia* in NW Europe. Costa & Davy (1992) describe saltmarsh development in subtropical Latin America. Whilst saltmarsh species in tropical Asia are poorly described, mention of saltmarsh in India can be found (Kathiresan & Rajendran, 2005). Beds of *Salicornia brachiata* are found along the coast of Gujarat, west India, in hyper-saline areas unsuitable for mangroves (Jagtap, Bhosale & Nagle, 2002). *Suaeda* and *Salicornia* spp. can be found in areas of degraded mangrove along the Krishna Delta in east India (Blasco & Aizpuru, 2002). Therefore, traditional maps of coastal wetland distribution probably underestimate the overall area of saltmarsh found in the tropics, leading to the presumption that latitude is the overriding constraint dictating marsh (temperate) *versus* mangrove (subtropical to tropical).

This review focuses on mangroves and saltmarsh from as much of their global distribution as is described in the literature, i.e. it is constrained by the geographical bias of previous research effort. We also discuss (predominantly subtropical) locations where mangroves and saltmarsh overlap at the

edge of their respective biogeographical ranges, especially the Southern US, Australia and New Zealand (Saintilan *et al.*, 2009). These ecotones are composed of the pioneer saltmarsh species *Spartina alterniflora* and the mangroves *Avicennia germinans* and *Laguncularia racemosa* in Louisiana and Florida, USA (Patterson *et al.*, 1997; Stevens, Fox & Montague, 2006; Krauss *et al.*, 2011), and multiple saltmarsh species with *Avicennia marina* in SE Australia (Saintilan & Williams, 1999). The tolerance and life-history factors described throughout this review play a particularly important role at latitudes where both ecosystems overlap and inter-specific interactions may occur.

III. TEMPORAL AND SPATIAL HIERARCHIES IN WETLAND DYNAMICS

To understand the interplay between physical and ecological bottlenecks and thresholds, we must identify the hierarchical scaling relationships that exist among coastal processes. To date, most scaling treatises have focused on morphological and ecological processes (Odum, 1996; Cowell *et al.*, 2003); however, a holistic understanding of coastal wetlands requires the incorporation of other physical processes (Fig. 1).

Hierarchy theory states that behaviour at any one scale results from higher order processes at smaller temporal and spatial scales, and is constrained by lower order processes that operate over longer temporal and spatial scales (Cowell *et al.*, 2003). Thus, changes occurring at a lower hierarchical level (i.e. mangrove stability) affect developments at higher order levels (diaspore availability for establishment). Processes occurring at a smaller scale are often the focus of research, but those processes may not be governed by the same factors at larger scales. For example, point-specific sedimentation is influenced by local water flow patterns and plant structure on m² scales, yet broader sedimentation patterns are related to sediment supply from upland land use, erosional processes and water flows at km² landscape scales. Hydrological manipulations, storms, and SLR are processes that may directly impact the ecological character of intertidal wetlands over all of these time classes (e.g. Kolker *et al.*, 2009). The temporal scale of wetland dynamics is particularly important, as different physical, biogeomorphological and ecological processes act during (i) initial wetland colonization (Section IV), (ii) ecosystem maintenance (Section V), and (iii) long-term reproductive success (Section VI).

IV. BOTTLENECKS AND THRESHOLDS TO WETLAND COLONIZATION AND ESTABLISHMENT

Knowledge of the major mechanisms influencing intertidal vegetation establishment is crucial to understanding plant community organisation and its restoration (McKee, Rooth & Feller, 2007b). Environmental and physiochemical

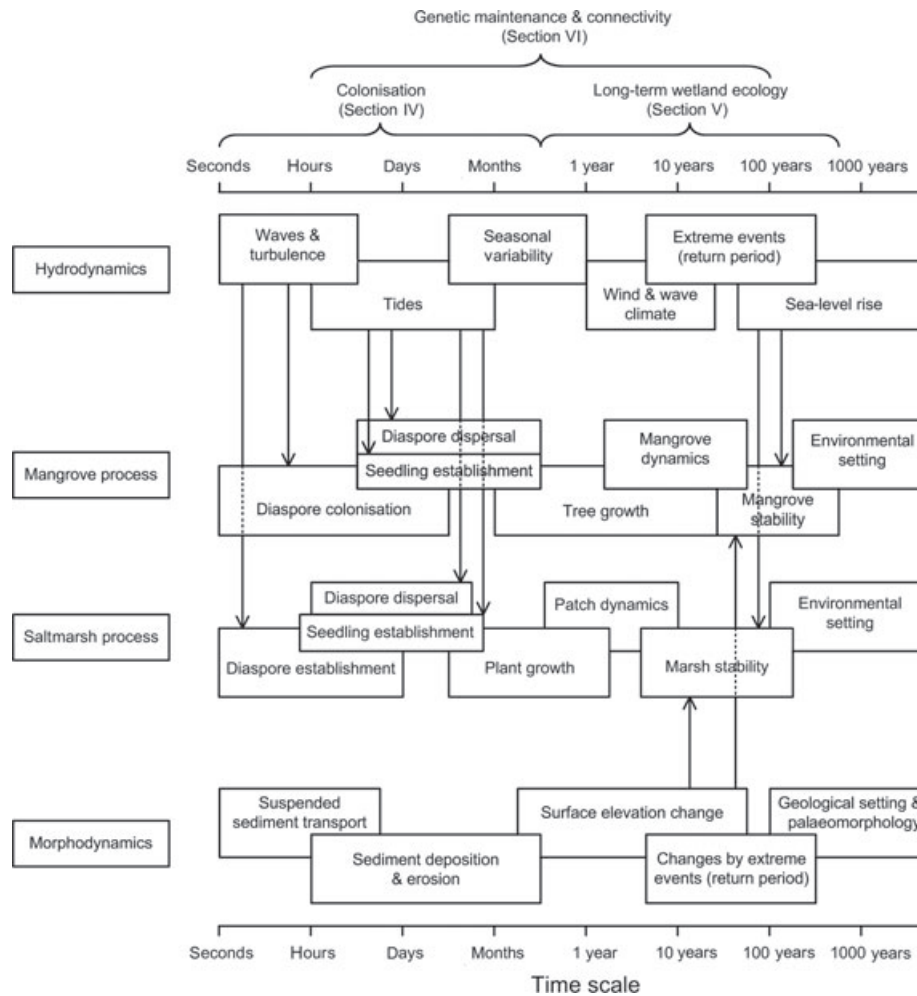


Fig. 1. Temporal scales of mangrove and saltmarsh ecosystem processes, including linkages between physical and ecological processes (arrows). Based on: Brommer & Bochev-van der Burgh (2009), Holling (2001), Stive (2002), Temmerman *et al.* (2007), Twilley (1998) and Van de Koppel *et al.* (2005).

constraints to colonization have been reviewed previously (e.g. salinity, light and nutrient controls on mangrove colonization by Krauss *et al.*, 2008). The following sections describe the main pioneer genera in saltmarshes and mangroves (Section IV.1), and focus on the pioneer traits that are essential to overcoming the two greatest constraints to intertidal wetland colonization, namely diaspore availability (Section IV.2) and hydrodynamic forcing (Section IV.3). We further discuss hydrodynamics in terms of tidal inundation thresholds at the site scale, and associated uprooting by hydrodynamic forces at the single-plant scale. Without sufficient diaspore material, and if bare intertidal surfaces are hydrodynamically unsuitable, colonization cannot occur.

(1) Pioneer traits to cope with physically harsh intertidal environments

The physiological adaptations needed to persist in anoxic and tidally inundated soils means that only a few specialized species successfully colonize intertidal mudflats. Temperate

saltmarshes are species-poor [only 45 species are found in saline areas in Britain (Adam, 1990)], with two pioneer genera evolving mechanisms to effectively colonize bare intertidal surfaces (Table 1).

- (1) Species comprising the genus *Salicornia* are annual succulent herbs found throughout NW Europe, the Mediterranean, the Black Sea and the Caspian Sea, the Arabian Gulf (Davy, Bishop & Costa, 2001) and North America, and in the latter are found in disturbed patches free from *Spartina* species (Ellison, 1987). As described previously, the genus *Salicornia* may also be found in subtropical wetlands of India (Jagtap *et al.*, 2002). The closely related chenopod genus *Sarcocornia* is found in southern Australia (Saintilan, 2009b), southern Africa (Steffen, Mucina & Kadereit, 2010) and the east coast of South America (e.g. Alberti *et al.*, 2010). Due to insufficient study, and since these genera along with *Salicornia* are monophyletic (Kadereit, Mucina & Freitag, 2006), it is assumed that those

Table 1. Bio/ecological characteristics of selected saltmarsh and mangrove pioneer species

