Exposure mediates transitions between bare and vegetated states in temperate mangrove ecosystems

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ABSTRACT: The resilience of mangroves is dependent on their regeneration capacity. Patchy mid-19th century clearing dramatically affected this capacity, creating stable vegetated and unvegetated states in a fragmented temperate mangrove ecosystem. Mechanisms of mediation between states were tested by monitoring the survival and growth of planted mangrove seedlings and propagules on formerly forested bare mudflats and inside patches of existing forest. Survival (1 to 76 %) and growth (-0.83 to 10.45 mm mo^{-1} increase in plant height) of seedlings was affected by (1) differing levels of exposure found at varying proximities to remnant forest and (2) differing inundation regimes both within and between sites that were randomly selected from locations that varied in aspect relative to prevailing winds. Increases in hydrodynamic energy within and between sites corresponded to a decrease in survival that was much more pronounced at locations that were exposed to prevailing winds. Growth rates were also generally lower at sites in exposed locations, but inundation regime was a more important determinant within sites, where growth was reduced at lower heights on the shore. Results suggest that stability of the bare mudflat state (caused by historical clearance of the mangrove forest) is dependent on level of exposure to hydrodynamic energy, and a return to a forested state is more likely where this exposure is lower. These results have implications for planning and implementing mangrove restoration projects and illustrate the role that physical factors can play in determining the resilience of disturbed temperate mangrove ecosystems.

KEY WORDS: Alternative stable states · Resilience · Temperate mangroves · Restoration · Hydrodynamics · *Avicennia marina*

INTRODUCTION

Mangrove forests are important intertidal ecosystems that have been degraded in many parts of the world, mostly due to coastal development and aquaculture industries, particularly pond aquaculture (Alongi 2002). Global declines of over 1% of the world's mangrove forests annually were recorded between 1980 and 1990 (reducing to 0.66% between 2000 and 2005; FAO 2007). Mangroves provide important habitat for a range of both terrestrial and marine fauna (Hutchings & Saenger 1987), and their loss has severe consequences for some of these spe-

cies, including a number of mangrove-obligate bird species which exist in the mangroves of northern Australia (Kutt 2007). Their value as nursery habitats for commercially harvested fish and shellfish highlights the importance of protecting these ecosystems from further destruction (Hindell & Jenkins 2005, Clough 2013). More recently, mangrove forests have been shown to have great potential for use in climate change mitigation and adaptation strategies (Duarte et al. 2013). Notably, they are very effective carbon sinks (Mcleod et al. 2011) and can provide protection for coastlines that would otherwise be exposed to the erosive forces of coastal storms (Alongi 2008, Feagin

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et al. 2011, Bouma et al. 2014). Additionally, the ability of mangrove forests to trap and retain sediments and nutrients has been shown to benefit adjacent coastal habitats, including seagrass beds and coral reefs (Gillis et al. 2014). Accordingly, restoration of disturbed mangrove ecosystems is likely to be a future focus of governments interested in reducing net carbon emissions and for coastal managers looking to reduce the impacts of coastal erosion and inundation and protect coastal habitats.

Mangrove restoration is common, although notoriously hampered by low success rates (Ellison 2000, Lewis 2005, Primavera & Esteban 2008, Winterwerp et al. 2013). Improved techniques for mangrove restoration are emerging and focus on understanding local mangrove ecology, including regeneration characteristics and hydrologic regime. Factors that restrict natural regeneration can then be manipulated to allow this process to occur without the need for planting mangroves (Lewis 2005). However, in instances where an entire section of mangrove forest has been removed, a suite of factors (which would be self-ameliorated within the forest) can reduce the likelihood of that area returning to forest.

Hydrodynamic forces associated with wind-generated waves and currents and tidal movement formerly attenuated by the forest (Mazda & Wolanski 2009) can become an important factor influencing natural regeneration processes. Hydrodynamic forces can inhibit initial settlement and establishment of propagules by washing them away, uprooting them or undermining them by eroding surrounding sediments (Balke et al. 2011, Van der Stocken et al. 2013). Increased hydrodynamic energy can also erode fine sediments and organic matter that had previously been trapped within mangroves (Bird 1986, Furukawa et al. 1997). The resultant reduction in mudflat height increases the length of time that seedlings are inundated, and this has been linked to negative effects on leaf and stem anatomy in *Avicennia marina* (Xiao et al. 2009). Erosion of sediments which once supported a mangrove forest can also lead to a reduction in nutrient pools and result in reduced productivity of seedlings (Ellis et al. 2004). Further, the loss of associated biota (e.g. crabs) with the removal of mangrove forests can lead to changes in substrate topography, bioturbation and propagule predation rates, which can also positively and negatively influence mangrove forest regeneration (Lee 1998, Minchinton 2001). Changes in microclimate that are important for mangrove survival and growth can also occur with forest removal. While increased light availability can facilitate growth of mangrove

seedlings to the sapling stage (Clarke & Allaway 1993, Osunkoya & Creese 1997), loss of shelter provided by a forest canopy can increase exposure of young seedlings to very hot or cold weather (D'Odorico et al. 2013). The incidence of frosts can greatly limit mangrove productivity at its latitudinal limits (Stuart et al. 2007, Wang et al. 2011).

It therefore seems likely that removal of mangrove forests, with associated physical and biological changes, could push the ecosystem beyond the point from which it can readily recover, resulting in a shift to an alternative stable state (e.g. Beisner et al. 2003). Transitions between alternative stable states are often driven by a combination of external environmental changes and internal feedbacks (Scheffer et al. 2001). In this case, disturbance caused by clearance of the forest along with the resulting overall increase in exposure, large-scale erosion and sedimentation processes are potential external mechanisms driving transition, while localised water and sediment dynamics, changes in biota and microclimate are potential internal feedbacks contributing to the stability of the alternative bare mudflat state. The ongoing existence of a particular stable state is reliant on its resilience, or the amount of disturbance it can absorb before it switches to another stable state (Gunderson 2000). Therefore, the ease of reversing the switch from a stable mangrove forest to a bare mudflat is dependent on how resistant the bare mud flat stable state is to natural regeneration or restoration activities.

