

Chapter 17

Kropotkin's Garden

Facilitation in Mangrove Ecosystems

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That is the watchword that comes to us from the bush, the forest, the river, the ocean – therefore combine, practice mutual aid.

Peter Kropotkin, Mutual Aid 1906

17.1 | Introduction

Ecologists have studied ‘mutual aid’ (or facilitation) since at least the time of Kropotkin (1842–1921). But the ‘watchword’ which he heard with such force has not always been heeded, remains poorly understood and is rather loosely defined. A seminal early use comes from Connell and Slatyer (1977), where building on the work of Clements (1916), they used ‘facilitation’ to describe a model of community succession in which pioneer species modify the habitat allowing the colonisation of later ones. While this successional implication remains common in the literature, the word is also applied more broadly to positive interactions between individuals and species. Some authors restrict the term to plant–plant interactions (e.g., Krebs, 2001), while others treat it as synonymous with ‘positive species relationships’ (He et al., 2013), although Munguia et al. (2009) argue that any relationship that does

not cause evolutionary changes to both parties is not a true ‘interaction’. Others expand the term to describe any positive relationships between individuals. For example Schöb et al. (2014) state that facilitation describes ‘the positive effects of one organism on others’, while Singer (2016) defines it as ‘interactions between two organisms, or two species, that benefit at least one of them and harm neither’. The latter definition covers interactions at all levels of complexity, from individual behaviour through to ecosystems, and includes obligate symbiosis, commensalism and looser associations.

The term therefore always involves the idea of benefit from association with another organism. This benefit is sometimes mutual, sometimes one-way and sometimes even negative for one partner, particularly over time (the facilitation model of succession allows for the competitive exclusion of the pioneer species by those that they facilitate). Given this broad use, any review of facilitation is in danger of losing focus or becoming overwhelmed. Here, we adopt another influential definition from Bertness and Calloway (1994), which includes interactions within and between species, but restricts the ambit of the term through a focus on stress: ‘the benefits to an organism by the minimisation by neighbouring organisms of biotic or physical stress’. Applications of this definition in the literature have

emphasised facilitation through the amelioration of physical stresses by habitat modification, biological stresses through associational defences and the existence of scale-dependant 'positive habitat switches' (Wilson and Agnew, 1992), in which sufficiently large or dense associations of organisms permit the presence of others. Here, we consider examples of all of these mechanisms in mangroves. We look at how relationships between individual plants can ameliorate physical and chemical stresses (particularly during establishment and colonisation), and how these effects can manifest at ecosystem scales. We consider how fauna are known to change the physical and chemical environments in favour of tree establishment and growth, and how the biological stress of herbivory may be mitigated by associational defences conferred by spatial aggregation of plants or through indirect interactions with epibionts or predators that defend plants against herbivory. Finally, we discuss the possible function of ecosystem-scale facilitation in the long-term resilience of mangroves to environmental change.

17.2 | Why Mangroves?

There are theoretical and practical reasons to look for facilitation within mangrove ecosystems. The dominant conceptual model used to explain and predict the occurrence of positive interactions in ecosystems is the stress gradient hypothesis (SGH; Bertness and Callaway, 1994). This suggests that physical and biological stresses will increase the frequency of facilitation, which will help mitigate these stresses through habitat amelioration or associational defences respectively. Later refinements of the theory show that particular outcomes of any interaction depend on the characteristics of the stress factors (resources or non-resources) and on the performance of the involved species (relative stress tolerance and competitiveness), which might change during their life cycles (Maestre et al., 2009).

Intertidal habitats are often used to exemplify stress in the ecological literature; they are places subjected to frequent physical and chemical

changes and require adaptations suited for aquatic and terrestrial survival. So it is not surprising that many of the studies demonstrating facilitation and testing the SGH have been conducted in the intertidal, with rocky shores and salt-marsh habitats predominating (see references in He and Bertness, 2014). Mangroves are exposed to the same stresses but are poorly represented in the facilitation literature. Trees and shrubs are the plant forms most likely to show strong facilitative interactions (He et al., 2013) so those growing intertidally – mangroves – should be particularly likely to demonstrate them. Facilitative interactions may also help explain the high productivity of mangrove ecosystems. Many of the adaptations to stress exhibited by mangroves, such as investment in succulent leaves with thick epidermal layers, metabolically costly salt exclusion, high root:shoot ratios and conservative resource capture and growth strategies, are usually associated with relatively low productivity (Chapin et al., 1993). The fact that mangroves show total productivity levels similar to terrestrial tropical forests (Alongi, 2009), despite these adaptive characteristics, suggests we lack a full understanding of how productivity is achieved in mangroves.

A growing literature indicates that fauna help explain this anomaly. The abundant burrows and mounds visible in most mangrove forests show ecosystem engineers – particularly crabs – at work. The activities of large and active bioturbators in areas where the edaphic conditions are stressful to plants creates conditions in which animals are likely to make important changes to growing conditions. While crabs are the focus of most of the relevant literature, there is good evidence of facilitatory importance to forest functioning of other faunal groups, including ants, birds and sponges. Here we review some of that evidence, with emphasis on the facilitatory roles of fauna in the establishment and productivity of mangrove trees.

Large-scale mangrove destruction combined with a growing awareness of the importance of mangroves for people and wildlife have led to global reforestation and restoration efforts. When modelled on silvicultural practices developed for terrestrial forests under benign

environmental conditions, these efforts are often unsuccessful (Kodikara et al., 2017). While planting seedlings in straight rows with large, even distances between them might minimize timber loss through density dependent mortality (self-thinning) once the vegetation is closed, growing evidence shows enhanced risk of mortality and reduced growth of single plants without neighbours. Facilitation theory and information on the importance of fauna provides a perspective that may inform restoration and rehabilitation of mangrove habitat (Gedan and Silliman, 2009), particularly in harsh and degraded settings and where positive biotic influences have been overlooked. This chapter considers the evidence for facilitation, as defined by Bertness and Callaway (1994), at the different successional stages of a mangrove forest and life stages of individual mangrove trees. We begin with the initial establishment and growth of seeds and propagules (while colonising new areas and within established forests), consider the growth of seedlings, saplings and young trees, and consider the positive role of biotic interactions in enhancing the long-term persistence of the mangrove ecosystem in the face of environmental change.