Species trait	Saltmarsh grasses/herbs			Mangrove trees	
	<i>Spartina</i> spp.	<i>Salicornia</i> spp.	<i>Avicennia</i> spp.	<i>Sonneratia</i> spp.	<i>Laguncularia racemosa</i>
Distribution	USA, NW Europe, China Australia ¹ , South Africa (see text)*	NW Europe, Mediterranean, Black Sea, Caspian Sea, Arabian Gulf, some parts of Atlantic North America ² , India (see text)	SE Asia, Australasia, Africa, neotropics ^{3,**}	SE Asia, Australia, east Africa ³	Florida, Central America, Atlantic South America, W Africa ³
‘Classic’ traits ⁴					
Shade intolerant	Yes	Yes ⁵	Yes ⁶	Yes ⁷	Yes ^{8,9}
Superficial rooting	Yes depending on elevation ¹⁰	Yes, <10–20 cm depth ²	Yes, large lateral spread ^{11,12}	Yes ^{11,12}	No information available
High fecundity (Section IV.2)	Yes (Poaceae)	Presumed	Yes ^{11,12} , most fecund of all mangroves	Yes ^{11,12,13}	Extensive carpets of seedlings ^{11,12}
Dormant seeds, seed bank, no recalcitrancy	Poor (though some) seedbank persistence, ^{14,15,16,17} recalcitrant ¹⁴	Some persistent seedbank, especially compared to other marsh species ^{15,17}	No dormancy, recalcitrant ¹⁹ , no seedbank	No dormancy or seedbank ¹¹	Recalcitrant, no dormancy ¹⁶
Wetland-specific traits					
Halophytic	Yes, though greatest germination in fresh water ¹⁹	Yes, adaptations (e.g. succulence), though greatest germination in fresh water ²⁰	Yes, (salt excretion glands) ^{11,18,21}	Yes ^{21,22}	Yes, can survive in hyper-saline lagoons, salt excretion glands, induced leaf succulence ^{11,21}
Tolerance to regular inundation (Section IV.3)	Characteristic of the lower intertidal zone ²³	Characteristic of the lower intertidal zone ²	Characteristic of the lower intertidal zone ¹¹	Characteristic of the lower intertidal zone ¹¹	Characteristic of the lower intertidal zone, rapid sinking to take advantage of short neap-tide window ¹²
Resistance to hydrodynamic (wave) energy (Section IV.3)	Stiff, but thin and long structure – high forces can be endured ²⁴ , clonal	Succulent—large surface area, short length	Moderate – rapid root growth initiation after stranding (T. Balke, unpublished data)	Can be clonal ¹¹	Greater tolerance than <i>A. germinans</i> ¹²
Seed/fruit dispersal and clonal spread	Hydrochorous, also clonal spread ²⁵	Hydrochorous, short dispersal distance ²	Hydrochorous, cryptoviviparous propagules ¹¹	Hydrochorous, seeds within large fruit, potential for clonal spread ¹¹	Hydrochorous ¹¹

¹Kriwoken & Hedge (2000); ²Davy *et al.* (2001); ³Spalding *et al.* (2010); ⁴defined by Swaine & Whitmore (1988); ⁵Ellison (1987); ⁶Smith (1987); ⁷Smith (1987); ⁸Saenger & Bellan (1995); ⁹Ball (1980); ¹⁰Bertness (1985); ¹¹Tomlinson (1986); ¹²Delgado *et al.* (2001); ¹³Ren *et al.* (2009); ¹⁴Wang *et al.* (2009); ¹⁵Erfanzadeh *et al.* (2010); ¹⁶Farnsworth (2000); ¹⁷Dixon *et al.* (2008); ¹⁸Osborne & Perjak (1997); ¹⁹Mooring *et al.* (1971); ²⁰Ungar (1979); ²¹Parida & Jha (2010); ²²Ball & Pridley (1995); ²³Bouma *et al.* (2009b); ²⁴Bouma *et al.* (2005a); ²⁵Nehring & Hesse (2008).

* *Spartina anglica* hybridised in the UK, introduced to China and Australia.

**The distribution of *Avicennia* extends to the neotropics, though may not be found in the pioneer zone.

species of the genera *Sarcocornia* and *Tecticornia* with a life history and morphology analogous to *Salicornia* spp. act similarly during colonization.

- (2) *Spartina* spp. are perennial grasses that colonize bare intertidal mudflats throughout the temperate zone, in regions as disparate as NW Europe, SW Mediterranean (Castellanos *et al.*, 1998), the Gulf and east coasts of the United States (Bertness, 1985; Travis & Grace, 2010), South Africa (Lubke *et al.*, 1997), Australia (Kriwoken & Hedge, 2000) and China (Ren *et al.*, 2009). The wide geographical distribution of the genus *Spartina* is due in part to the artificial introduction of *Spartina anglica* to many regions for shore stabilisation purposes. It has subsequently spread and established elsewhere due to its pioneer characteristics of fast growth and the ability to spread both vegetatively and by seed (Nehring & Hesse, 2008). Clonal spreading is likely to explain *Spartina* spp.'s greater resistance to regular tidal inundation and water movement compared to *Salicornia* spp. This mechanism, potentially along with observations of higher root porosity (fraction of root volume occupied by air space) in *Spartina* spp. (Justin & Armstrong, 1987), means that *Spartina* spp. vegetation can often be found lower in the intertidal zone than *Salicornia* spp., where hydrodynamic pressures are greater.

Similarly, mangroves are also species-poor for a tropical ecosystem, consisting of 70 vegetation species or hybrids globally (Duke *et al.*, 1998a). Spalding *et al.* (2010) gives an in-depth overview of the distribution of 65 mangrove species. While many true mangrove species exhibit pioneer-phase characteristics to some extent (Alongi, 2008), we consider the three main mangrove pioneer genera.

- (1) *Avicennia* spp. are well known globally as the first colonizers of many tropical mudflats, with *A. alba* dominating in SE Asia (Thampanya, Vermaat & Duarte, 2002a; Wong, 2005), *A. marina* in east Africa and Australia (Clarke, 1993) and *A. germinans* in the Americas (Perry & Mendelssohn, 2009). Colonization of *Avicennia* spp. in disturbed patches within existing forests is poor, and is dependent upon the demography of shaded patches when developing in an existing understorey (López-Hoffman *et al.*, 2007).
- (2) *Sonneratia* spp. are well-known mangrove pioneers throughout their range (Tomlinson, 1986; Thampanya, Vermaat & Terrados, 2002b; Wong, 2005; Ren *et al.*, 2009), which for *S. alba* stretches from East Africa to the Pacific Island groups of Melanesia and Micronesia (Tomlinson, 1986; Spalding *et al.*, 2010). In SE Asia, *S. alba* may be associated spatially with *Avicennia* spp. in the pioneer zone (Thampanya *et al.*, 2002a), although it can also be found further seaward due to the ability of *Sonneratia* spp. to spread vegetatively in a manner similar to *Spartina* spp., especially on muddy substrata.

- (3) The pioneer *Laguncularia racemosa* is restricted to the neotropics (Florida, the Caribbean and Latin America, and the east coast of South America) and western Africa (Tomlinson, 1986; Spalding *et al.*, 2010). *L. racemosa* most commonly colonizes low-elevation shoals in riverine environments (Delgado *et al.*, 2001), and is often a dominant tree species in young forests (<100 years: Chen & Twilley, 1998) until replacement by more shade-tolerant species.

There is some debate over the role of *Rhizophora* in the lower intertidal zone, specifically in the neotropics, so it is not discussed here in the context of pioneer species. *Rhizophora* spp. are generally considered opportunistic gap species rather than primary colonizers (López-Hoffman *et al.*, 2007). A comparative study of *Laguncularia racemosa*, *Avicennia germinans* and *Rhizophora mangle* by McKee (1995) distinguished *R. mangle* as non-pioneer, and *L. racemosa* and *A. germinans* as pioneers, because the latter two species exhibited classic pioneer traits of partitioning a greater proportion of resources to leaf area and rapid shoot growth.

The wetland pioneer genera *Salicornia*, *Spartina* (saltmarsh), *Avicennia*, *Sonneratia* and *Laguncularia* (mangrove) represent a range of colonization strategies, with each having distinct biotic traits that enable them to establish successfully in physically dynamic coastal environments. Many of these traits are similar to those classically ascribed to the terrestrial pioneer guild (defined by Swaine & Whitmore, 1988), such as high fecundity and rapid stem growth (Table 1). Some traits (specifically tolerance to high salinity and frequent inundation, and high fecundity compared to other intertidal species within the same system) are similar for all the pioneer genera listed, irrespective of wetland system, and are therefore interpreted to be essential for colonization of intertidal mudflats. However, there are some clear morphological differences between pioneer herbaceous marsh and woody mangrove tree species. Diaspore size is often larger in mangroves than saltmarsh plants [small marsh herb/grass seeds *versus* larger (crypto)viviparous mangrove propagules], though contradictory examples can be found. *Spartina* spp. spikelets (groups of seeds) can be up to 21 mm in length (Marchant, 1967), and *Sonneratia* spp. fruits contain a large number of small seeds a few mm in length. There is a further difference in seed dormancy and subsequent soil seedbank presence, which affects species ability to regenerate rapidly after disturbance. Most mangrove species have evolved (crypto)vivipary, where the seed germinates while still attached to the parent tree to allow rapid seedling growth after dispersal; such propagules are recalcitrant and do not persist in the seedbank. By contrast, seeds of *Salicornia* spp. (and to a lesser extent, *Spartina* spp.) show some potential for soil seedbank production (Dixon *et al.*, 2008; Erfanzadeh *et al.*, 2010).

(2) Diaspore availability as an ecological bottleneck

Mudflats are only colonized when sufficient diaspore material is available in the water column to be deposited on a surface that exists within key physical boundaries (see Section IV.3).

Diaspore availability is therefore a potential bottleneck for successful colonization. Ecological characteristics relating to species fecundity and dispersal capacity (see Section VI.2) affect the potential number of recruits to be transported. Saltmarsh community recruitment is based on a larger number of smaller diaspores compared to mangroves due to plant form (chenopods/graminoids *versus* trees). Diaspore numbers produced by the mangroves *Avicennia*, *Sonneratia* and *Laguncularia* spp. are considerably lower than those of saltmarsh pioneers, though still high relative to non-pioneer mangrove species (Tomlinson, 1986).

While fecundity determines the potential number of diaspores available to transport, physical factors dictate the potential route of diaspore transport, and include hydrodynamics, tidal circulation and distance from the nearest diaspore source. Medium/long-distance diaspore dispersal is rare in saltmarsh systems except in extreme weather events (Chang, Veeneklaas & Bakker, 2007), due to species-specific constraints (described in the context of long-term ecosystem maintenance in Section VI.2). While most mangrove propagules are not exported from their source population, there is potential for long-distance transport due to their high buoyancy characteristics. For both ecosystems, diaspore dispersal probability is inversely related to distance from source population, so distance between neighbouring patches is important (Wolters, Garbutt & Bakker, 2005), especially when the neighbouring mudflat is accreting into the appropriate hydrodynamic conditions. Tidal and current patterns dictate how diaspores traverse this distance, determining whether patches act as diaspore sources or sinks.