This study aimed to examine the resilience of disturbed temperate mangrove forests by investigating how resistant bare mudflats, formerly occupied by a mangrove forest, are to mangrove recolonization and restoration and how this resistance changes in relation to (1) proximity to remnant mangrove forest and (2) inundation duration. Effects of wave energy and associated erosion of sediments on propagule settlement and initial establishment (over a period of days to weeks) were examined by Balke et al. (2011). They found that successful establishment depends on periods of low hydrodynamic energy that prevent new seedlings from being wrenched out of the mud or toppled due to erosion of surrounding sediments. Their study and others that have further developed these findings (Balke et al. 2013a,b) were undertaken by recreating hydrodynamic conditions using flume studies. A field experiment in Pak Phanang Bay, Thailand, using transplanted seedlings within forests showed differing effects related to hydrodynamic energy between forests of different species and densities but did not examine the effects of wave

energy on bare restoration sites and forest fringes (Thampanya et al. 2002). In contrast to earlier work, our study was undertaken in the field using seedlings that were raised in a nursery and planted deeper in the sediment with a well-developed root system and therefore improved survival by avoiding threats at earlier life stages shown in the flume studies. Additionally, the location of our experimental sites on mudflats that had previously been occupied by mangroves allowed us to consider the stability and resilience of potential alternative states found in disturbed mangrove ecosystems of temperate areas. It was expected that successful establishment and growth of seedlings and propagules would decrease with distance to remnant mangrove forests and with shorter inundation duration. It follows that the stability of either bare mudflat state or forested state would also decrease closer to the interface between bare mudflat and mangrove forest, and at this point it becomes easier to reverse the switch to an alternative state through restoration activities.

MATERIALS AND METHODS

The study consisted of planting and monitoring *Avicennia marina* seedlings and propagules in 2 separate experiments at a range of distances within and away from remnant patches of mangroves and at a number of heights on the shore (inundation durations) within their natural tidal extent. Physical factors that are affected by these varying levels of exposure (sediment characteristics, hydrodynamic energy and temperature) were also measured.

Study site

Western Port Bay (38° 12′ to 38° 31′ S) is a large tidal bay located around 70 km southeast of Melbourne, Australia (Fig. 1). The bay covers an area of 680 km^2, which includes approximately 270 km^2 of intertidal mudflats (Marsden et al. 1979). Tides are semidiurnal and range from 1.2 m near the southern entrances to 3.3 m during spring tides at the embayment head in the northeast of the bay (Marsden et al. 1979). The climate is temperate with warm summers and no substantial dry season (Peel et al. 2007). Mean annual rainfall is 665 mm and mean temperature is 18.5°C. Although temperatures are moderated near the bay, extremes occur, and there is an average of 1.5 d yr^{-1} with a maximum temperature greater than 35°C and 1.8 d with minimum temperatures less than 2°C (0.8 d
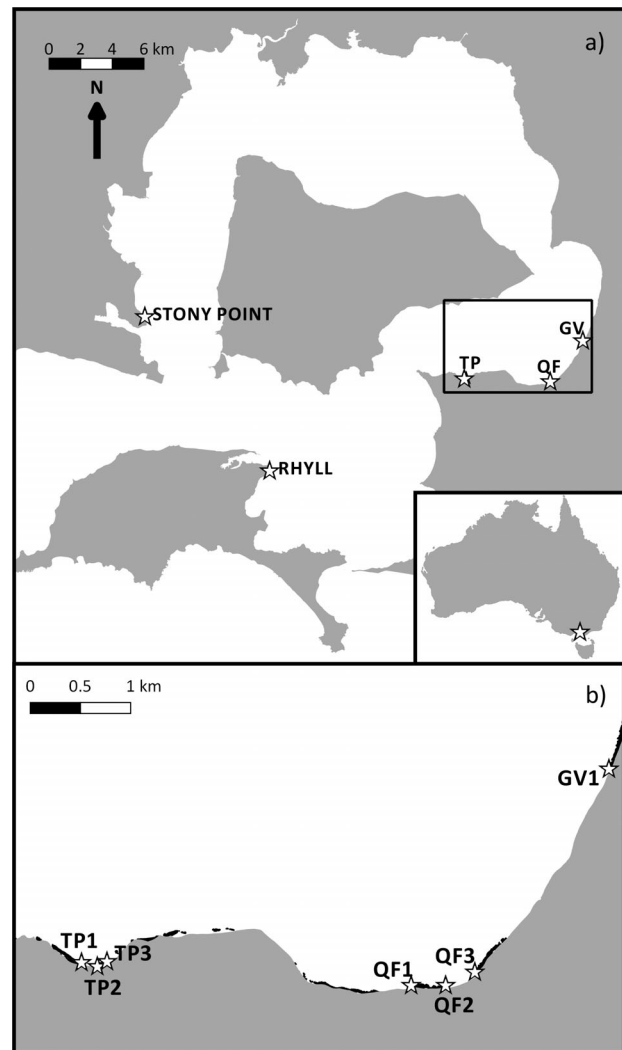

Fig. 1. (a) Western Port Bay, Australia, with experimental locations (TP: Tenby Point, QF: Queensferry, GV: Grantville) shown in the box. (b) Location of 7 experimental sites shown in close-up of boxed area in (a). The local distribution of the mangrove *Avicennia marina* is indicated in black (Boon et al. 2011)

< 0°C) (Bureau of Meteorology: www.bom.gov.au/climate/data/). Sea surface temperatures in the bay range from around 11°C in July/August to 21°C in January/February (Commonwealth Scientific and Industrial Research Organisation, www.cmar.csiro.au/). Salinities in the bay peak at approximately 37 PSU in March and are lowest in September when they can drop just below 35 PSU. Total suspended solids are generally below 10 mg l^{-1} in western parts but can exceed 50 mg l^{-1} in the eastern segments of the bay (Melbourne Water 2011).

In temperate mangrove forests of Australia, mangrove species diversity decreases with increasing lat-

itude (Morrisey et al. 2010). In Western Port Bay, temperate mangrove forests are close to their latitudinal limit of distribution, and *A. marina* (Forsk.) Vierh. var. *australasica* (Walp.) Moldenke is the only species present. A large proportion of the forests are 'fringe' type (Lugo & Snedaker 1974) which grow in bands along shorelines and face open expanses of water. Fringe forests, as opposed to 'riverine' forests located in sinuous tidal waterways, are generally more exposed to wind-generated waves and currents. In some areas, mangrove forests were cleared during colonial settlement in the mid-19th century (Bird 1975) and, according to historical aerial photography, only some of these fragmented forests have regenerated naturally, indicating that the cleared areas may have switched to a stable bare mudflat state. Attempts have been made to replant these areas (to restore habitat and prevent coastal erosion), but these attempts have generally resulted in low survival rates.

Seven sites for this study were randomly selected within 3 locations (Grantville: GV; Queensferry: QF; and Tenby Point: TP) around the fragmented mangrove forests along the eastern shores of the bay (Fig. 1). Topographical cross-sections taken through the intact forest adjacent to the planting sites showed an existing elevation range of approximately 0 to 0.8 m above Australian Height Datum (AHD ≈ mean sea level), and elevations of planting sites were surveyed using an amphibious vehicle to select consistent tidal heights for planting that also corresponded with remnant forests.