17.3 Establishment and Colonisation

17.3.1 Hydrodynamics at the Seaward Edge

Mangrove seedlings and propagules are particularly vulnerable stages and early growth and establishment is often prevented due to physical and biological stresses. For example, Balke et al. (2011) identify 'windows of opportunity' during which mangroves may establish on tidal flats. These are periods during which hydrodynamic forcing is low enough to allow the initial growth of the plants; without such periods, seedlings are washed away. Because the critical drag force of water required to dislodge a new seedling increases exponentially with the maximum root length (Balke et al., 2011), the very early days during which roots are small are the most vulnerable. Hence, the physical impacts of waves and

fast-moving water are critical stresses at the seaward mangrove fringe and on open tidal flats. Hydrological stresses limit establishment of new plants beyond current vegetated areas. The plants themselves modify these stresses by slowing water down, reducing wave heights, stabilising sediments against erosion with their roots and by encouraging sediment accretion and depositing organic material into the sediment. This generates biogeomorphic feedbacks that can lead to alternative states (open mud flat versus dense forest) with very sharp and rapid transitions (both spatially and temporally) between them (Figure 17.1).

Mangroves are effective in attenuating the energy of waves; for example, *Kandelia candel* trees of only five to six years old reduced wave energy by 20 per cent over 100 m (Mazda et al., 1997), while Barbier et al. (2008) show reductions of up to 60 per cent over 100 m of *Sonneratia caseolaris*. Some mangroves, such as *Rhizophora mucronata*, are incapable of establishment without sheltered conditions (Thampanya et al., 2002). In many sites, such species effectively rely on the protection from waves and water movement provided by the seaward forest, consisting of pioneer species such as *Avicennia marina* and *Sonneratia alba* to establish and regenerate. This differential susceptibility to wave impact and biogeomorphic feedbacks between tree density and water movement provides one explanation for species zonation within mangrove forests and is an example of an ecosystem-wide facilitation effect.

Researchers have long discussed whether mangroves can act as active 'land builders' or whether they simply passively follow new accretion (see for example the discussion on p. 106 of Smith (1992) citing examples more than 120 years old). While elements of this debate continue (Alongi, 2008), there is now compelling evidence that mangroves enhance sediment accretion, enable forest surface elevation and reduce erosion (Winterwerp et al., 2005; Mcivor et al., 2012; Krauss et al., 2014; Huxham et al., 2015). Measuring the changes in coastlines over time has shown how mangrove removal can enhance rates of erosion, while forest preservation can reduce erosion and cause land progradation (Thampanya et al., 2006). Hence, mangrove

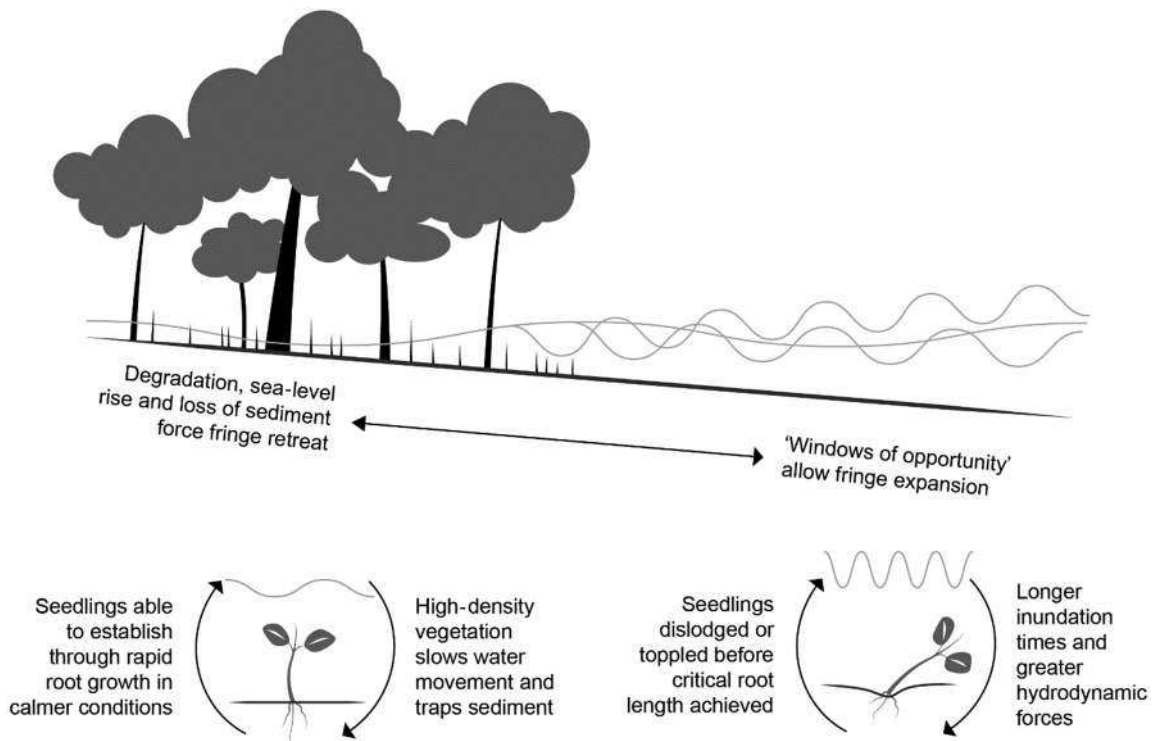


Fig. 17.1 Biogeomorphic feedbacks between hydrodynamic stresses (including wave height and current speed) and the impacts of mangroves on water movement help to determine the sharp transition zone between the mangrove forest and open shore.

ecosystems help create stable conditions for their persistence and, in some cases, expansion, through the facilitative effects of tree density on water and sediment dynamics.