If a wetland restoration site is far from potential diaspore source populations, location-specific planting may be required to overcome a propagule-availability bottleneck. This is particularly true if species composition must be controlled (Field, 1998) or if rapid vegetation cover is required to reduce erosion (Garbutt *et al.*, 2006). However, many coastal wetland restoration trials have shown that if restoration sites are located close to existing wetlands, diaspore availability is typically not the primary limitation to colonization for both temperate (Garbutt *et al.*, 2006; Elsey-Quirk, Middleton & Proffitt, 2009) and tropical wetlands (Lewis, 2005), if physical site conditions are appropriate.

Thus, diaspore availability is a potentially important bottleneck for the colonization of sites at a distance from propagule source areas, though is not insurmountable, as high fecundity is a consistent marsh/mangrove pioneer trait (Table 1). Therefore, if diaspore availability is not the greatest limiting factor to establishment, more insight is required into the physical process thresholds that influence diaspore, and later seedling loss (Bouma *et al.*, 2009b).

(3) Hydrodynamic forces at the pioneer zone

Energetic hydrodynamic conditions impose multiple stresses on pioneer diaspores during initial colonization, and on seedlings during subsequent establishment, especially (i) repeated tidal inundation, and (ii) drag forces from hydrodynamic energy. Intertidal vegetation establishes in

a zone below a threshold of tidal inundation, associated with surface elevation in both saltmarsh (Adam, 1990) and mangrove ecosystems (Watson, 1928; Smith, 1992). Furthermore, wetland communities will only establish successfully if the hydrodynamic pressures on colonization remain below critical threshold values. While many authors qualitatively discuss the inhibiting role of hydrodynamic action on the large-scale establishment of mangrove pioneer seedlings (Clarke, 1995; Delgado *et al.*, 2001; Huisman & van Langevelde, 2009), little quantitative data exist on such hydrodynamic thresholds (Lewis, 2005). Previous research has focused on growth, productivity, and physiological proficiency of saltmarsh and mangrove species at different hydroperiods (Morris *et al.*, 2002; Krauss *et al.*, 2006, 2008). Here, we focus on how inundation and hydrodynamic forcing influence initial colonization success.

(a) The importance of inundation period in determining system-scale thresholds

Inundation frequency is a function of both intertidal surface elevation (lower surfaces are flooded more frequently than higher areas) and local tidal characteristics. The spring-neap tidal cycle allows a number of days to pass with no inundation, depending on surface height. Krauss *et al.* (2006) state that the positioning of intertidal wetlands marginally above mean sea level means that most natural mangrove forests and saltmarshes are flooded less time per year than they are drained. Hydrographs of mangrove forests in Tampa Bay, Florida (Lewis, 2005) and mangroves and saltmarshes occurring within 4.3 km of each other in Naples, Florida illustrate this point (Fig. 2).

Only basic system-scale inundation thresholds have been described for intertidal wetlands. Watson (1928) described broad inundation classes for a shallow-sloping mangrove under a diurnal tidal regime on the west coast of Peninsular Malaysia, with *Avicennia* and *Sonneratia* species colonising in areas flooded 45–59 times per month. Other mangroves are flooded 30% of the time at sites in Tampa, Florida (Lewis, 2005), 29–53% of the time for sites in southwest Florida (Krauss *et al.*, 2006), and as little as 9% along the Klong Ngao estuary in west Thailand (reported in Lewis, 2005). Similarly, mangrove community establishment at a site in Vietnam was

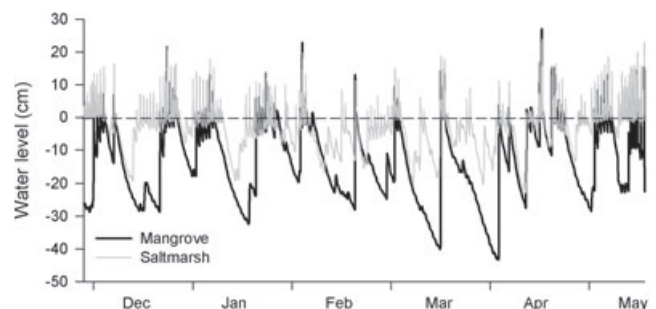


Fig. 2. Mangrove and saltmarsh hydrology relative to soil surface elevation (0 cm) in Ten Thousand Islands National Wildlife Refuge, Naples, Florida, USA.

Table 2. Average inundation thresholds for *Spartina* spp.

Location	<i>Spartina</i> spp.	Submergence at seaward extent (hours year ⁻¹)	Reference
Mariager Fjord, Denmark	<i>S. townsendii</i> and <i>S. anglica</i>	3100	Christiansen & Møller (1983)
Poole Harbour, UK	<i>S. anglica</i>	5800	Ranwell <i>et al.</i> (1964)
Bridgewater Bay, UK	<i>S. anglica</i>	6760	Morley (1973)
Poole Harbour, UK	<i>S. anglica</i>	7372	Reported in Hubbard & Partridge (1981)
Davis Bay, Mississippi, USA	<i>S. alterniflora</i>	7645	Eleuterius & Eleuterius (1979)
Invercargill estuary, New Zealand	<i>S. anglica</i>	7873	Hubbard & Partridge (1981)

not possible in areas inundated for >13 h per day (Van Loon, Dijkema & Van Mensvoort, 2007). Similar to Watson (1928), pioneering work was conducted in British saltmarshes by Wiehe (1935), who recorded a lack of establishment of *Salicornia europaea* in areas of low elevation on a riverine saltmarsh flooded on average >12 h per day. Studies describing the inundation threshold for various *Spartina* spp. are shown in Table 2, with most suggesting that the limit of *Spartina* spp. tolerance is approximately 5800–7800 inundated hours per year. Christiansen & Møller (1983) attribute the reduced inundation tolerance of their studied *Spartina townsendii* and *S. anglica* populations (3100 hours per year) to unusual local tidal dynamics and frost damage adding an additional stressor. By contrast, low water turbidity in the Invercargill estuary, New Zealand permitted sufficient light to penetrate the water column, allowing *Spartina anglica* to establish at lower elevations (Hubbard & Partridge, 1981). These examples suggest that thresholds of inundation period and frequency may be influenced by location-specific factors (Van Loon *et al.*, 2007). So, while statements regarding the broad inundation tolerance of *Spartina* spp. can be made from Table 2, further studies are required to show the impact of differing location and coastal regimes.

Restored wetlands are an experimental opportunity to study the importance of adequate surface elevation for colonization. In NW Europe, saltmarsh has been created by ‘managed realignment’, where sea defences protecting previously reclaimed agricultural land are breached to allow the formation of saltmarsh between the former, and new, more landward defences (Dixon *et al.*, 2008). However, such sites are often lower in elevation than the surrounding intertidal zone due to compaction, organic matter oxidation in reclaimed agricultural soil, surface reprofiling and curtailed sediment input following their original closure to tidal exchange (Crooks *et al.*, 2002; Dixon *et al.*, 2008). Hence, pioneer saltmarsh colonization was often less successful (in terms of percentage vegetation cover) for early trials on old reclamations with the lowest elevations, even though saltmarsh vegetation surrounded the site. Restoration efforts have been most successful at sites with a shorter reclamation history, and therefore high site surface elevation for colonization (Wolters *et al.*, 2005). In some cases, the surface to be restored can be artificially raised to an elevation appropriate for vegetation development; the productivity of marsh macrophytes in a restored site in Louisiana was maximized when sediment slurries were added to the soil surface to bring them

up to mid-high intertidal elevations (Stagg & Mendelssohn, 2010).

Unfortunately, many mangrove restoration projects, especially in SE Asia, have proven unsuccessful because of a mismatch between inundation (surface elevation) and species tolerance. Donor-funded mangrove restoration projects in SE Asia often support large-scale mangrove planting on the fronting low-elevation mudflat, where mangroves either did not previously exist, or because non-pioneer, but commercially attractive species—e.g. *Rhizophora* spp.—were planted in the pioneer zone (Lewis, 2005; Samson & Rollin, 2008). Thus, knowledge (and acknowledgment) of the correct surface elevation and its control on hydroperiod and water depth is one of the most important factors determining the success of mangrove restoration (Lewis, 2005; Gilman & Ellison, 2007).

(b) Wave and current thresholds to single-plant scale establishment

Single-plant establishment requires significantly longer than the average period free from inundation over a lunar tidal cycle, so the emerging seedling can develop sufficient root anchoring to withstand a threshold drag force by hydrodynamic energy when inundated. Wiehe (1935) showed that 65% of *Salicornia europaea* seedlings established during inundation-free periods of 2–3 days. The mangrove pioneer *Avicennia germinans* requires approximately five days to anchor (Rabinowitz, 1978). As a contrasting example, rooting success of the non-pioneer mangrove *Xylocarpus granatum* is greatest in the upper intertidal zone due to reduced tidal action (Allen, Krauss & Hauff, 2003). Therefore, successful colonization will only occur where the surface elevation is high enough relative to the tidal frame, and the lunar tidal cycle allows for an adequate inundation-free period for seedling rooting, dependent on species-specific characteristics.

Pioneer characteristics such as rapid anchoring and growth enable plants to establish during short periods of calm hydrodynamic conditions or no tidal inundation. While some work has characterised root architecture of saltmarsh (Bouma *et al.*, 2001a, b) and mangrove species (summarised by Tomlinson, 1986) there is a distinct lack of data on early root growth rates. Such a knowledge gap is surprising, given that information on rooting is critical to understanding the success of early establishment.