Seedling planting experiment

Ripe propagules (i.e. dispersal units) were picked from trees less than 2 km from the experimental sites in early December 2010. Propagules were soaked overnight to remove pericarps and planted individually into 600 ml coated cardboard containers that were half-filled with a 50% commercial potting mix and 50% sand mixture. The containers were stored in a nursery in plastic-lined frames half-filled with water and watered daily with fresh water. Salinity of the water was monitored, and salt was added to maintain the storage solution at approximately 10 PSU (Clarke & Hannon 1970, Farrell & Ashton 1974, Clough 1984). Before planting, salinity was increased to full strength seawater (35 PSU) over 2 wk to acclimatise the seedlings as recommended by Bhat et al. (2004).

In total, 3024 seedlings were planted across all sites in May 2011 at 3 proximities to existing stands of man-

groves (0 m: Close; 40 m: Mid; and 100 m: Far) and at 3 heights on the shore (0.1 m: Low; 0.4 m: Mid; and 0.7 m: High, ± 0.05 m AHD). Heights and positions were located with GPS using coordinates of contours and features derived from the elevational survey and verified by visual assessment of incoming tides. The average percentage of time that each of the heights on shore treatments were inundated was 46.8% at 0.1 m, 35.5% at 0.4 m and 20.9% at 0.7 m, based on 2 yr of tidal data during the experimental period from the nearest tide gauge at Stony Point (Bureau of Meteorology, www.bom.gov.au/climate/data/). At each height-on-shore/proximity combination, 3 replicate plots of 16 seedlings were planted. Seedlings were selected randomly and planted at a density of 1 per m^2 which approximated average natural seedling density determined from an earlier survey of a nearby forest. Elsewhere, planting density has been shown to have little effect on survival and growth of seedlings (Osunkoya & Creese 1997). Seedling height (mean ± SE: 73.31 ± 0.34 mm) and number of leaf pairs (mean 2.08 ± 0.01) of each seedling were recorded before planting, and stem diameter (mean 2.91 ± 0.01 mm) was measured from a subsample of randomly selected seedlings (25%). Individual seedlings were remeasured at 3, 6, 9, 12, 18 and 24 mo after planting. For analysis, data were converted to a growth rate in mm mo^{-1} for height and stem diameter or leaf pairs per month for leaf pairs (G) using Eq. (1), where h_1 and h_2 are the pre- and post-planting measurements of the seedling in mm (or leaf pairs), t_1 is planting month (month 0), and t_2 is monitoring month:

$$G = \frac{(h_2 - h_1)}{t_2 - t_1} \qquad (1)$$

Propagule planting experiment

Based on initial results from the seedling planting experiment and a separate propagule planting pilot, a further experiment investigated seedling survival and growth at a finer spatial scale across the fringe of existing mangroves. Propagules that had shed their pericarps were collected from the ground at the experimental sites in January 2012. Fifteen propagules were directly planted (radicle side down, pushed half into substrate) within a marked 1 m^2 quadrat and covered with a square of coarse wire mesh for 2 mo to keep them from washing out. Three replicate quadrats were established at the boundary between mangrove forest and bare mudflats as well as 5, 15 and 25 m both away from the forest and into the forest along a single height on shore (0.25 ±

0.05 m AHD, visually verified as per seedling planting experiment). This arrangement was repeated at 1 randomly selected site from each location of the seedling planting experiment (GV1, QF1 and TP2). Seedling height, stem diameter and number of leaf pairs were recorded at 3, 9, 15 and 21 mo after planting. In this experiment, individual plants were not successively monitored, and data were pooled from each replicate plot. Growth data were converted to growth rate per month as per the seedling planting experiment using 3 month data as t_1 (see Eq. 1).

Environmental data collection

Estimates of hydrodynamic energy

Weight losses of clod cards (blocks of plaster of Paris) were used as a relative measure of hydrodynamic energy which includes wave energy, tidal and wind-driven currents and inundation (Doty 1971, Porter et al. 2000). Three 250 ml clod card replicates were mounted onto stakes within each height-on-shore/proximity combination for the seedling planting experiment (at sites GV1, QF1 and TP2 only) and for each set of replicates for the propagule planting experiment (all sites). Clod cards were weighed before and after 14 d in the field (24 February to 10 March 2012).

Temperature

Temperature was monitored at the experimental sites over a period of 109 d in 2012 (28 June to 15 October). Temperature data loggers (Onset HOBO Pendant Temperature Data Logger) were deployed at the 3 heights on shore for the Close and Far proximities and also at the same 3 heights 100 m into the forest to determine temperature effects of an intact mangrove canopy. The loggers were deployed at 3 of the 7 experimental sites (GV1, QF1 and TP2) and logged temperature at 5 min intervals.

Sediment

A visual/tactile estimate of sediment grain size (McKenzie 2007) was conducted by hand-sampling surface and sub-surface (10 cm depth, the approximate level of seedling root zone when planted) sediments. Three replicate samples were taken from each height-on-shore/proximity combination at all 7

sites and each set of propagule planting replicates. The method involves estimating the order of abundance of mud, fine sand, sand, coarse sand and gravel. The most dominant constituent is given a score of 3, the next most dominant is given a 2 and the third most dominant is given a 1. This allows a percentage of each grain size to be calculated (e.g. a sample which was mostly sand, followed by mud and then gravel would be called sand-mud-gravel. Sand is given a 3 [50%], mud a 2 [33.3%] and gravel a 1 [16.6%]). The estimated composition allowed sample statistics to be generated (using GRADISTAT; Blott 2010). For comparability with other studies describing mangrove sediments (e.g. Balke et al. 2013a), the resulting median grain size was chosen for analysis. Sediment strength (i.e. surface firmness) in the vertical direction ($kg\ cm^{-2}$) was also measured at each height-on-shore/proximity combination at all 7 sites using a penetrometer.

Wind condition and fetch length

Three years (2011–2013) of wind speed and direction data from Rhyll (Bureau of Meteorology, www.bom.gov.au/climate/data/stations/) were used to derive a 12 angular sector wind rose showing dominant wind directions and speeds. At each location, wind sectors that were angled greater than 15° from the shoreline were used to calculate fetch distance using orthographic images of Western Port Bay and then used to determine average fetch distance.

Data analysis

Data were analysed using mixed-model ANOVAs in Systat (version 13) where site was considered a random factor and all other factors were considered fixed. Assumptions of normality and constant variance were tested *a priori* with Q–Q plots of residuals and scatter plots of residuals versus predicted values, respectively. Data were transformed when these assumptions were not met, and the method of transformation is indicated in plot captions. Post hoc tests for significant factors and interactions were undertaken using Tukey's Honestly Significant Difference test.