17.3.2 Desiccation at the Landward Edge

At Gazi Bay, southern Kenya, there are many hectares of bare sediment between the landward fringe of the natural mangrove forest and the terrestrial vegetation. These forlorn areas are studded with the stumps of long-dead mangrove trees, testament to an historical transition from forest to bare ground. Local sources suggest this was caused by commercial extraction of wood at least forty years ago (Kirui et al., 2008). Hence, the loss of trees caused an enduring change from forest cover to a new ecosystem, characterised by bare ground and very low biodiversity. This sharp transition between two states is similar to that found at the seaward mangrove fringe and

suggests strong feedback processes are operating; in this case, driven not by water energy, but by salinisation and desiccation (Figure 17.2). Canopy removal exposes the sediment to the sun and allows rapid evaporation of pooling saline water. At Gazi this has resulted in salinisation (with sediment pore water at 89 PSU or more), preventing seedling establishment and leaving ‘salty barrens’ which are hostile to the growth of all higher plants. Under such conditions, forest recovery may follow the opening of natural ‘windows of opportunity’, such as unusually heavy rainfall events coinciding with periods of seed or propagule production. The lengthy persistence of the Gazi salty barrens suggests that no such windows have opened here over at least the past forty years and active restoration involving the planting-out of seedlings was required to restore mangrove coverage. New seedlings and propagules are very vulnerable to desiccation. However *Avicennia*

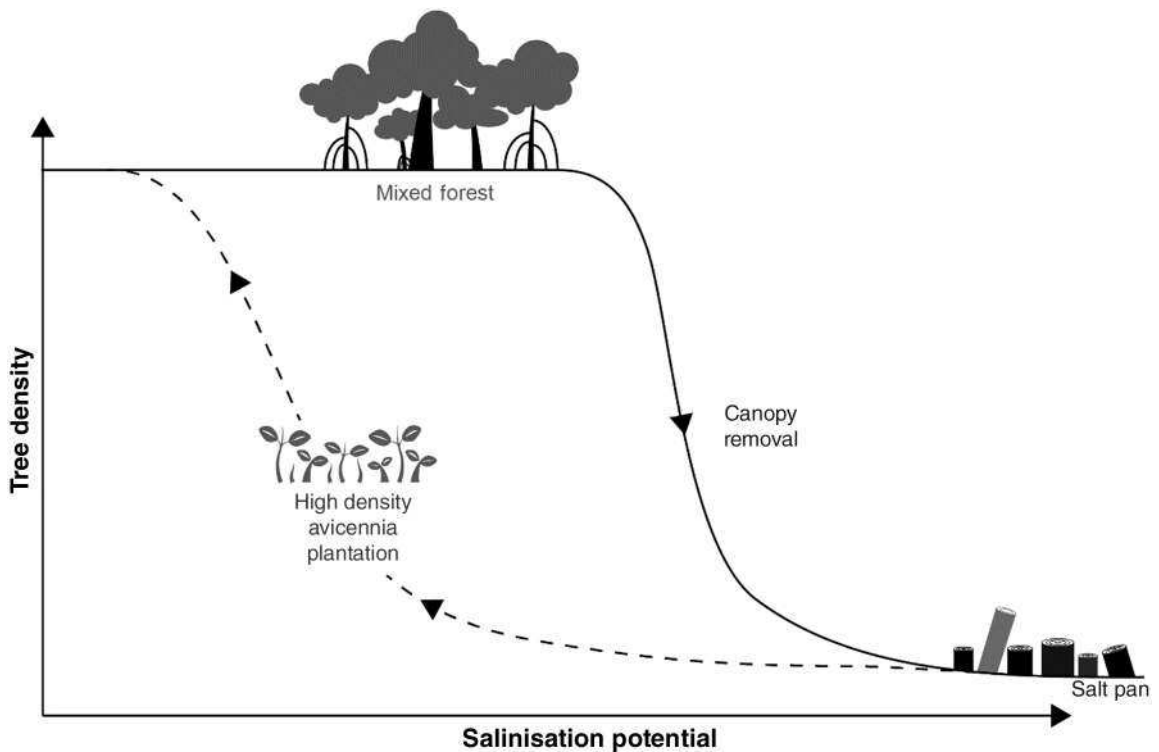


Fig. 17.2 Canopy removal at the landward fringe can result in salinisation, as salt water evaporates without the protection of shade. This may establish a stable state characterised by hysteresis; rapid transitions and non-linear processes mean that it is difficult to reverse the condition of the ecosystem. Here, planting of high-density *Avicennia marina* seedlings allows mangrove recovery through intra- and inter-specific facilitation, as the seedlings cast shade, enhance soil organic matter and permit colonisation of other species.

marina is exceptionally tolerant of salt (Jayatissa et al., 2008), and seedlings older than three to four months were able to survive and grow (Kirui et al., 2008). *Avicennia marina* subsequently acted as a nurse species at this site, allowing the establishment of wild seedlings of other mangrove species under the protection of shade and with enhanced sediment moisture and reduced salinity, an example of inter-specific facilitation (Huxham et al., 2010).

Similar interactions have been reported between salt marsh vegetation and the black mangrove *Avicennia germinans*, which shows enhanced survival and growth when associated with salt-marsh vegetation under high-stress conditions in the USA (Guo et al., 2013). In the Caribbean, forbs and grasses can also act as nurse species for mangroves, both through

ameliorating soil conditions and by physically trapping and supporting propagules (McKee et al., 2007b).

Intra-specific facilitation is also common during the early growth stages of intertidal plants, including mangroves, and such interactions can be harnessed to enhance restoration (Gedan and Silliman, 2009). For example, Silliman et al. (2015) showed increased biomass of tidal marsh grass *Spartina* sp. when planted in clumped rather than dispersed configurations at temperate sites. This effect was largely due to the amelioration of soil anoxia, with high densities of plants sharing oxygen leaked from roots. Similar mechanisms, along with mutual shading, may explain why high-density clumps of *Avicennia marina* seedlings showed enhanced survival in Kenya (Huxham et al., 2010).