Post-colonization dislodgement occurs when the drag forces by waves and currents exerted on the seedling exceed

its root anchorage to resist this force. Several wetland pioneer species exhibit rapid root emergence and development, with associated sediment binding and dewatering increasing local soil shear strength around the seedling [shown for *Salicornia* spp. and to a lesser extent, *Spartina* spp. in salt-marshes (Pestrong, 1969), and *Avicennia* and *Sonneratia* spp. in mangroves (Augustinus, 1995)]. After anchoring, seedling survival is dependent on resistance to dislodgement by higher energy events (e.g. spring tides and storms). Dislodgement is well studied for macroalgae and benthic organisms that anchor on subtidal rocky shores (Denny, 1994), but threshold values for saltmarsh and mangrove dislodgement at the single-plant scale are poorly understood. Existing studies tend to be qualitative or comparative. For example, Wiehe (1935) described how *Salicornia europaea* seedlings at lower elevations did not show lower growth rates but were more likely to be dislodged by 'tidal action' compared to individuals at higher elevations. The seedlings of the pioneer genera *Avicennia* and *Sonneratia* are better able to withstand water movement than *Rhizophora* spp. (Thampanya *et al.*, 2002a) because of their below- and above-ground morphologies. Such root morphologies include long star-shaped cable roots (in plan view) extending across the mudflat, and are shared by *Avicennia*, *Sonneratia* (Augustinus, 1995) and *Laguncularia* spp.

While quantitative data on the threshold for dislodgement are scarce, the biological factors that contribute to drag force (and plant adaptations to them) are better understood. The drag force applied by current or wave action to a seedling is proportional to seedling surface area in the water column, which is mitigated by shoot stiffness (Bouma *et al.*, 2005b; Bouma, De Vries & Herman, 2010). Small seedlings with low above-ground biomass and flexible stems experience low drag forces, which increase non-linearly as the plant adds above-ground biomass. Pioneer species have evolved growth form and life-history characteristics to reduce drag force and reduce dislodgement in hydrodynamic environments. *Avicennia marina* seedling stems are flexible compared to terrestrial tree seedlings, owing to the presence of aerenchyma tissue (Ashford & Allaway, 1995), with foliage predominantly at the tip of the seedling. These adaptations allow for significant stem bending and reduced drag, respectively. Herbaceous saltmarsh species such as *Salicornia* spp. have independently evolved the same solution of high stem flexibility. However, for succulent *Salicornia* spp. this adaptation is counterbalanced by a high relative stem height-width ratio compared to long and thin mangrove seedlings, which may increase susceptibility to erosion. Self-scouring due to hydrodynamic energy is often evident around *Salicornia* individuals, especially at the end of the growing season when biomass is highest, and contributes to the dislodgement of established seedlings/yearlings (Jefferies, Davy & Rudmik, 1981; Fig. 3). This interesting biogeomorphological feedback may not play an important role on an ecosystem scale, although it is important for individual mortality, and may aid in seed dispersal. Self-scour is a mechanism that remains poorly studied for coastal vegetation, despite its known importance for riverine vegetation (Bouma *et al.*, 2009a).

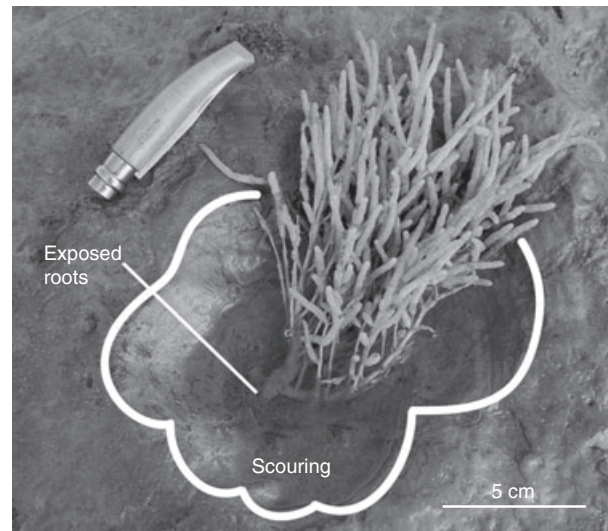


Fig. 3. Self-scouring of *Salicornia europaea*. Photograph by T. Balke.

Whether similar scouring occurs with mangrove seedlings is not known in the literature. Research can be designed to determine whether mangrove seedlings possess a morphology that inhibits self-scouring (e.g. smaller surface area, only one shoot), or whether dislodgement occurs quickly and/or without obvious signs of scouring.

Vegetative propagation is another independently evolved strategy to increase establishment success in hydrodynamically energetic areas that would otherwise limit diaspore anchoring. The hybrid *Spartina anglica* has spread along the coast of NW Europe [and later introduced to areas as disparate as Australia and China (Kriwoken & Hedge, 2000)] since the introduction of the exotic *S. alterniflora* to the UK in the mid 1800s, and its subsequent hybridization with the native species *S. maritima*. *S. anglica* has been a particularly effective invasive species primarily due to its ability to spread vegetatively after initial diaspore introduction, at elevations lower in the tidal frame than many native saltmarsh species can colonize. Vegetative spread allows colonization in areas where diaspore material may otherwise be unable to settle and anchor sufficiently. Despite a vastly different morphology and life-history strategy, the mangrove *Sonneratia alba* has independently evolved vegetative spread, with 37 m long clones of *S. alba* being discovered (Holbrook & Putz, 1982). Similar to *Spartina* spp., *Sonneratia alba* can establish at low elevations along the seaward edge of a mangrove forest (Tomlinson, 1986; Ball & Pidsley, 1995). Vegetative spread by roots at shallow depths means that *Sonneratia* species such as *Sonneratia caseolaris* probably perform better than other mangrove species when colonizing areas with very high sedimentation rates (Thampanya *et al.*, 2002b), and *S. alba* growth has shown to be compromised in eroding environments (Krauss *et al.*, 2007). Vegetative spread is a viable method of establishment for both *Spartina* spp. and *Sonneratia* spp. in areas where inundation period and hydrodynamic forces are above a physical threshold that constrains seed

colonization, or may dislodge established seedlings. Clonal spread may also facilitate later establishment by providing structures that protect seeds and seedlings, and improve the chances of permanent seedling anchoring.

(c) *Facilitation between saltmarshes and mangroves to overcome wave and current thresholds*

Saltmarshes and mangroves have so far been considered independently in terms of their tolerance to hydrodynamic thresholds, in keeping with their generally separate global distribution. However, a saltmarsh-mangrove ecotone is formed over large areas of the tropics and subtropics (Section II). Mangroves and saltmarshes can co-exist as a mosaic or remain spatially separated by inhabiting different zones within an ecotone, depending on broad geographic location and local site conditions, e.g. (i) *Avicennia* spp. along creek banks in estuarine sites, with *Spartina* spp. at lower interior elevations, (ii) *Spartina* and *Juncus* spp. behind mangroves on hypersaline soils, or (iii) the vegetative spread of *Spartina* spp. at lower elevations fronting the mangrove margin (Burns & Ogden, 1985; Patterson *et al.*, 1997; Rogers, Saintilan & Heijnis, 2005b; Saintilan *et al.*, 2009).

In saltmarsh-mangrove ecotones, initial colonization of the lowest intertidal zone by saltmarsh vegetation has an important facilitative impact on mangrove vegetation. Establishment and successional processes in Florida mangroves are often facilitated by the initial colonization of marsh nurse species such as *Spartina alterniflora* (Lewis, 2005). Saltmarsh vegetation acts as a nurse species by two main mechanisms. First, dense saltmarsh vegetation physically traps mangrove propagules (Stevens *et al.*, 2006). Observations and manipulative experiments on a saltmarsh-mangrove ecotone in Belize, Caribbean, showed marsh species *Distichlis spicata* and *Sesuvium portulacastrum* promoting mangrove recolonization by trapping buoyant *Rhizophora mangle*, *Avicennia germinans* and *Laguncularia racemosa* mangrove propagules, whereas mangrove seedlings on bare surfaces were quickly removed by tidal exchange (McKee *et al.*, 2007b). This facilitative mechanism is species specific: *Distichlis spicata* trapped a higher number of mangrove propagules due to its greater vegetation height and stiffer structure. Secondly, saltmarsh vegetation attenuates incoming hydrodynamic energy, providing calmer physical conditions for rooting by mangrove species and structural support to mangrove seedlings requiring upright posture. Furthermore, the short height of saltmarsh vegetation provided structural support (facilitation), while not shading mangrove seedlings (inter-specific competition). Such facilitative interactions are important for mangrove restoration, and it has been suggested that marsh nurse species should be planted alongside mangrove seedlings in sites where hydrodynamic thresholds may be too high for mangrove establishment alone (Lewis, 2005).

There is a (currently undefined) threshold where facilitation of mangrove seedlings by marsh nurse species turns to competition, and mangrove seedling survival is reduced even with preferential fertilization (McKee & Rooth, 2008).

Shrubby saltmarsh species above a certain stem density may exclude mangrove seedlings through shading [for example, species of the saltmarsh chenopod genus *Tecticornia* can exclude *Avicennia marina* seedlings in Australia (Rogers, Wilton & Saintilan, 2006)], or saltmarshes can raise the surface elevation to favour other saltmarsh species (Rogers *et al.*, 2005b; Saintilan *et al.*, 2009). Established mangroves may also exclude saltmarsh seedlings by shading (Kangas & Lugo, 1990).

A discussion of the facilitative role of marsh vegetation for mangrove seedling establishment also begs the question: why do mangroves not facilitate the establishment of saltmarsh plants? McKee *et al.* (2007b) attribute this one-sided relationship to the fact that some marsh nurse species are already better adapted to hydrodynamic constraints due to vegetative spread, while mangroves (with the exception of *Sonneratia* spp.) rely overwhelmingly on propagule production for regeneration. Saltmarsh vegetation also contributes more to facilitation due to the rapid growth of annual/perennial herbaceous vegetation, and its establishment at higher stem densities. Marshes thus buffer wave energy more effectively at shallow water depths, that equate to mangrove seedling height. It is thus biotic adaptations to hydrodynamic thresholds that predispose a species to positively affect the establishment of other vegetation types lacking sufficient biological adaptation. The dominant community type, or the proportion of marsh *versus* mangrove that exists at a particular location is a combination of temporally variable physical factors, the species present and their life-history mechanism.