Very low survival in some treatments meant that growth rates could not be analysed using a full ANOVA, and therefore growth rates were analysed with a series of partial analyses using data from plots with surviving seedlings (see Table 2).

Table 1. Summary of environmental data collected. Fetch and temperature data were collected for locations (see Fig. 1) only, while sediment characteristics were collected for each experimental site. Values are means ± 1 SE (except for fetch, which is mean only). Sediment grain size data are based on a semi-quantitative estimate as described in the 'Materials and methods'

Location	Fetch Average distance (km)	Temperature			Experimental site	Sediments		
		Average (°C)	Average minimum (°C)	Average maximum (°C)		Grain size (µm) at surface	Grain size (µm) at 10 cm depth	Sediment strength (kg cm^{-2})
Grantville	7.16	12.52 ± 0.11	8.00 ± 0.13	22.28 ± 0.18	GV1	73 ± 4	44 ± 3	0.09 ± 0.003
Queensferry	7.26	12.41 ± 0.11	8.38 ± 0.13	20.95 ± 0.16	QF1	84 ± 14	70 ± 11	0.10 ± 0.004
					QF2	159 ± 21	110 ± 16	0.11 ± 0.007
					QF3	326 ± 9	299 ± 20	0.12 ± 0.004
Tenby Point	5.88	12.52 ± 0.11	8.59 ± 0.12	21.42 ± 0.16	TP1	43 ± 3	26 ± 3	0.11 ± 0.009
					TP2	45 ± 3	122 ± 61	0.11 ± 0.007
					TP3	33 ± 1	21 ± 3	0.20 ± 0.008

RESULTS

Environmental data

Temperature varied very little between locations, whereas sediments did (Table 1). In general, surface and subsurface sediments were finest at the TP location and coarsest at the QF location, with very coarse sediments found at site QF3. Sediment strength was similar at all experimental sites except at site TP3, which was firmer due to hard clay outcrops. Average wind fetch was similar between the QF and GV locations but approximately 20% shorter at the TP location. Analysis of wind data revealed that strong winds can occur from the north, but the most frequent winds are derived from the south through to the northwest (Fig. 2).
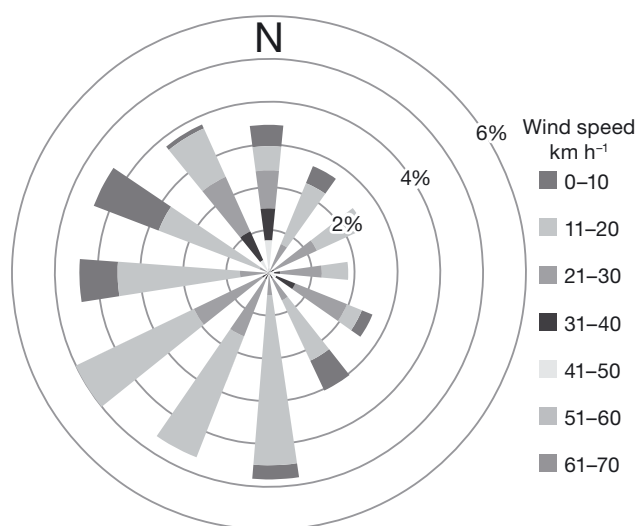

Fig. 2. Average percentage of wind direction and speed at Western Port Bay, Australia, over 3 yr (2011–2013). Wind speeds increase towards the center of the wind rose

Weight loss from clod cards placed at the sites where seedlings were planted displayed significant spatial variability (Fig. 3). Weight loss was progressively greater ($F_{2, 53}$ = 68.86, p = 0.001) lower on the shore (Fig. 3a). This was expected due to longer periods of inundation and therefore exposure to currents and waves. Independent of the effect of elevation, the interaction between location and proximity was also significant ($F_{4, 53}$ = 25.29, p < 0.0005) where substantially less weight loss resulted from clod cards nearest existing stands at TP, a pattern that was significant but less marked at GV and absent at QF (Fig. 3b). Weight loss from clod cards placed with the propagule planting experiment was also affected significantly by an interaction between location and proximity ($F_{12, 42}$ = 7.28, p < 0.0005). Losses increased steadily from 25 m within the forest to the fringe, after which the rate of losses plateaued outside of the forest, with no significant differences between outermost positions between locations (Fig. 3c). The significant interaction between location and position indicates that effect of location on weight loss at each position was inconsistent, largely due to significantly less weight loss at 25 m within the forest at GV. However, the general pattern described above was observed at all locations.

Seedling planting experiment

Due to heavy rain in the months after planting, the majority of seedlings were smothered by sand from creeks near sites QF2 (Mid and Far proximities, all heights) and QF3 (all proximities and heights). These sites were excluded from the survival analyses and most of the growth analyses, as there were too many missing values to successfully undertake an ANOVA.
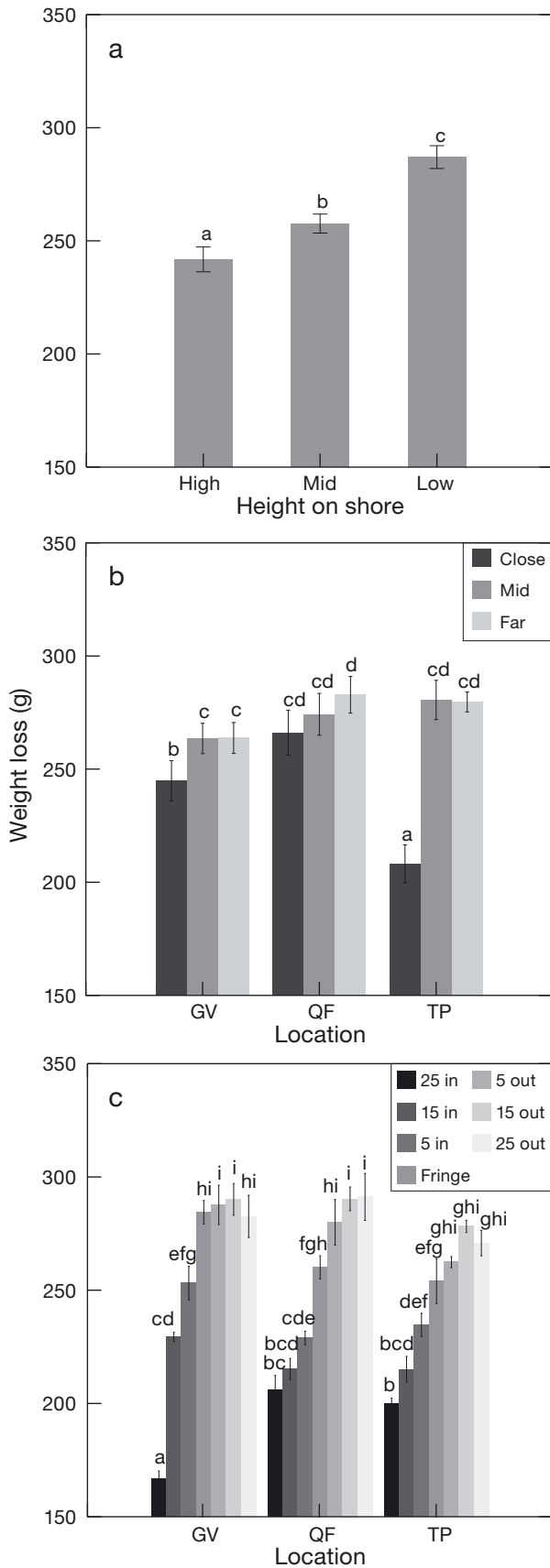
Fig. 3. Weight loss of clod cards after 14 d of deployment. (a) Effect of the height-on-shore treatment and (b) the interaction between location and proximity to the nearest mangrove forest within the seedling planting experiment. (c) Effect of the interaction between location and position (in: within the forest; out: outside of the forest; numbers in the key indicate distance in metres) within the propagule planting experiment. Bars are means (± 1 SE) and those with the same letter are not significantly different (p ≤ 0.05). For sites see Fig. 1