17.3.3 Degradation Due to Changes in Hydrodynamics and the Role of Phenotypic Plasticity in Ecological Recovery

Regular flooding is essential for the normal functioning of most mangrove ecosystems; physical changes that prevent this usually result in the loss or degradation of forests. For example, there was rapid dieback after the construction of a road cutting through the Ajuruteua Peninsula, northern Brazil, in 1974. The road, constructed parallel to the watershed, blocked inundation by tidal channels and led to desiccation and a lethal accumulation of salt of the sediment. The erosion of the uppermost soil layer by wind contributed to a regime shift from a tall mangrove forest (with a maximum canopy height of 30 m; Mehlig et al., 2010) to a bare, hypersaline ground, similar to the salty barrens of Gazi. This lasted almost thirty years before *A. germinans* seedlings were able to recolonize the area (Vogt et al., 2014), presumably during a natural window of opportunity. The colonisers developed as shrubs and thus adapted to the salinity-induced osmotic constraints and water scarcity (Peters et al., 2014). As nurse plants, the shrubs facilitated the survival and growth of con-specific followers (Vogt et al., 2014; Pranchai, 2015), which eventually switched back to tree architecture (Vogt et al., 2014) and an onset of neighbourhood competition (Pranchai, 2015). The change of morphology from shrub to tree architecture was key for this self-rescuing effect and is a feature distinct from other nurse plant systems, e.g., from alpine regions (Schöb et al., 2014), where nurse plants are not conspecifics of the facilitated plants.

17.3.4 Faunal Facilitation of Seedling Recruitment

While plant interactions dominate the literature on facilitation during colonisation of new areas, the effects of fauna become increasingly apparent as forests mature. The burrowing and sediment feeding activities of crabs, mud shrimps and mud skipper fish collectively transform what would have been a relatively flat forest floor into a variable-height topography of burrow digging spills, burrow ‘hoods’ and burrow openings.

Minchinton (2001) speculated that such topography provides opportunity for propagules to become trapped on the forest floor during tidal flooding. Burrow mounds were particularly common under canopy cover, accounting for up to 44 per cent of the forest floor. Minchinton (2001) found that 75 per cent more propagules were trapped in areas with mounds than those without, and that propagules were more likely to establish as seedlings when growing on mounds. The establishment of seedlings was also faster on mounds than on flats (Minchinton, 2001), possibly as the window of opportunity for propagule settlement (*sensu* Balke et al., 2011) is extended by the amelioration of hydrological stress by elevation in surface topography. The study showed crab burrowing can have a positive effect on mangrove recruitment in mature forests and in forest gaps and might aid in the recovery of forests after disturbance events. Crabs are also avid propagule predators (Sousa and Dangremond, 2011) and the effective outcome of crabs on seedling establishment is likely to be dependent on contextual variation in offsetting of propagule trapping against propagule predation. Nevertheless, the effect of crab mounds on propagule establishment is similar to that offered by mussels in the establishment of salt marsh vegetation. Angelini et al. (2015) found that mussel patches, which account for a much smaller proportion of marsh area cover than do crab burrows in mangroves, had significant and large-scale facilitating implications for marsh functioning, including the boosting of primary production.

17.4 Early Growth – Facilitation in Seedlings and Saplings

17.4.1 Sedimentation and Nutrient Supply

Positive density-dependent effects operating over small scales may persist well beyond the initial establishment and growth of mangrove seedlings, although the mechanisms causing this intra- and inter-specific facilitation are likely to change as plants mature. In Sri Lanka, *R. mucronata* seedlings planted at high densities grew faster and showed better survival than those at

low densities (Kumara et al., 2010), an effect that persisted for at least six years (Kumara, personal communication). Thampanya et al. (2002) also recorded positive effects of density on the same species in Thailand. Macronutrients, in particular nitrogen and phosphorus, are typically limiting factors of mangrove growth (Alongi, 2009), and biophysical processes that enhance the delivery and absorption of nutrients will usually improve growth. In the Sri Lanka case, denser stands of trees accumulated more allocthonous sediment with high nitrogen content and this was the likely cause of the better performance of high-density plants (Phillips et al., 2017).

17.4.2 Associational Resistance to Herbivores

A plant's spatial associations with other plants can alter its detection by and/or vulnerability to herbivores. Interspersion of a host plant with other species can decrease (associational resistance) or increase (associational susceptibility) its herbivore load, compared to what it experiences when growing in monospecific stands (Barbosa et al., 2009). To our knowledge, the beneficial effects of associational resistance to herbivory have not been studied explicitly in mangrove ecosystems. This may be a consequence of the long-standing belief that mangrove vegetation is structured primarily by responses of plants to physical and chemical, rather than biological, stressors. The apparent low rates of folivory in mangroves compared to terrestrial forests has reinforced this view (Komiya et al., 2008; Alongi, 2009). However, most estimates of folivore damage to mangroves are based on the level of standing leaf damage, which has been shown to greatly underestimate true rates of loss, since leaves that are completely consumed are not included in the estimates. When Burrows (2003) marked individual leaf buds and followed their fates to maturity, he estimated leaf damage of 5–8.3 per cent for *Rhizophora stylosa* and 19.3–29.5 per cent for *Avicennia marina*, substantially higher than earlier estimates based on standing leaf damage. In addition, other, less obvious, herbivorous niches, such as stem wood-borers, are functionally important in mangroves and typically are overlooked when estimating biomass lost to

herbivory. For example, stem-boring beetles killed more than 50 per cent of a fringing *Rhizophora mangle* canopy on offshore islands in Belize (Feller and McKee, 1999; Feller, 2002). Hence, it is clear that mangrove stands must cope with both the stressful chemical and physical conditions already discussed and the biological stress imposed by herbivore damage comparable to that observed in other types of forests.

Associational resistance has been well-documented in terrestrial vegetation. Among the first studies to experimentally demonstrate it were Root and colleagues' investigations of herbivore–plant interactions in gardens planted into old field habitat (Tahvanainen and Root, 1972; Root, 1973), which showed an inverse relationship between herbivore load on collard (*Brassica oleracea*) and the diversity of neighbouring vegetation (pure stands of collard versus a diverse mix of meadow grasses and forbs). Alternative (but not mutually exclusive) mechanisms that could account for this relationship include: (1) the enemies hypothesis: diverse vegetation harbours a greater number of natural enemies of herbivores (predators and parasitoids) than single-species stands and (2) the resource concentration hypothesis: a host plant is more likely to be found, particularly by specialist herbivores, if it grows in a dense monoculture of conspecifics than in a mixed-species stand, and such herbivores are more likely to aggregate and reproduce in these areas of high resource availability and are less likely to emigrate from them (Root, 1973; Bach, 1980). Since the publication of this classic garden-meadow study, associational resistance to herbivores has been experimentally demonstrated in a variety of natural communities, including nearshore marine habitats (e.g., Pfister and Hay, 1988), open woodlands with shrub understory (Baraza et al., 2006) and shoreline vegetation (Hambäck et al., 2000).