V. PHYSICAL THRESHOLDS FOR LONG-TERM WETLAND ECOLOGY

Natural intertidal habitats often exhibit broad community zonation [see Watson (1928) for mangroves, Adam (1990) for saltmarshes] once pioneer species have colonized and other wetland species can establish. Zonation is a recurrent feature of intertidal communities, and is a culmination of physical processes such as tidal inundation frequency (described previously, Adam, 1990) and edaphic factors that change along a gradient from seaward to landward. Species positioning in the tidal frame is often determined by (i) continued thresholds to physical processes at their seaward limit, and (ii) competitive ability at their upper range (Pennings & Moore, 2000).

The physical forces constraining intertidal vegetation establishment continue to act once a mudflat has been successfully colonized and as it develops into a stable ecological unit. The scale of biogeomorphological interactions also changes. Whereas short-term processes such as drag forcing at the single-plant scale are most important during early colonization, surface elevation change relative to SLR and feedbacks between vegetation and hydrodynamic forces increase in importance at the ecosystem scale and over the long term. Importantly, these factors do not act in isolation, and the strength of interaction will vary across space.

(1) Accretionary status over the long term

The relationship between surface elevation and vegetation presence crucial to pioneer establishment is not static over the long term. The intertidal surface elevation changes through time by physical processes of tectonic activity, accretion and/or erosion, shallow and deep subsidence, and biogeomorphological interactions of sediment trapping and root zone expansion, while the tidal frame moves due to SLR. Intertidal ecosystems must maintain their relative position in the tidal frame by (i) lateral migration landward to higher elevations (Egler 1952) and/or (ii) vertical substratum adjustment by sediment accumulation and accretion (McKee, Cahoon & Feller, 2007a), or else exceed a threshold beyond which vegetation succumbs to increasing tidal inundation (Fitzgerald *et al.*, 2008) and reverts to pioneer vegetation or bare intertidal surface. Excluding changes in sediment supply, the ecological consequences of SLR are greatest for coastal wetlands in micro-tidal locations where SLR is proportionally larger compared to the tidal frame (Stevenson, Ward & Kearney, 1986; Kirwan & Guntenspergen, 2010), such as Baltic and Mediterranean saltmarshes in Europe and mangroves in the Caribbean, Pacific and Middle East (Alongi, 2008).

In locations where landward system migration is restricted, long-term ecosystem survival is primarily a balance between rates of SLR and positive vertical surface elevation change (Fig. 4). The difference between these rates determines a wetland's 'accretionary' or 'sedimentary' status (French *et al.*, 1995), a threshold determining wetland loss, stability or expansion over the long term.

(a) Physical and biological variables contributing to intertidal surface elevation change

While SLR occurs at the regional-global scale and is completely physical in nature, the variables contributing

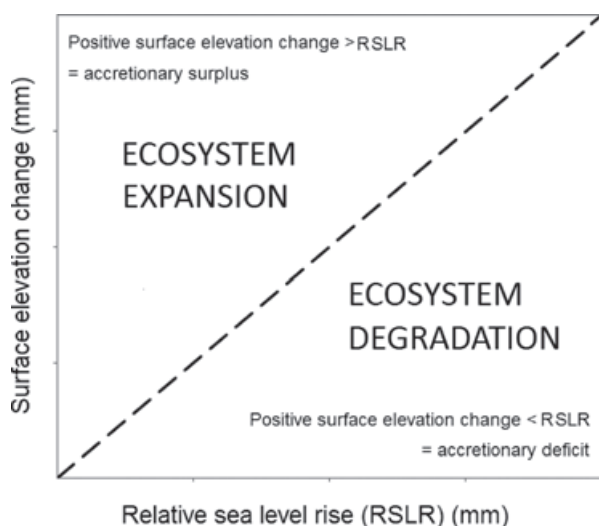


Fig. 4. Conceptual classification of wetland stability by accretionary status. SLR, sea level rise. Modified from Stevenson *et al.* (1986).

to surface elevation change (and hence potential wetland resilience to SLR) are spatially heterogeneous, range from regional to highly site-specific, and are affected by four main tectonic, geomorphological and biological processes:

- (1) Vertical wetland movement operates under boundary conditions imposed by long-term tectonic and deep geological movements. Surface elevation change by deep tectonic processes is due to (a) large-scale isostatic adjustment in response to the last glacial maximum [see Shennan & Horton (2002) for the effect of isostatic adjustment on the coastline of the UK], and (b) low-frequency, high-magnitude tectonic events over smaller spatial scales. The 1964 Alaskan earthquake caused uplift of 1.8 to >3 m along the coast, suddenly shifting areas of saltmarsh above the spring tidal height and significantly changing inundation characteristics (Reimnitz & Marshall, 1965). Similarly, areas of *Rhizophora* spp. mangrove in the Andaman Islands increased significantly in elevation due to tectonic movement after the 2004 Asian tsunami, and are expected to be replaced by terrestrial flora due to their disconnection from tidal inundation (Alongi, 2008). Another (anthropogenic) cause of negative surface elevation change of importance to coastal wetlands is deep, non-tectonic subsidence due to natural resource extraction (The Netherlands: van Wijnen & Bakker, 2001; Mississippi delta: Coleman, Robert & Stone, 1998). This further exacerbates the accretionary deficit experienced by systems such as the Mississippi delta that may already be suffering from the effects of reduced sediment input and SLR.

As per hierarchy theory (Section III), smaller scale sedimentological processes act within boundaries set by larger scale tectonic processes, and are the focus of most study. Surface elevation change within such boundaries is determined by vertical sediment accretion on top of the mud surface (point 2 below), plus below-surface soil expansion (point 3), minus processes contributing to shallow subsidence (point 4).

- (2) Vertical accretion is controlled by long-term sediment availability and accumulation, especially for allochthonous systems. The magnitude of vertical accretion is thus determined by: (a) *Sediment supply*. Sediment supply on a small scale is a function of intertidal surface elevation; lower surfaces are inundated more frequently and experience greater sediment deposition, so show greater accretion over the long term (van Wijnen & Bakker, 2001), if hydrological connections are maintained. On a larger scale, sediment is inputted into the broad coastal system from rivers, cliff erosion or the reworking of offshore sediments (Allen, 2000) and may vary seasonally. Upstream land use and coastal management decisions impact upon sediment availability from these sources. Extensive levee construction and river damming reduces terrestrial sediment input into

the coastal zone, contributing to accretionary deficit for deltas such as the Mississippi (Coleman *et al.*, 1998) and Yangtze (Yang *et al.*, 2006). Short-term, high-magnitude sedimentation events can also contribute significantly to accretionary status. Erosion caused by Hurricane Mitch completely buried some adjoining mangroves with sediment in Honduras (Cahoon *et al.*, 2003), while Hurricane Wilma deposited 42.8 mm of soil at one study site in south Florida (Whelan *et al.*, 2009). In some instances, a single event may introduce an order of magnitude more sediment into a field location than typically deposited in an entire year or longer.

(b) *Sediment trapping and consolidation by vegetation.* Complex above-ground root and stem morphologies can attenuate tidal flow velocity and wave height sufficiently for sediment particles to fall out of suspension, increasing sediment deposition (Morris *et al.*, 2002; Krauss, Allen & Cahoon, 2003; Cahoon *et al.*, 2006). Vegetation also reduces sediment resuspension, as reduced tidal flow velocities do not exceed a threshold bottom shear stress force [especially on the flood tide (Webster & Lemckert, 2002)]. Vegetation-accretion dynamics have been well quantified experimentally: Langlois, Bonis & Bouzillé *et al.* (2003) showed higher accretion on a *Puccinellia maritima* saltmarsh compared to a bare intertidal surface at the same elevation within close proximity. Increases in production and biomass of the saltmarsh species *Spartina alterniflora* in North Carolina, USA has also been shown to increase sediment trapping, thus facilitating surface elevation increase (Morris *et al.*, 2002). The degree of hydrodynamic attenuation (and hence sediment deposition) varies with vegetation structure and density; for example, *Rhizophora* spp. prop roots caused greater sediment deposition, and ultimately accretion compared to pencil-shaped pneumatophores in a Micronesian (*Sonneratia alba*: Krauss *et al.*, 2003) and Singaporean mangrove (*Avicennia alba*: D.A. Friess, unpublished data). It is currently unknown whether one ecosystem is more effective at trapping sediment than the other within a saltmarsh-mangrove ecotone. Perry & Mendelssohn (2009) showed that *Avicennia germinans* trees moving into marshes in Louisiana were too young to establish structurally complex root systems to affect sediment deposition significantly more than saltmarsh vegetation. Research is required to compare the relative sediment-trapping efficiency of coexisting mature mangrove and saltmarsh vegetation.

- (3) An ecological component to surface elevation change that has implications for differential responses of marshes and mangroves to SLR is soil expansion due to organic matter accumulation by below-ground productivity (McKee *et al.*, 2007a; Perry & Mendelssohn, 2009). Soil expansion by root biomass and organic matter production has been demonstrated to be an important process in mangroves (Rogers, Saintilan & Cahoon, 2005a), allowing mangroves to adjust over century time scales during periods when SLR (upwards

of 5 mm year⁻¹) far exceeded present-day eustatic rates (McKee *et al.*, 2007a). In many systems such as Caribbean mangroves that are disconnected from fine sediment input, organic below-ground productivity is the main driver of positive elevation change (Cahoon *et al.*, 2006). By contrast, many saltmarsh systems, such as those of NW Europe and Eastern Canada are highly minerogenic (Allen, 2000; Davidson-Arnott *et al.*, 2002), so accumulate proportionally lower levels of soil organic matter. Therefore, under similar conditions of sediment input, minerogenic marshes may be more likely to exhibit accretionary deficits than mangroves or biogenic saltmarsh systems such as those in the Mississippi River delta, USA (Nyman *et al.*, 1993), which exhibit much faster rates of organic matter accumulation. Further comparative research focusing on below-ground productivity between saltmarshes and mangroves is required to inform attempts at modelling subsurface processes underlying medium- to long-term surface elevation change and ecosystem vulnerability of both ecosystems to SLR.