However, the Close proximity treatment at site QF2, which was not affected by sand smothering, was used in some of the partial analyses of growth.

Survival of seedlings

Overall mortality was greatest in the first 6 mo, slowing during the remaining 18 mo of the experiment (Fig. 4a). By the end of the experiment, significantly greater survival near existing stands occurred at some sites, with no clear pattern at others. This is reflected in the significant interaction between proximity and site ($F_{8,90} = 5.12$, p < 0.0005), where the pattern was apparent at the 3 sites within the TP location but absent at sites GV1 and QF1 (Fig. 5a). Spatial variability in the effect of the interaction between site and elevation on survival was also significant ($F_{8,90} = 3.23$, p = 0.003), but with no consistent patterns (Fig. 5b).

Growth rates

Similar to survival, there was substantial spatial variability in growth rates (Table 2). Patterns between sites were broadly consistent with survival rates, with greater growth at locations with high survival. Unlike the survival results, however, proximity was not found to be a significant factor in any of the analyses. In contrast to its effects on survival, height on shore played a much larger part in seedling growth. There was a significantly lower increase in seedling height and number of leaf pairs at the Low treatment (site TP1) and significantly greater growth at the High treatment compared to Mid (sites TP1, TP2 and QF1). Additionally, there was a decrease in number of leaf pairs and stem diameter from High to Low treatments for all sites at Close proximities.
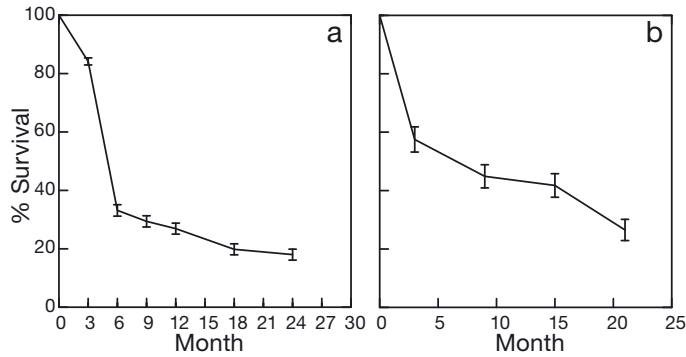
Fig. 4. Survival curves of planted *Avicennia marina* (a) seedlings and (b) propagules showing change in mean % survival (±1 SE) over 24 mo (seedlings) and 21 mo (propagules). Sites QF2 and QF3 were excluded from the data in (a)

Propagule planting experiment

Almost all of the propagules at site GV1 failed to establish because they were buried by drifting sand during the month after they were planted. This site was therefore excluded from the survival and growth analyses of the propagule planting experiment.

Survival

Similar to survival rates from the seedling experiment, survival of *in situ* germinated propagules fell sharply in the first 3 mo (Fig. 4b). Patterns of survival with position relative to forest edge differed between sites ($F_{6,28} = 4.56$, p = 0.002), with overall survival

higher at TP (Fig. 6). There was a general decrease in survival at QF from inside the mangroves to the fringe before dropping dramatically outside the forest (Fig. 6). On the other hand, survival across positions at TP was much more stable, with no significant difference between positions (except for a peak at the fringe position).

Growth

Position had a significant effect on both stem diameter ($F_{6,20} = 5.75$, p = 0.03) and number of leaf pairs ($F_{6,20} = 9.96$, p = 0.007). These showed no change or a slight decrease from post-germination (3 mo) to 21 mo after planting at all positions within the mangrove forest (Fig. 7a,b). In contrast, both of these growth rate measures were significantly greater at the fringe and outside forest positions. A similar pattern was observed for increased plant heights within the fringe and outside of mangrove forests compared with inside the forest (Fig. 7c), but this was not consistent between locations, with greater growth near the forest fringe at the QF site (interaction: $F_{6,20} = 7.51$, p < 0.0005).

DISCUSSION

By examining early post-settlement dynamics both in and outside existing forests, this paper augments recent studies addressing effects of hydro-

Table 2. Growth results of *Avicennia marina* seedlings by plant height, number of leaf pairs and stem diameter after 24 mo; values shown are mean height increase rate (mm mo⁻¹), mean increase in number of leaf pairs (leaf pairs mo⁻¹) and mean stem diameter increase (mm mo⁻¹), respectively. S: site, P: proximity to remnant mangrove forest. H: height on shore, NA: not applicable. All means are presented ± 1 SE. #Data were square root transformed to improve normality. *p < 0.05, **p < 0.02, ***p < 0.001. Means with the same superscript are not significantly different (p ≤ 0.05). See Fig. 1 for locations of study sites