As described earlier, the resource concentration hypothesis posits that a host plant is at greater risk of herbivory when growing in a monoculture than in a mixed-species stand, particularly if it is primarily fed on by specialists. However, an increase in local density within monocultures could lower the per capita risk of attack if the herbivore does not exhibit a

sufficient numerical response (through behavioural aggregation or in situ reproduction) to keep pace with plant growth or compensatory recovery from herbivore damage. In effect, as the local density of host plants increases, the resident herbivore population becomes swamped/satiated and per capita rates of damage and mortality decline (Crawley, 1997; Otway et al., 2005). This is more likely to occur if the specialist herbivore is univoltine (i.e., a single brood of offspring per year), has low fecundity and/or a complex life cycle, with a grazing larval stage that metamorphoses into a mobile, non-grazing adult stage (e.g., Lepidoptera). In the latter instance, the reproductive adult disperses away from the host plant and is unlikely to return to lay eggs in the same patch of plants in which it grazed as a larva (Cromartie, 1975).

As noted earlier, we know of no published investigations that specifically test for associational resistance to herbivory in mangrove habitats. The study that comes closest is Johnstone's (1981), which quantified rates of standing insect grazing damage to mature leaves of twenty-three mangrove species growing in mixed stands in coastal swamps of the Port Moresby region of Papua New Guinea. He found no relationship between rates of herbivory and the species richness of mangroves growing within 25 m of the sampled tree, and no correlation between leaf area eaten and the densities of individual species. However, patterns could have been obscured by large species-specific variation in susceptibility among the twenty-three species he sampled.

New evidence that associational resistance to herbivory occurs in mangroves comes from an unpublished field experiment that one of us (Sousa) conducted to assess the roles of intra- and inter-specific competition on growth and survival of mangroves along the tidal gradient on the central Caribbean coast of Panama. In this experiment, young (~ 1-month-old) mangrove seedlings of the three canopy mangrove species *A. germinans*, *Laguncularia racemosa* and *R. mangle* were planted into single- and mixed-species treatments, both inside and outside of replicate canopy gaps created by past lightning strikes. The complete design and results of this study will

be reported elsewhere; here we focus on patterns of survivorship of *A. germinans* seedlings as a function of density and species composition inside three upper-intertidal gaps, within forest stands dominated by conspecific adults. These stands are where populations of the specialist lepidopteran *Junonia genoveva*, or black mangrove buckeye, are concentrated (Sousa, unpublished data). *J. genoveva* larvae feed exclusively on the leaves of *A. germinans* and can strongly impact seedling populations (Elster et al., 1999). We analysed rates of survival over the first six months of the experiment; young seedlings are the most attractive life stage to egg-laying, adult *J. genoveva*, and are the most likely stage to be killed by their larvae (Sousa, unpublished data).

The experiment yielded evidence of both herbivore swamping by high host plant density and interspecific associational resistance (Figure 17.3). Survival rates differed significantly among treatments ($F_{5,12} = 12.72$, $P = 0.0019$). Among the *A. germinans* monocultures, the mean rate of survival was higher in the three-fold density treatment than either the two-fold or one-fold seedling densities. Survival was also higher in the 1:1 and 1:2 mixed treatments than the one-fold density monoculture, which contained the same number of *A. germinans* seedlings, a pattern indicative of associational resistance. Survival in the 2:1 mixed treatment appeared to be greater than in the two-fold monoculture, also suggestive of associational resistance, but the difference was not significant ($P = 0.095$).

This experiment did not directly manipulate *J. genoveva* densities to confirm that grazing by its larvae was responsible for seedling mortality. We did observe numerous larvae feeding on the plants and many adult butterflies flying around the study forests, laying eggs on host plants. In a subsequent experiment of similar design, an herbivore-exclusion treatment was added; it confirmed that *J. genoveva* caterpillars are responsible for most of the mortality of young *A. germinans* seedlings in upper-intertidal basin forests, where this experiment was conducted.

The specific mechanisms accounting for associational resistance in this system are not known. The presence of neighbouring non-host plants may physically interfere with the adult

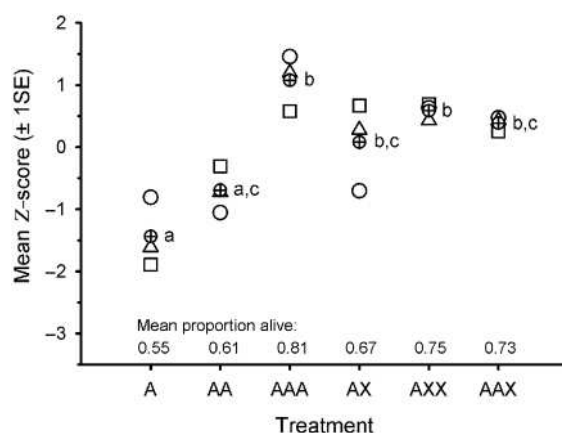


Figure 17.3 Survival to six months of *A. germinans* (A) seedlings planted in three monospecific treatments of one-, two- and three-fold density (A, AA, AAA), and three mixed-species treatments of 1:1 (AX), 1:2 (AXX) and 2:1 (AAX) density combinations of *A. germinans* with one of two other mangrove species (X = *L. racemosa* or *R. mangle*). Treatments were established in 0.5 m² plots at densities of twenty-five, forty and eighty-one seedlings per plot; the design was replicated inside three upper-intertidal gaps. The three mixed-species treatments contained twenty-five, twenty-seven and fifty-four *A. germinans* seedlings, respectively. Survival values for the pair of plots (one with *L. racemosa* and the other with *R. mangle*) that contained a 1:1, 1:2 or 2:1 ratio treatment were averaged for the analysis. Because seedlings in one of the gaps suffered nearly four-times higher mortality across all treatments than the other two, we standardised the proportion surviving values from each gap by converting them to z-scores, based on the respective gap means and standard deviations. Open symbols (○, △, □) represent values from the three replicate light gaps. The ⊕ symbol marks the mean Z-score of the three replicates. Letters to the right of these symbols summarize results of a Tukey honest significant difference test; those not sharing a letter are significantly different at $P < 0.05$. The mean proportions alive at six months in each of the six treatments are presented just above the x-axis, SE, standard error.