- (4) Surface elevation change also includes negative processes related to soil properties such as shallow subsidence caused by soil autocompaction, dewatering, sediment settling, water table depth and organic matter oxidation (van Wijnen & Bakker, 2001; Cahoon *et al.*, 2006; Rogers *et al.*, 2006; Fitzgerald *et al.*, 2008). Dewatering and sediment compaction can account for a large proportion of negative elevation change in minerogenic systems with high rates of vertical accretion (van Wijnen & Bakker, 2001). Mangroves and biogenic marsh systems, on the other hand, are vulnerable to net subsidence caused by greater organic matter oxidation (Cahoon *et al.*, 2006; McKee *et al.*, 2007a), if rates of soil expansion cannot compensate.

The relative importance of each of the tectonic and biogeomorphological processes described above will differ according to location. Importantly, in areas with high rates of shallow subsidence, measurements that consider only accretion will overestimate the magnitude of positive surface elevation change. Precise data on true surface elevation change are crucial for the accurate determination of accretionary status, which is especially important in assessing potential vulnerability of wetlands to SLR.

(b) *The impact of surface elevation change on saltmarsh-mangrove ecotones: a case study*

We have shown that accretionary status can be affected by ecosystem-specific traits such as sediment trapping and below-ground productivity. Changes in accretionary status can in turn explain observations of dominance shifts within saltmarsh-mangrove ecotones. Coastal wetlands in SE Australia are showing a shift to a mangrove-dominated ecotone, by their landward encroachment onto areas of

saltmarsh (Saintilan & Williams, 1999; Rogers *et al.*, 2005*b*). Indeed, encroachment of *Avicennia marina* has been the leading cause of widespread saltmarsh loss in SE Australia since the 1930–50s (Saintilan & Williams, 2000). While there are a range of variables that could promote mangrove dominance, the main determining factor is assumed to be surface elevation and inundation (Rogers *et al.*, 2006). Areas of minerogenic saltmarsh in Western Port Bay (Rogers *et al.*, 2005*b*) and the broader SE Australia region (Rogers *et al.*, 2006) that exhibited high rates of accretion also experienced high subsidence due to autocompaction, which was not compensated for by below-ground productivity. Net elevation in these locations was either static or decreasing ('accretionary deficit') relative to current and anticipated SLR. Areas experiencing an accretionary deficit were more suitable for *Avicennia marina* establishment (Rogers *et al.*, 2006), potentially due to its higher threshold to inundation compared to the local saltmarsh species. Saltmarsh species such as *Tecticornia* spp. were more competitive in areas experiencing accretionary surplus (Rogers *et al.*, 2005*b*). These observations suggest that in SE Australia, further mangrove encroachment will be aided by future accelerated SLR over the long term (Saintilan *et al.*, 2009).

Surface elevation does not control ecosystem dominance in saltmarsh-mangrove ecotones in other locations in the subtropics, but is species specific. For example, in the Gulf of Mexico the flood-tolerant *Spartina alterniflora* is found at lower elevations than *Avicennia germinans* (Saintilan *et al.*, 2009). Thus, shifts in ecotone composition over time rely on the interplay between surface elevation change and inundation thresholds described in Section IV.3*a*.

(2) Hydrodynamic thresholds in well-established ecosystems

Intertidal vegetation attenuates incoming hydrodynamic energy over an entire system due to friction caused by the accumulation of individual-level drag forces (Möller, 2006 for saltmarshes; Mazda *et al.*, 1997 for mangroves). Established vegetation produces a positive feedback; its very presence reduces incoming hydrodynamic energy, creating calmer hydrodynamic conditions for subsequent plant establishment. Modelling of coastal wetland development shows that such positive feedback ultimately results in self-organizing landscapes (Kirwan & Murray, 2007; Temmerman *et al.*, 2005, 2007). Hydrodynamic attenuation occurs non-linearly (Koch *et al.*, 2009) and at two scales, within and between patches (Fig. 5). At the single-patch scale, drag forces are highest at the edges and are reduced within the patch (Bouma *et al.*, 2010). In a multiple-patch scenario, the fronting patch(es) attenuate a larger proportion of hydrodynamic energy, 'protecting' patches behind. Mid-back-zone wetland species with a potentially lower hydrodynamic threshold compared to pioneer species may be better able to establish in the protected area, so it can be assumed that the modification of hydrodynamic energy is self-sustaining.

The magnitude of hydrodynamic attenuation by vegetation differs according to vegetation type and site-specific

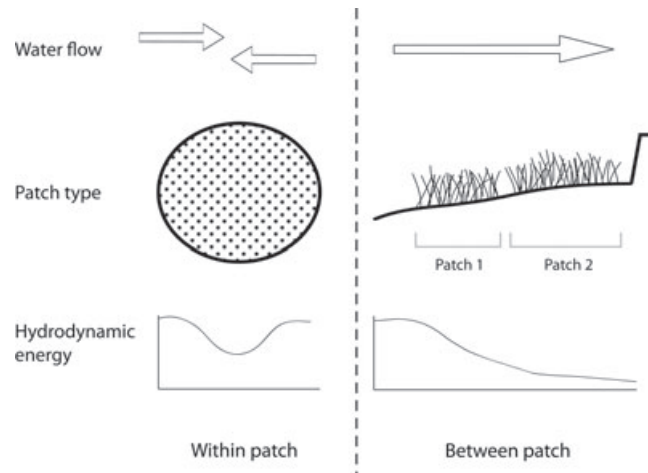


Fig. 5. Hydrodynamic energy attenuation within and between vegetation patches.

vegetation characteristics such as stiffness, density and standing biomass (Bouma *et al.*, 2005*b*, 2010). It is generally acknowledged that tall, stiff and structurally complex mangrove vegetation is capable of attenuating waves of greater heights compared to saltmarsh vegetation (Wolanski, 2007; Koch *et al.*, 2009). The mechanism of wave attenuation by mangroves changes from seaward to landward. In SE Asian mangroves, wave height drops rapidly as short pioneer seedlings of *Avicennia* and *Sonneratia* species absorb incoming hydrodynamic energy due to their complex canopy structures and large surface areas (Quartel *et al.*, 2007). In the back mangrove, the complex aerial root structures of *Rhizophora* spp. further attenuate hydrodynamic energy. The interaction between hydrodynamic energy and vegetation can decrease wave heights from 1 m at the seaward edge to 0.05 m in the back mangrove along a 1.5 km width of mangrove forest (Mazda *et al.*, 1997), or by 9.45 cm km^{-1} of mangrove during a storm surge (Krauss *et al.*, 2009). In contrast to mangroves, short, herbaceous and woody saltmarsh plants tend to be found in higher density stands. The structural characteristics of saltmarsh vegetation thus force sheet flow over the top of the vegetation layer. Within the vegetation, hydrodynamic energy is effectively attenuated. However, a distinct water-level threshold exists, above which vegetation does not interact with water flow, and wave attenuation capacity is decreased (Möller, 2006).

Finally, site-specific characteristics of established intertidal wetlands affect the attenuation of hydrodynamic energy, especially 'normal' waves, as opposed to high-magnitude, low-frequency storm surge or tsunami waves. For example, stem density can vary greatly within a mangrove stand as a function of natural gap dynamics or human-induced disturbances. Modelling efforts have suggested that there is a nonlinear relationship between stem density and wave energy dissipation in mangrove forests (Massel, Furukawa & Brinkman, 1999). This implies that stem-density reduction may have important implications for wave attenuation by degraded mangrove forests. It seems plausible that because

establishment of vegetation is a positive feedback for further establishment and wave attenuation, reductions in stem density may also produce a positive feedback, where loss of vegetation increases erosion (by not sufficiently attenuating wave and current energy below a species-specific threshold), thus underlying a non-linear trajectory towards an accretion deficit. To date, there has been little empirical or modelling research that addresses possible non-linear, positive feedback of vegetation loss on wave attenuation. However, given the widespread degradation of coastal ecosystems globally (Valiela *et al.*, 2009), such research would be critical to wetland protection and restoration efforts.

VI. REPRODUCTIVE BOTTLENECKS TO LONG-TERM ECOSYSTEM MAINTENANCE AND CONNECTIVITY

Once successfully established and maintained, the continued maintenance of single populations, and the further spread of wetland habitats over the long term requires the exchange and dispersal of genetic material within and between populations. Reproductive success and genetic maintenance over long timescales is limited by ecological bottlenecks associated with pollinator availability and diaspore dispersal. Differing pollination and dispersal strategies between saltmarshes and mangroves could cause differential vulnerability to large-scale habitat dynamics such as fragmentation. Within-patch genetic exchange is limited by pollinator availability, while between-patch genetic exchange is limited by patch isolation, which may reduce the flow of pollinators and diaspores.