| Site(s) analysed	Analysis	Significant factors	Proximity		
			Close	Middle	Far
Plant height					
TP1	P × H	H***	3.69 ± 0.26	3.25 ± 0.32	3.17 ± 0.34
QF1, TP1, TP2	P × H × S (no Low)	S***, H**	3.38 ± 0.20	2.73 ± 0.28	3.33 ± 0.28
All (except QF3)	P × S (Close only) × H#	S***	NA	NA	NA
QF1, TP1, TP2, TP3	P × H × S (High only)	S**	3.22 ± 0.30	3.56 ± 0.32	4.22 ± 0.40
GV1, QF1, TP1, TP2	P × H × S (Mid only)	S***	2.96 ± 0.21	2.11 ± 0.35	2.57 ± 0.27
Leaf pairs					
TP1	P × H	H***	0.10 ± 0.01	0.10 ± 0.01	0.07 ± 0.01
QF1, TP1, TP2	P × H × S (no Low)	H*, S**	0.10 ± 0.01	0.09 ± 0.01	0.09 ± 0.01
All (except QF3)	P × S (Close only) × H	H**, S***	NA	NA	NA
QF1, TP1, TP2, TP3	P × H × S (High only)	None	0.11 ± 0.01	0.11 ± 0.01	0.10 ± 0.01
GV1, QF1, TP1, TP2	P × H × S (Mid only)#	S***, S × P*	0.08 ± 0.01	0.07 ± 0.01	0.07 ± 0.01
Stem diameter					
QF2, TP1, TP2, TP3	P × S (Close only) × H#	S***	NA	NA	NA
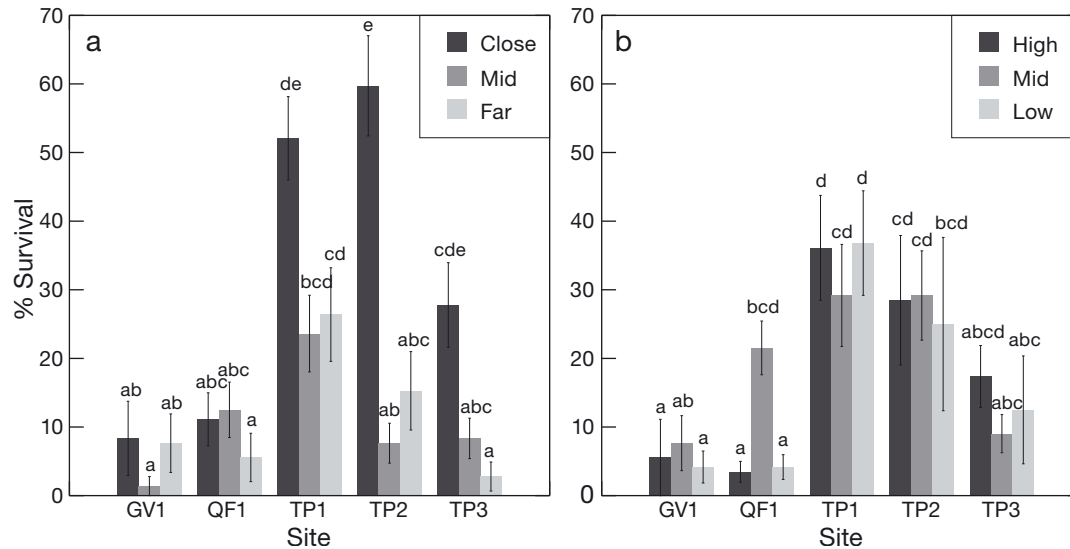
Fig. 5. Interaction plots showing percentage survival of *Avicennia marina* seedlings at 24 mo after planting. Survival by (a) proximity to remnant mangrove forest and site (see Fig. 1) and (b) height on shore and site. Bars are means (± 1 SE), and those with the same letter are not significantly different (p ≤ 0.05)

dynamic forces and existing forests on the establishment and early growth of mangroves. We found that when mangrove seedlings establish outside of a mangrove forest, their survival is affected by their proximity to that forest and that this effect can vary depending on the location of the forest. Higher rates of dissolution of clod cards at increasing distances from the same forests indicates that excessive hydrodynamic energy is a likely cause of a decrease in survival. Additionally, duration of inundation of mangrove seedlings is less important in their survival, but has a significant effect on their growth rates.

Survival of planted seedlings and propagules

The high variability in survival rates resulting from this study (1–60% for the seedling planting experiment and 2–76% for the propagule planting experiment) is not uncommon in comparable studies (e.g. 39–69%: Osunkoya & Creese 1997; 16–86%: Bhat et al. 2004). In our study, significantly higher survival was observed in seedlings planted close to existing forests at sites in 1 of 3 locations (namely TP). The clod card results indicate that hydrodynamic energy was significantly lower at close proximity to existing stands at TP than for any other proximity/location

| Height on shore			Site			Site		
High	Mid	Low	GV1	QF1	QF2	TP1	TP2	TP3
4.46 ± 0.30^a	3.56 ± 0.26^a	2.39 ± 0.25^b	NA	NA	NA	NA	NA	NA
3.73 ± 0.23^a	2.77 ± 0.16^b	NA	NA	2.01 ± 0.21^a	NA	4.05 ± 0.21^b	2.78 ± 0.22^a	NA
3.00 ± 0.25	2.81 ± 0.17	2.41 ± 0.15	1.64 ± 0.44^b	2.14 ± 0.23^b	2.27 ± 0.24^b	3.69 ± 0.26^a	2.67 ± 0.19^b	1.93 ± 0.17^b
NA	NA	NA	NA	2.81 ± 0.39^{ab}	NA	4.46 ± 0.30^a	2.93 ± 0.36^{ab}	2.47 ± 0.34^b
NA	NA	NA	1.31 ± 0.37^b	1.89 ± 0.23^b	NA	3.56 ± 0.26^a	2.64 ± 0.26^b	NA
0.13 ± 0.01^a	0.10 ± 0.01^a	0.05 ± 0.01^b	NA	NA	NA	NA	NA	NA
0.11 ± 0.01^a	0.07 ± 0.01^b	NA	NA	0.05 ± 0.01^b	NA	0.11 ± 0.01^a	0.08 ± 0.01^{ab}	NA
0.09 ± 0.01^a	0.07 ± 0.01^a	0.04 ± 0.01^b	0.02 ± 0.01^c	0.05 ± 0.01^{abc}	0.04 ± 0.01^{bc}	0.10 ± 0.01^a	0.06 ± 0.01^b	0.05 ± 0.01^{bc}
NA	NA	NA	NA	0.07 ± 0.02	NA	0.13 ± 0.01	0.10 ± 0.01	0.09 ± 0.01
NA	NA	NA	0.03 ± 0.01^b	0.05 ± 0.01^b	NA	0.10 ± 0.01^a	0.07 ± 0.01^{ab}	NA
0.16 ± 0.02	0.10 ± 0.01	0.08 ± 0.01	NA	NA	0.08 ± 0.01^b	0.15 ± 0.02^a	0.07 ± 0.01^b	0.07 ± 0.01^b
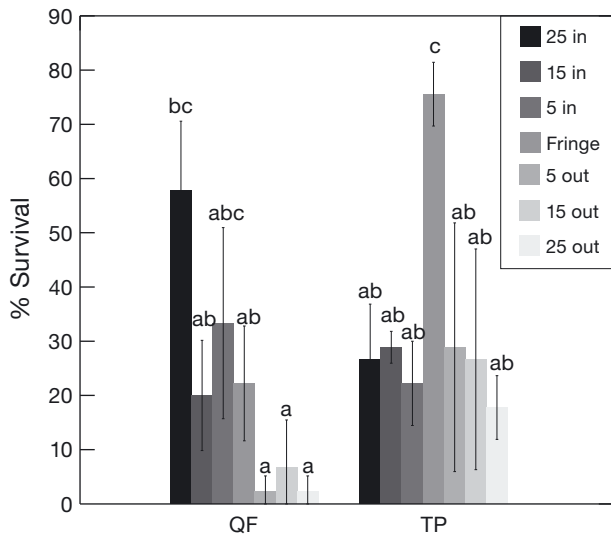
Fig. 6. Effect of interaction between position (in: within the forest; out: outside of the forest; numbers in the key indicate distance in metres) and site (see Fig. 1) on survival of planted *Avicennia marina* propagules after 21 mo. Bars are means (±1 SE), and those with the same letter are not significantly different (p ≤ 0.05)