butterfly's ability to locate and oviposit on a host plant. In addition, *A. germinans* leaves contain iridoid glycosides (Fauvel et al., 1995). This class of chemical compounds has been shown to act as oviposition stimulants for *J. genoveva*'s temperate zone congener, *Junonia coenia* (Pereyra and Bowers, 1988); therefore, it is conceivable that there may also be some interference with chemical signalling in patches of mixed-species composition.

17.5 Mature Trees and Forests

17.5.1 Faunal Enhancement of Mangrove Primary Production

There is good evidence that crabs facilitate mangrove production. Removing crabs from the benthos of *Rhizophora*-dominated stands in Australia led to a reduction in forest primary production and reproductive output (Smith et al., 1991); an outcome that is very similar to the result of crab exclusion experiments in salt marshes (Bertness, 1985). Bioturbation by crabs aerates mangrove soils and reduces soil sulphide content (Smith et al., 1991), a chemical that depresses the primary productivity of coastal wetland plants in general (Bertness, 1985). Burrowing by crabs also regulates other soil characteristics that influence forest production. Smith et al. (2009) found that field exclusion of fiddler crabs reduced the growth of *L. racemosa* seedlings, probably because soil salinity rose in the absence of crab burrowing. Faunal burrows aid the flushing of sediments by tidal water (Stieglitz et al., 2013), which dilutes salinity and reduces sulphate reduction (Kristensen, 2000; Smith et al., 2009). Crab burrowing is also thought to boost nitrification and thereby plant growth (Bertness, 1985), and Skov and Hartnoll (2002) proposed that selective feeding of crabs on mangrove leaf litter facilitates the retention and remineralisation of litter nutrients for the benefit of crabs themselves, as well as forest productivity. So far, the experimental evidence of this happening in coastal wetlands is limited (Daleo et al., 2007; Kristensen et al., 2008).

Crab burrowing might also indirectly enhance forest production by facilitating the activity of other species that stimulate tree growth. In salt marshes, the aeration of soils by crab burrowing facilitated the development of mycorrhizal fungi, which boost the availability of nitrogen for plant production (Daleo et al., 2007). The fungi need soil aeration to grow and the removal of crabs, and their burrows, reduced the growth of salt marsh *Spartina* plants by 35 per cent (Daleo et al., 2007). Mycorrhizal fungi are abundant in the soils of coastal wetlands (Carvalho et al., 2004), and it is likely that crab

facilitation of mycorrhiza will also boost mangrove tree production.

Exclusion of crabs does not always result in a reduction of tree growth. A year-long removal of a dominant semi-terrestrial crab from a high-shore *Rhizophora* stand in Brazil did not have any measurable impact on forest growth (Pülmanns et al., 2016). While the lack of effect might be because crab removal was not complete (approximately a third of all crabs were removed), it may equally well be that the facilitatory role of crabs in forest production is context-dependent and influenced by a range of geomorphological, physio-chemical, seasonal or biological factors (Pülmanns et al., 2016). Theoretical and empirical work emphasises the influence of environmental context on the relative importance of facilitation, particularly along gradients of stress (Bruno et al., 2003; Maestre et al., 2009; Schöb et al., 2014). The influence of stress gradients on faunal facilitation has not been addressed in mangroves.

While the evidence for crab facilitation of mangrove production is considerable, other fauna can also positively affect forest production. Ellison and colleagues (Ellison and Farnsworth, 1990; Ellison et al., 1996) described an intriguing facultative mutualism between *Rhizophora* trees and their prop root-colonising sponges. Trees fringing creeks in Belize, with permanently submerged roots, grew adventitious rootlets within sponge tissues to extract nitrogen from sponges. Sponges in return were offered colonisation substrate as well as organic carbon by the trees and both organisms grew substantially faster when coexisting. Facilitation may also be instigated by vertebrates. For example, birds can boost tree production through providing growth-limiting nutrients. Mangroves offer preferential roosting sites to many bird species that feed on adjacent mudflats (Buelow and Sheaves, 2015). Bird roosting sites may be restricted to select areas of the forest, the preference for which may last for years (Pearse, 2010). Bird guano in such habitual roosting areas can offer a locally significant and steady supply of nutrients that ultimately boost tree growth (Onuf et al., 1977; Feller, 1995).

17.5.2 Indirect Protection from Herbivores by Epibionts or Predators

A variety of indirect ecological interactions have been shown to reduce the negative impacts of stem-borers on mangrove prop roots and folivores on mangrove leaves. Mats of epibionts, comprised of colonial ascidians and sponges, commonly grow on the surfaces of submerged young *R. mangle* prop roots. As described earlier, these may include organisms that lessen the chemical stress of nutrient limitation through mutualistic associations, and they can also affect biological stresses by deterring attacks by stem-boring isopods (Ellison and Farnsworth, 1990, 1992). The mechanism(s) by which an encrusting layer of ascidians and sponges blocks isopods is unknown; it may act as a physical and/or chemical barrier to their recruitment and boring activity.