(1) Pollination as a limitation

Pollen limitation has been demonstrated experimentally in both saltmarsh and mangroves through hand-pollination experiments (Bertness & Shumway, 1992; Coupland, Paling & McGuinness, 2006). Limited evidence suggests that many mangrove species are self-compatible to some degree, although almost all favour outcrossing (Tomlinson, 1986). Adaptations to promote outcrossing include functional protandry/protogyny (where maturation of male and female sexual organs is asynchronous) and maternal regulation (abortion of self-fertilized fruits). Such adaptations are prevalent in genera such as *Avicennia*, *Ceriops*, *Rhizophora* and *Sonneratia* (Tomlinson, 1986; Kathiresan & Bingham, 2001). Equally, a number of saltmarsh species also favour out-crossing, even if self-compatibility is possible (e.g. Bockelmann *et al.*, 2003; Steffen *et al.*, 2010). *Spartina patens* and *S. alterniflora* are protogynous (Bertness & Shumway 1992), as are many *Sarcocornia* (Steffen *et al.*, 2010) and *Salicornia* spp. to varying degrees (Ferguson, 1964). Similarly, *Limonium vulgare* and *L. humile* are protandrous (Boorman, 1967).

A preference for out-crossing requires both systems to rely heavily on pollen movement between individuals. Pollen transport within and among wetlands is a function of the

pollen vector. Saltmarsh species are pollinated by wind and a wide array of invertebrate pollinators, with no species known to be vertebrate-pollinated (Pojar, 1973; Mackay & Whalen, 2009). Mangroves are almost exclusively animal-pollinated; it was once thought that *Rhizophora* had the potential for wind-pollination, but flowers within this genus produce nectar, are linked with invertebrate visitation, and lack a suitable stigma for the reception of wind-borne pollen (Tomlinson, 1986). One would expect similar general constraints to pollen movement within and among populations of insect-pollinated mangrove and saltmarsh species, specifically limitations to invertebrate movement. Other mangrove species are pollinated by vertebrates such as nectarivorous birds (*Bruguiera gymnorrhiza*: Tomlinson, 1986; Noske, 1993) and bats (*Sonneratia* spp.: Coupland *et al.* 2006).

Vulnerability of pollination syndromes—i.e. resistance to negative effects caused by habitat loss or isolation through fragmentation—is strongly dependent on the syndrome employed and the specificity of the pollinator-plant relationship. Saltmarsh species that utilize wind as a primary or alternative pollen vector may at first be thought to be relatively resistant to habitat fragmentation, as wind patterns are somewhat independent of patch distance. However, there is still a maximum distance that pollen can be transported by this vector, dictated by a probability curve; thus, wind-dispersed species can also be pollen-limited, with implications in fragmented landscapes (Koenig & Ashley, 2003). Saltmarsh and mangrove species that have non-specific invertebrate relationships may also be more resistant to the impacts of habitat fragmentation, as they can potentially switch their pollen vector. However, mangrove species pollinated by vertebrates show highly specific plant-pollinator relationships, such as the pollination of *Sonneratia* spp. (especially *Sonneratia alba*) by bats (Tomlinson, 1986) and pollination of *Bruguiera gymnorrhiza* by nectarivorous birds (Noske, 1993). Owing to a smaller pollinator array, it would be plausible to expect that *Sonneratia alba* and *Bruguiera gymnorrhiza* would be more vulnerable than non-specific insect-pollinated species such as *Kandelia candel* (Tomlinson, 1986; Sun, Wong & Lee, 1998) to pollinator-specific population fluctuations. For example, habitat loss may reduce bat populations, leading to reductions in pollination success (Henry, Cosson & Pons, 2007; Meyer *et al.*, 2008). In another example, the introduction of the brown tree snake (*Boiga irregularis*) in Guam resulted in extirpation of nectarivorous bird populations, leading to a collapse in the reproductive output of *Bruguiera gymnorrhiza* (Mortensen, Dupont & Olesen, 2008). However in Singapore, where mangrove habitat declined from 13% to <0.5% of Singapore's land area (Ng & Sivasothi, 1999), populations of two sunbird species (*Nectarinia jugularis* and *N. calcostetha*) and two nectarivorous bat species (*Cynopterus brachyotis* and *Macroglossus minimus*) remain extant and continue to provide pollination services to *Bruguiera* spp. and *Sonneratia alba*, even in highly isolated mangrove populations, as well as outside mangroves (D.A. Friess, E.L. Webb, personal observations). This may be due to two reasons. First, the remaining vertebrate pollinators may be cosmopolitan

and able to tolerate non-mangrove habitat. Secondly, vertebrate pollinators such as birds and bats have longer flight distances than many invertebrates, increasing the potential for long-distance pollen dispersal. For example, the bat *Syconycteris australis* has been tracked moving up to 5.8 km through a fragmented landscape in Australia (Law & Lean, 1999). Large *Pteropus* spp. bats associated with mangrove habitat in SE Asia and Australia have been tracked travelling 12 to more than 61 km over a seven day period across mixed vegetation types, urban areas and open sea (Breed *et al.*, 2010).

In some instances, when vertebrate pollinator populations decline, mangrove species may alter flowering to adapt to an alternative suite of pollinators. For *Sonneratia alba*, reductions in bat populations in Kosrae, Micronesia may have provided greater pollination opportunities by birds (e.g. *Myzomela rubra-tris*); a crepuscular flowering habit by *S. alba* tends to support this observation (James A. Allen, unpublished observations). Pandit & Choudhury's (2001) observations of diurnal flowering and nectar production in *Sonneratia caseolaris*—typically observed to be nocturnally flowering—were explained by an ecotypic adaptation to maintain flexibility in pollinating agents.

If pollen is limited, and pollination rates decline because of changes in pollinator abundances, habitat area or plant populations, then there could be long-term feedbacks on population growth rates. In saltmarshes, pollen limitation was linked to an Allee effect (a positive correlation between population density and population growth rate) in *Spartina alterniflora* (Davis *et al.*, 2004). By contrast, data collected from populations of *Avicennia marina* at its range limit, and compared with core populations in Southeast Asia do not support an Allee effect for mangroves; in fact, it is suggested that inbreeding may be advantageous because of higher probabilities of mating success (Arnaud-Haond *et al.*, 2006). Accordingly, *Avicennia marina* populations at range extremes in Asia are maintaining high levels of genetic structure despite inbreeding. Nevertheless, the Allee effect has been suggested as a possible threat to mangroves where populations occur at low densities, such as *Lumnitzera littorea* at the edges of its range (Su *et al.*, 2007). Low rates of pollen flow at the range extremes for mangroves, where densities are lower, could make mangrove populations more vulnerable to habitat degradation (loss of individuals from the population) than at the centre of its distribution.

(2) Diaspore dormancy and dispersal—what are the implications for habitat fragmentation?

Wetland species are unique in that they utilize water as a medium to disperse diaspores within and between wetlands. Diaspore characteristics differ markedly between saltmarsh and mangrove species, which suggests different dispersal pathways and distances over which genetic material can be exchanged.

Some saltmarsh species exhibit limited dormancy, so a seedbank can aid within-patch marsh renewal (especially of

annuals that do not spread vegetatively). Seedbank composition is determined by existing vegetation composition, seed dormancy characteristics, seed size/mass and rates of seed production (Wang *et al.*, 2009; Erfanzadeh *et al.*, 2010). In contrast to the dormancy strategy of most saltmarsh plants, the majority of true mangroves produce diaspores that undergo continual development (Clarke, Kerrigan & Westphal, 2001) with no strict dormancy phase in viviparous (and many non-viviparous) species (Burns & Ogden, 1985; Tomlinson, 1986; Clarke *et al.*, 2001). Hence, genetic renewal from a dormant store is not possible for mangroves.

To aid within- and especially between-patch dispersal, saltmarsh species (especially Poaceae and Amaranthaceae) produce seeds that are generally small and lightweight, and released annually in large numbers. However, dispersal capability is generally low (Wolters *et al.*, 2005) owing to a short period of buoyancy. Mangroves, on the other hand produce a smaller number of larger and more buoyant (Souza *et al.*, 2007) propagules compared to saltmarsh species (Table 3). Tomlinson (1986) describes particular modifications of the propagule to facilitate flotation, such as a fibrous mesocarp (e.g. *Heritiera*), a cork-like testa (*Xylocarpus*) and aerenchyma (*Rhizophora*). Fine hairs on *Avicennia* propagules may also trap air bubbles. Differences in buoyancy, flotation time and ultimately dispersal efficiency within and among mangrove species are linked to diaspore size and buoyancy. Across the Hawaiian archipelago, *Rhizophora mangle* has colonized a number of islands in this chain since its introduction, but *Bruguiera sexangula* has not spread from the few locations on Oahu where it was introduced in 1922 (Allen, 1998). Dispersal was a bottleneck to *B. sexangula* expansion because it was less buoyant than *R. mangle*, and because it is a back mangrove species and therefore has a lower probability of export than *R. mangle*, which in Hawaii is found throughout the intertidal zone (Allen & Krauss, 2006).