combination and is the likely explanation for higher survival rates. Orientation away from prevailing winds and a shorter fetch distance (Table 1, Fig. 2.) as well as finer surface sediments (Table 1) found at TP provide additional evidence that this location is more protected from hydrodynamic energy. Nearby creeks are a probable explanation for the relatively coarse sediments found at some of the other locations; however, coarser sediments are also found at sites where creeks are absent. This is likely a symptom of more vigorous water movement which is able to transport coarser sediments onto the mudflats at these sites and/or continually remove the smaller size fractions (Quartel et al. 2007). In estuarine environments, smaller sediment particles have lower settling velocities, and therefore particle size is negatively related to water velocity (Gray 1981).

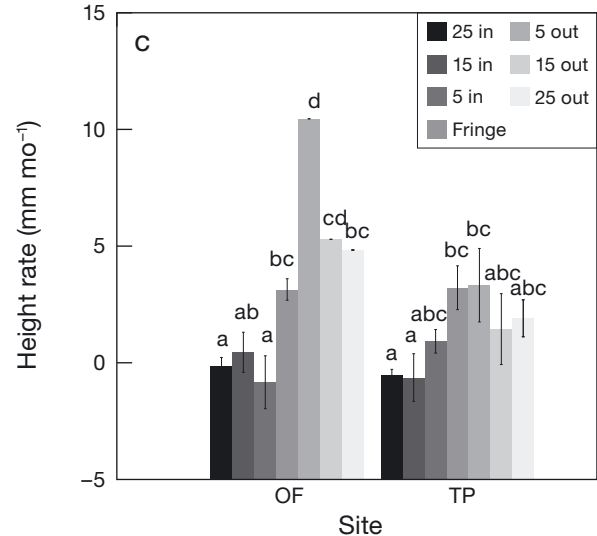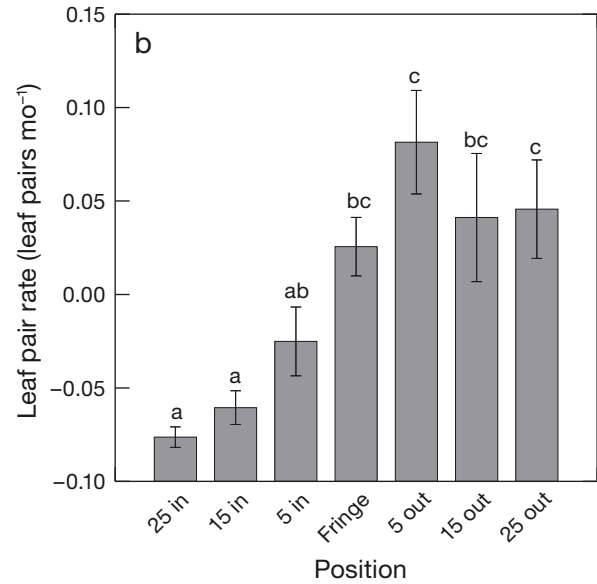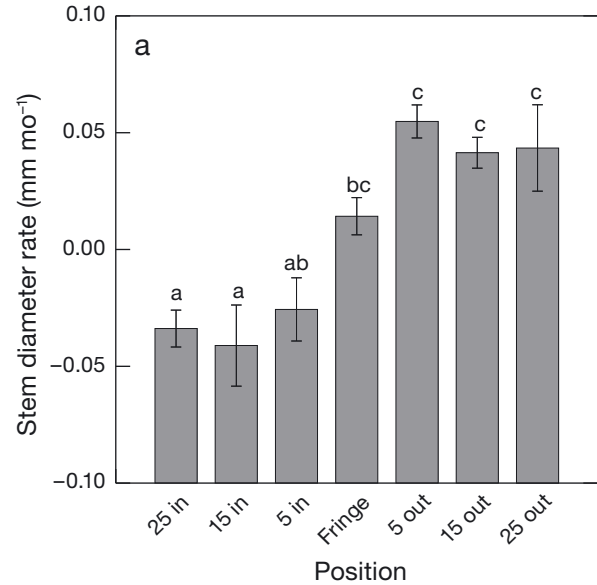The clod card results from the propagule planting experiment indicate that protection from the man-

Fig. 7. Growth of planted *Avicennia marina* propagules after 21 mo. (a) Increase in stem diameter (mm mo^{-1}) across positions (in: within the forest; out: outside of the forest; numbers in the key indicate distance in metres); (b) increase in leaf pairs (leaf pairs mo^{-1}) across position; and (c) increase in plant height (mm mo^{-1}) across positions and sites (see Fig. 1). Bars are means (± 1 SE), and those with the same letter are not significantly different (p ≤ 0.05)

grove forest is gained very quickly with distance into the forest (Fig. 3c). The high mortality of planted propagules at the more exposed QF site was consistent with the rapid increase of hydrodynamic energy outside of the forest, whereas survival across this boundary at the more protected TP site was more stable. At QF, some deaths were caused by the physical wrenching out or toppling of the seedlings, consistent with mechanisms of mortality identified in related flume studies (Balke et al. 2011). Interestingly, observations did not reveal that uprooting and toppling was a common cause of mortality in the seedling planting experiment. This is likely due to the method of planting employed in this study which was developed through earlier community plantings in Western Port in response to the uprooting of seedlings planted straight into the mudflat. The deeply-placed carton stabilises the plant more effectively, and results here suggest that mortality is also caused by factors additional to the uprooting or toppling of the seedling suggested by others (Clarke & Allaway 1993, Clarke & Myerscough 1993, Balke et al. 2011). Observations of defoliation and necrosis of leaves and stems suggest that conditions away from existing forests, including mechanical stress, may be having negative physiological effects on the seedlings similar to stress caused by wind in terrestrial plants (Jaffe & Forbes 1993, McArthur et al. 2010). Leaf necrosis is also common in frost-affected mangroves (Wang et al. 2011). While protection from frosts is a potential effect of proximity to existing forests, it is an unlikely mechanism in this case based on the temperature data collected. Mechanical stress at the anatomical/physiological level may be an important mechanism affecting mangrove regeneration and restoration and requires further research.