Emergent portions of mangrove trees may be indirectly protected from insect herbivory by associated predators, including ants and lizards. In these tri-trophic interactions, the predators reduce the density of insect herbivores, indirectly benefitting the plant. Mangrove protection by ants is well documented, with examples from both comparative and experimental studies. Ozaki et al. (2006) compared rates of predation on populations of the scale insect, *Aulacaspis marina* (Homoptera: Diaspididae) infesting potted seedlings of *R. mucronata* introduced into mature natural forests and young plantations growing in abandoned shrimp ponds, on Bali Island, Indonesia. In the natural forests, two species of ants (*Monomorium floricola* and *Paratrechina* sp.) preyed heavily on the scale insects, suppressing their density by 88 per cent in seven days. By comparison, only 28 per cent were eaten in the plantation sites, probably because the young trees in these sites afforded few ant nesting sites and the inundated soils prohibited ants from nesting in the ground. A second experiment in which ants were excluded from half the seedlings with sticky barriers applied to their lower stem confirmed that ants accounted for almost all the scale insect mortality.

Offenberg et al. (2004) documented a negative correlation between the density of arboreal weaver ants (*Oecophylla smaragdina*) and levels of herbivory on *R. mucronata* leaves in a Thai mangrove forest. Trees lacking ants had more than three times the herbivore leaf damage of trees with ant nests. On trees with ants, leaves near the nest suffered less damage than those in other areas of the canopy. Most of the leaf damage was caused by chrysomelid beetles and sesamid crabs; both were deterred by the presence of ants, and ants were observed preying on the beetles. In this case, the relationship might be considered a weak form of ant–plant mutualism, since the ants weave the host mangrove leaves together to build their nest (Offenberg et al., 2004). Weaver ants have long been used for herbivorous insect pest control in a variety of tree crop systems (Van Mele, 2008). An earlier study of insect herbivory rates in a Papua New Guinea mangrove forest (Johnstone, 1981) did not detect a statistically significant relationship between standing leaf damage and the presence of *O. smaragdina* colonies. While the mean percent of leaf area eaten tended to be higher on trees that had no ants, compared to those with ant colonies, there was high variation in herbivory rates among trees with similar densities of ants. The difference in the findings of Offenberg et al. (2004) and Johnstone (1981) likely stems from a fundamental difference in method. The former study focussed on a single host plant species that is frequently occupied by weaver ants, while the latter compared rates for a pooled sample of leaves from twenty-three different species of mangroves, which varied in their attractiveness to the ants. This undoubtedly introduced considerable variation in other leaf attributes that affect rates of herbivory.

Ants also play a defensive role on small Bahamian islands, where the buttonwood mangrove, *Conocarpus erectus*, dominates the shoreline vegetation. This plant has extrafloral nectaries that attract a variety of insects, including nine species of ants. Its leaves come in two morphs, a silver form that has a dense layer of leaf hairs or trichomes on their surface, and a green form that has very few trichomes. Trichomes function as a structural defence against folivorous insects

(Schoener, 1987, 1988; Agrawal and Spiller, 2004); silver plants have fewer extrafloral nectaries than green plants, and they produce less nectar and attract fewer ants (Piovia-Scott, 2011). Experimental exclusion of ants from low-trichome plants resulted in higher herbivore damage and lower new leaf production compared to control plants accessible to ants. In contrast, ant exclusion from silver plants had no measurable effect of either leaf damage or leaf production (Piovia-Scott, 2011). *Anolis* lizards also prey on insect folivores of *C. erectus* on these islands; some islands support lizard populations and others lack them. In a survey of seventy-four islands, total leaf damage was 42–59 per cent greater on no-lizard- than lizard-inhabited islands (Schoener, 1988).

17.5.3 Facilitation Cascades and the Scaling-Up of Faunal Facilitation of Mangroves

Mangrove trees act as foundation species, creating complex habitats that support multiple other species which together constitute the mangrove ecosystem. When an independent foundation species supports other, dependent foundation species, which themselves facilitate the survival of different organisms, a facilitation cascade may ensue, with facilitatory effects rippling between trophic levels (Angelini et al., 2011). Bishop et al. (2012) describe such a cascade in *Avicennia marina* forest, where beyond a threshold density of pneumatophores capture of algae facilitate fauna that depend on algae to ameliorate environmental stressors, including desiccation risk. Such facilitatory cascades may have profound implications for ecosystem functioning, when the array of facilitated species has distinct functional roles. Angelini et al. (2015) found that colonisation by mussels, which are secondary foundation species in North American salt marshes, facilitated an array of species that together stimulated marsh accretion, carbon sequestration, marsh grass production and faunal functional richness. Crabs could be argued to have a similar secondary foundation role in mangroves, potentially leading to facilitatory cascades of benefit to trees. Their facilitation of other organisms is certainly diverse, from providing habitat to other

invertebrates, to facilitating the growth of mycorrhizal fungi and microphytobenthic species (Alongi, 1994; Gillikin et al., 2001; Daleo et al., 2007). Predatory as well as herbivorous crabs may act as facilitators. An observed reduction in salt marsh plant production in the USA has been attributed to 40–80 per cent reductions in predatory blue crab and fish populations and their natural control of herbivorous snails and crabs (Altieri et al., 2012). So far, there is no firm evidence of fauna regulating facilitation cascades in mangroves, but the likelihood of it occurring is high.

17.6 | Forest Resilience in the Face of Long-Term Change

The intertidal zone is a place of daily, seasonal and decadal flux. Colonising new areas in response to long-term change, driven for example by sea-level rise (SLR) or altering river flows, allows mangroves to adapt. This spatially based resilience relies in part on the facilitative mechanisms discussed earlier; the ability for pioneer plants to exploit windows of opportunity in bare substrate, often supported by interactions with other organisms. But there are many locations where the prospects for forest migration, inshore or offshore, are limited; for example, some mangroves grow on coral islands with no hinterland and forests are increasingly restricted from movement in-land by anthropogenic structures and activities. The absence of room to move does not, however, mean that a mangrove forest lacks resilience and the ability to persist over time. For example, Caribbean mangroves growing in areas without alluvial deposits and with limited opportunities to move spatially are able to adjust to rising sea level through the deposition of organic matter, with some now growing on 10 m of peat representing thousands of years of adjustment (McKee et al., 2007a). This ability of mangroves to elevate their soil surfaces in response to rising sea levels relies on a large range of factors, including the above- and below-ground productivity stimulated by fauna and the sediment trapping assisted by conspecific density (Krauss et al.,

2014), and burrowing crabs may also be important agents in helping to store organic carbon below ground (Andreotta et al., 2014).