The morphological adaptations of mangrove propagules allow them to disperse better and maintain viability during dispersal [up to several months according to Clarke (1993)] in the water column, and lead to clear qualitative distinctions between saltmarsh and mangrove capacity to disperse to new areas for colonization (see Section IV.2), and to disperse among existing wetland fragments. From Table 3 it is clear that gene flow from diaspore exchange between saltmarsh populations will be constrained to a greater extent than mangroves due to short flotation times, and hence a smaller distance that diaspore material can travel between marsh populations (Erfanzadeh *et al.*, 2009). As a result, saltmarshes develop most rapidly from a local community species pool (Wolters *et al.*, 2008) such as an existing seedbank and/or adjacent marsh, as opposed to mangroves in which site-specific species composition reflects a subset of the regional species pool (Ellison, 2002). Dispersal of saltmarsh seeds by methods other than hydrochory could overcome this constraint to a certain extent; a small proportion of species (such as those belonging to Asteraceae) produce seeds that are dispersed aurally by wind, a dispersal trait not observed

Table 3. Buoyancy and dispersal characteristics of selected saltmarsh and mangrove species

Ecosystem	Species	Flotation time	Reference(s)
Saltmarsh	<i>Spergularia media</i>	1–1.5 h (50% residence time) (max. 7 h)	Koutstaal <i>et al.</i> (1987)
Saltmarsh	<i>Salicornia europaea</i>	1.5–2 h (50% residence time) (max. 24 h)	Koutstaal <i>et al.</i> (1987); Huiskes <i>et al.</i> (1995)
Saltmarsh	<i>Aster tripolium</i>	7–15 days	Huiskes <i>et al.</i> (1995)
Mangrove	<i>Lumnitzera racemosa</i>	<20 days (15 parts per thousand salinity)	Ye <i>et al.</i> (2004)
Saltmarsh	<i>Spartina alterniflora</i>	25 days	Elsey-Quirk <i>et al.</i> (2009)
Mangrove	<i>Avicennia marina</i>	25 days	Clarke (1993)
Saltmarsh	<i>Elymus athericus</i>	10% floating after 30 days	Bockelmann <i>et al.</i> (2003)
Mangrove	<i>Laguncularia racemosa</i>	31 days (median, salt water)	Rabinowitz (1978)
Saltmarsh	<i>Atriplex portulacoides</i>	45 days	Koutstaal <i>et al.</i> (1987)
Mangrove	<i>Xylocarpus granatum</i>	60 days (max.)	Steele (2006)
Mangrove	<i>Bruguiera sexangula</i>	12–63 days (10% floating after 63 days)	Allen & Krauss (2006)
Mangrove	<i>Rhizophora stylosa</i>	75 days (max.)	Steele (2006)
	<i>R. apiculata</i>	15 days average (max. 89 days)	Drexler (2001)
	<i>R. mucronata</i>	53 days average (max. 150 days)	Drexler (2001)
	<i>R. mangle</i>	>80% floating after 63 days (estimated up to 302 days)	Allen & Krauss (2006)
Mangrove	<i>Heritiera littoralis</i>	1 year (max.)	Davis (1940)
		104 days (max.)	Steele (2006)
		150 days (15 parts per thousand salinity)	Ye <i>et al.</i> (2004)

with heavier mangrove propagules. Anecdotal observations suggest that saltmarsh diaspores can adhere to the feet and plumage of saltmarsh waterfowl (Vivian-Smith & Stiles, 1994; Figuerola & Green, 2002), such as the bar-tailed godwit (*Limosa lapponica*), which can travel nearly 12 000 km across the Pacific Ocean, possibly in one flight (Gill *et al.*, 2009). However, there is currently a large knowledge gap relating to the distance that adhered saltmarsh diaspores could travel by such a vector and remain viable. With the exception of humans (*sensu* Fourqurean *et al.*, 2010), the role of animal vectors in the dispersal of mangrove propagules is expected to be minimal.

Saltmarshes and mangroves are naturally disjunct due to natural breaks and barriers such as estuaries, headlands and beaches. Despite this, recent land conversion and subsequent fragmentation of saltmarshes and mangroves raises concern that already disparate, poorly connected (genetically) communities may be further isolated, leading to long-term genetic degradation. However, there is a distinct knowledge gap regarding the implications of dispersal characteristics on gene flow among intertidal wetland populations, and therefore the impact of habitat fragmentation on the long-term genetic maintenance of coastal wetlands. Research addressing this subject requires genetic studies, of which there are currently few. Of these studies in saltmarsh systems, most have concerned gene flow in *Spartina* spp. Incremental ‘stepping stone’ gene flow between patches (within the potential dispersal distance of this species) and low probability of founder effects from geographically spread populations led to low genetic diversity across the species range, such as that observed in *Spartina anglica* populations across France (Baumel, Ainoche & Levasseur, 2001) and *S. alterniflora* in the United States (Travis & Grace, 2010).

Mangroves may also exchange genes in a ‘stepping stone’ manner, as there is still a low probability of extreme long-distance dispersal (Duke *et al.*, 1998b) and the relatively

rare success of founders in establishing new populations leads to genetic erosion (Sun *et al.*, 1998). In contrast to saltmarshes however, mangroves—with greater buoyancy and longer potential seed-dispersal distances (*cf.* Duke, Lo & Sun, 2002)—can potentially exchange genetic material over larger distances, even if this is still considered rare. It can thus be hypothesized that the capacity for longer distance dispersal may reduce the effects of habitat fragmentation on mangroves (meaning that ‘stepping stone’ patches can be spaced further apart) if a sufficient number of mangrove propagules are exported from remaining patches. This, in turn, would be dependent upon local site conditions such as community position (riverine, fringe, overwash), vegetation structure, currents, and population fecundity, as well as transport probabilities between isolated patches.

In summary, both systems appear to have the capacity to maintain genetic connectivity among spatially dispersed populations up to a species-specific distance, determined by diaspore flotation characteristics. Diaspore dispersal is more likely to form a major constraint to genetic exchange in coastal wetlands that are spatially explicit or undergoing habitat fragmentation, if fragmentation increases the distance between populations beyond the capacity of diaspore dispersal. Along with the presence of seedbanks, gene flow between fragments and the introduction of diaspore material to new colonizable intertidal surfaces (Section IV) occurs at a smaller spatial scale in saltmarshes compared to mangroves, and may increase the vulnerability of saltmarshes to fragmentation and population isolation in the long term if key ‘stepping stone’ marsh patches are removed. Hydrodynamic modelling of local-regional current patterns in combination with accurate, standardized data on flotation characteristics would help ecologists determine the potential dispersal kernel, the importance of distance as a constraint to dispersal, and begin to identify locations where wetland habitat restoration is most needed from the perspective of habitat connectivity.

VII. CONCLUSIONS

(1) This review took a comprehensive, interdisciplinary and comparative approach to reviewing colonization, establishment and long-term functioning in saltmarsh and mangrove ecosystems, encompassing a wide temporal scale and both physical and ecological thresholds and bottlenecks. Wetland ecosystem science requires an interdisciplinary approach; physical processes are the overarching control on wetland establishment, although biotic traits greatly influence vegetation establishment and stability below the thresholds of tidal inundation and hydrodynamic energy. Thresholds to wetland ecosystems are mostly physical in nature and crucial during early establishment and for long-term ecosystem persistence in the face of SLR. Bottlenecks often relate to biological traits (e.g. diaspore availability, pollination limitation) that play a crucial role in long-term and large-scale ecosystem functioning.

(2) Physical constraints are broadly similar for both habitats, as saltmarshes and mangroves occupy similar intertidal positions. However, morphological differences between saltmarsh and mangrove pioneers determine thresholds to vegetation establishment, above which an alternative stable state (e.g. mudflat) is reached. Tidal inundation and hydrodynamic forcing are considerable constraints to the establishment of both ecosystems, and saltmarsh and mangrove species have evolved morphological and reproductive mechanisms to cope with these thresholds. Hydrodynamic thresholds also act similarly through time on both systems, with vulnerability to SLR depending on appropriate hydrodynamic conditions for biogenic *versus* minerogenic settings. This has major implications for wetland vulnerability assessment and modelling; it may be unwise to treat mangroves and saltmarsh surface elevation similarly within a SLR vulnerability model, even if they have similar sediment inputs.

(3) The importance of facilitation to overcome constraints to ecosystem success must be considered when examining subtropical and tropical ecotones where both saltmarshes and mangroves intergrade. In many situations, saltmarsh nurse species play a crucial role in the succession of mangroves; the benefit of such interactions should be considered during wetland restoration, where appropriate. However, uncertainty remains regarding the threshold at which facilitative interactions between saltmarsh and mangrove vegetation become competitive.

(4) Major differences between mangroves and saltmarshes are evident in reproductive traits; differences in pollination syndromes and alternative dispersal strategies in particular suggest that mangrove and saltmarsh ecosystems may have differential vulnerabilities to habitat fragmentation. The scope for long-distance saltmarsh diaspore dispersal is limited, so large-scale exchange of genetic material is potentially constrained by distance between saltmarsh populations due to poor diaspore buoyancy and flotation compared to mangrove propagules. Virtually no research exists on this topic, but it is essential to understand the

relative contributions of pollination and diaspore dispersal to gene flow for wetland species.

(5) This review has highlighted some important knowledge gaps that limit our understanding of key processes in tidal wetland establishment and long-term functioning; these gaps undermine current restoration and management efforts. Two key gaps can be identified. First, while the interactions between hydrodynamics and vegetation are understood at the single-plant scale, we have little quantitative knowledge of system-scale hydrodynamic thresholds. What is the critical average current velocity or wave height threshold over a whole intertidal surface that prevents colonization, and how does this change with coastal regime? It is surprising that so little attention has been paid to this area since the pioneering work of Watson (1928) in mangroves and Wiehe (1935) in saltmarshes. Such knowledge will greatly improve wetland restoration success, which fails especially for mangroves because hydrological thresholds are poorly understood (Lewis, 2005). Linked to this, we have little knowledge on aspects of single-plant adaptations to hydrodynamic thresholds, such as rates of rooting for different coastal wetland species. Can we quantify dislodgement thresholds under different coastal regimes? Secondly, more research is needed regarding constraints to gene flow at the landscape level, especially potential and actual seed/propagule dispersal, and the impact of increasing habitat fragmentation and isolation. The combination of accurate landscape-level hydrodynamic data with knowledge of diaspore properties will allow modelling of diaspore dispersal, from which vulnerability to habitat fragmentation can be defined. Such information will help identify species at risk locally and regionally, and support proactive conservation and management.

(6) Against a background of large-scale accelerated SLR, and with coastal wetlands increasingly threatened by anthropogenic forcing, a synthesis of knowledge relating to important physical and biological constraints to the short-term establishment and long-term success of tidal marshes and mangroves will contribute to greater vulnerability assessment, protection and restoration of these important habitats. It is crucial that wetland restoration and protection first focus on establishing and maintaining acceptable hydrodynamic conditions for tidal wetland development, then follow by ensuring habitat connectivity at the landscape level.

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