Growth of planted seedlings and propagules

Reflecting their latitudinal position, overall growth rates in this study were low, ranging from 1.31 to 4.46 mm increase in plant height per month for the seedling planting experiment and −0.83 to 10.45 mm mo^{-1} for the propagule planting experiment. This is comparable to another study conducted at a similar latitude in New Zealand, where stem height increase was 4.67 mm mo^{-1} over 12 mo (Burns & Ogden 1985), and during an earlier study in Western Port Bay, where seedlings grew 5–7 mm mo^{-1} over 4 mo (Farrell & Ashton 1974). However, these rates are substantially lower than growth rates in subtropical *Avicennia marina* of between 56 and 75 mm mo^{-1} in the

United Arab Emirates (Anwahi et al. 1998). A concern in our study was that raising seedlings in cartons would limit their growth through the restriction of their root system. This did not appear to be the case, and growth rates of successful seedlings were comparable between the seedling and propagule planting experiments.

Within sites, and unlike survival, plant growth was not enhanced by the proximity to existing stands but was greater at the TP site. Results show that for growth, height on shore is a far more important factor with seedlings planted at the high position growing at almost double the rate of those planted at the low position. This is consistent with tropical studies that have shown longer inundation periods to reduce survival and growth rates (Smith 1987, Kitaya et al. 2002), but not with a study by Clarke & Myerscough (1993), who recorded an increased growth rate at lower intertidal levels of a temperate Australian forest. These disparities may relate to differences in species, location or in descriptions of planting level relative to tide. Additionally, salinity can be very high at higher elevations of mangrove forests, especially where precipitation is low and evaporation is high, and this can reduce growth rates of mangrove seedlings (Krauss et al. 2008). However, direct comparisons are difficult, as many field studies examining effects of inundation on survival and growth of mangroves have not demonstrated how elevation of planting sites relative to tide was determined.

The propagule planting experiment showed that growth rates are significantly affected by finer-scale position across the transition zone between the forest and the bare mudflat. Growth seems to be hindered within the forest, and this is consistent with studies showing that seedlings are able to establish in shady areas but their ongoing growth and survival depends on sufficient sunlight (Clarke & Allaway 1993, Osunkoya & Creese 1997, Minchinton 2001). It appears there is an optimum growth area around the fringe and 5 to 15 m outside of it before growth is reduced farther away (Fig. 7).

Resilience and stable states

The hypothesis that the resistance of the bare mudflat state to regeneration/restoration decreases with increasing proximity to an existing mangrove forest appears to hold true. Our results suggest that this resistance is linked to the protection the forest provides from hydrodynamic energy and its associated physical effects. The likelihood of an ecosystem mov-

ing from one stable state to another is driven by changes in state variables (e.g. population density) and/or parameters (e.g. environmental drivers) (Beisner et al. 2003). In this case, a large disturbance, viz. clearance of an entire section of mangrove forest fringe affecting the state variable of mangrove forest density (reduced to 0), has resulted in a shift from the former stable state (intact forest) to the new stable state (bare mudflats). Clearance of the forest has led to the change in at least 1 of the parameters (i.e. exposure to hydrodynamic energy). This parameter has been shown to reduce the capacity for natural recruitment and establishment of mangrove seedlings (Balke et al. 2011) and, in our study, survival of planted mangroves adjacent to disturbed forests. Reduced outside-forest survival at locations with greater exposure suggests that this parameter varies spatially in its importance in maintaining the bare state and that forests with less shelter from hydrodynamic energy are less resilient to disturbance. Historical aerial photography in such locations indicates little natural regeneration over a number of decades, demonstrating that the bare state is highly resilient and resistant to natural mangrove regeneration.

Implications for mangrove restoration

This study has shown that successful restoration of the mangrove forest through planting appears to be more likely at sites protected from hydrodynamic energy, although long-term experiments following survival and growth of trees to maturity would be required to fully assess this conclusion. It has also highlighted that seedlings in bare areas outside of existing forests are not only susceptible to being uprooted or pushed over by strong hydrodynamic forces, but the constant mechanical stress caused by these forces may be having a chronic effect on the seedlings. In this case, it appears that using existing mangrove forests as a node from which to expand their extent would be a sensible strategy for undertaking mangrove restoration. However, mass plantings in exposed/semi-exposed areas (e.g. for sequestering meaningfully large amounts of carbon or protecting long stretches of coastline) would not necessarily have the luxury of protection from existing vegetation. In these cases, physical protection from hydrodynamic energy during the vulnerable period in which they are most susceptible to mortality from excessive water movement appears to be necessary. Potential artificial protection can be provided by temporary breakwaters (Hashim et al. 2010) or perme-

able groynes (Winterwerp et al. 2013), although resulting changes in sediment dynamics can have negative geomorphological effects. Recent trials of more local protection of seedlings using short lengths of PVC pipe placed over individual plants have resulted in a substantial increase in survival compared to unprotected seedlings and have a lower risk of unexpected changes to sediment dynamics (T. Hurst unpubl. data).

The protection of coastal areas from climate-change-driven increases in wave energy through the establishment (or eco-engineering) of coastal vegetation is an idea that is gaining popularity (Arkema et al. 2013, Duarte et al. 2013, Bouma et al. 2014). Given the widespread destruction of mangrove forests around the globe, there are likely to be many places where protection of the coastline can be improved or restored through establishment of mangrove forests. However, our study highlights that it may not be as easy as replacing what was once there. The reason for this is that the original disturbance of the forest can result in a change in the level of protection that a mature mangrove forest provides to new seedlings. We argue that this leads to the initiation of an alternative stable state (also identified in other degraded coastal ecosystems by Bouma et al. 2014), and the effort required to restore the ecosystem to its former state is much greater than through simple replanting projects.

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