Hence, facilitatory processes assist in the long-term persistence of mangroves and contribute to the enormous carbon density of these forests (Figure 17.4). Change (over space and time) is a central feature of mangrove systems. Over the past twenty years, the paradigm of ‘balance of nature’ has largely been replaced among ecologists by ‘resilience thinking’ (Walker and Salt, 2012), but conservation of the status quo is still a common goal for managers and the broader conservation movement. A focus on resilience mechanisms is essential to identify the relevant spatial and temporal scales at which ‘self-similarity’ (Jax et al., 1998), ‘integrity’ (Cumming and Collier, 2005) and ‘persistence of relationship’ (Holling, 1973) self-guard ecosystem functioning.

17.7 | Conclusions

Benignity is seldom found in alliance with strength.

Alexander von Humbolt

The SGH suggests that searching for facilitation within mangrove ecosystems should be fruitful; these forests are miracles of productivity and persistence in the face of the multiple stresses that they naturally face. Our brief review confirms this prediction. Facilitation can be found at all stages of the lives of individual trees and of the forest ecosystems themselves. While reports of the amelioration of physical and chemical stresses predominate, we also present evidence of how facilitative interactions can help limit the biological stress of herbivory. What remains unclear, however, is whether these diverse observations can inform a coherent theory of facilitation in mangrove ecosystems. While the complex interplay of plant diversity, density and environmental stressors in creating context-specific outcomes is slowly being understood in other, much simpler, plant communities, such as alpine cushion plants (Schöb et al., 2014), a comparable understanding of

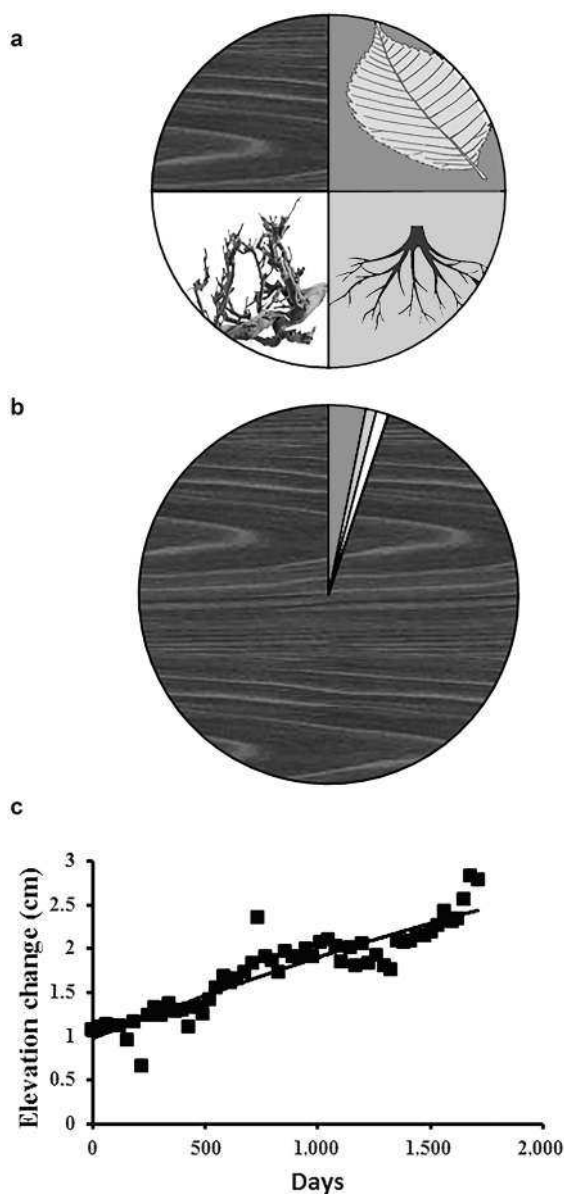


Figure 17.4 The accumulation of carbon in the *R. mucronata* forest of Gazi Bay, helping with resilience of the forest in the face of SLR and resulting from multiple forms of facilitation. There are four main components of the long-term (years, decades or longer) carbon pool: (a) (clockwise from top-left) soil organic carbon, above-ground biomass, below-ground biomass (living roots) and dead root materials. (b) These four pools, in the same order, but here represented as the percentage contribution to the total pool at Gazi, with soil organic carbon constituting 95 per cent of the total (data from Tamooch et al., 2008; Cohen et al., 2013; Gress et al., 2017; figures converted to $t\ C\ ha^{-1}$ equivalents, assuming carbon

contingent ecological outcomes that structure mangrove communities is yet to emerge. In part, this is because we are still in the process of discovering how these unique forests work. Modern methods of ecological research, particularly manipulative field experiments and mathematical as well as computational modelling, have been applied for a much shorter time and by fewer investigators in mangroves than in terrestrial habitats. Not surprisingly, new findings frequently contravene standard explanations derived from studies in other ecosystems. Mangroves contain pronounced stress gradients on relatively compact spatial scales. These gradients consist both of resources (e.g., nitrogen or phosphorous) and of non-resources (e.g., salinity or temperature). Mangrove flora and fauna must cope with multiple, interacting stress factors and all species vary in their stress tolerance and competitiveness. These factors make mangrove systems difficult to understand. But they also mean that mangroves provide an extraordinary laboratory for building a more comprehensive and general understanding of the role that facilitation and other processes play in structuring communities. Achieving this will require a coordinated and hypothesis-driven effort to experimentally disentangle the predictions of the refined stress-gradient hypothesis (Maestre et al., 2009) and its extensions by considering the interactive influences of abiotic and biotic processes across a range of environment settings. Mangrove researchers will need to work together to do this – therefore combine, and practice mutual aid.

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content of living roots, dead roots and living stems of 0.39, 0.5 and 0.47, respectively). (c) Surface elevation measured in ten plots from Gazi over fifty-eight months, showing 3.1 mm elevation per year, driven by below-ground accumulation of carbon.

and share ideas at the Aquatic Biodiversity and Ecosystems Conference in 2015 and the Mangrove and Macrobenthos Meeting 4 in 2016; thank you to all those who organised these meetings and invited us.

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