


A general framework for propagule dispersal in mangroves

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ABSTRACT

Dispersal allows species to shift their distributions in response to changing climate conditions. As a result, dispersal is considered a key process contributing to a species' long-term persistence. For many passive dispersers, fluid dynamics of wind and water fuel these movements and different species have developed remarkable adaptations for utilizing this energy to reach and colonize suitable habitats. The seafaring propagules (fruits and seeds) of mangroves represent an excellent example of such passive dispersal. Mangroves are halophytic woody plants that grow in the intertidal zones along tropical and subtropical shorelines and produce hydrochorous propagules with high dispersal potential. This results in exceptionally large coastal ranges across vast expanses of ocean and allows species to shift geographically and track the conditions to which they are adapted. This is particularly relevant given the challenges presented by rapid sea-level rise, higher frequency and intensity of storms, and changes in regional precipitation and temperature regimes. However, despite its importance, the underlying drivers of mangrove dispersal have typically been studied in isolation, and a conceptual synthesis of mangrove oceanic dispersal across spatial scales is lacking. Here, we review current knowledge on mangrove propagule dispersal across the various stages of the dispersal process. Using a general framework, we outline the mechanisms and ecological processes that are known to modulate the spatial patterns of mangrove dispersal. We show that important dispersal factors remain understudied and that adequate empirical data on the determinants of dispersal are missing for most mangrove species. This review particularly aims to provide a baseline for developing future research agendas and field campaigns, filling current knowledge gaps and increasing our understanding of the processes that shape global mangrove distributions.

Key words: fecundity, abscission, retention, predation, buoyancy, viability, obligate dispersal period, release–recapture, particle tracking, seascape ecology.

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I. INTRODUCTION

Dispersal is a critical process that determines a species' potential to colonize new habitats and unoccupied niches suitable for establishment (Howe & Smallwood, 1982), and for tracking favourable environmental conditions under climate change (Travis *et al.*, 2013). Species may survive climatic alterations through phenotypic plasticity or evolutionary adaptation, or *via* dispersal, by shifting geographically to track the conditions to which they are adapted (Berg *et al.*, 2010; Moritz & Agudo, 2013; Valladares *et al.*, 2014). Changing climate conditions have led to distributional shifts in a diverse range of marine and terrestrial taxa, typically to higher latitudes and higher elevations (Parmesan & Yohe, 2003; Chen *et al.*, 2011; Poloczanska *et al.*, 2013). Hence, quantifying dispersal and identifying the physical and biological factors that contribute to this process is of particular importance to understanding the distributional responses of species under future climate conditions. However, collecting dispersal data becomes increasingly difficult at larger spatial scales and information on ecological processes at regional and global scales cannot simply be obtained by extrapolating local-scale observational data (Bullock & Nathan, 2008). The difficulty in measurement and obtaining empirical dispersal data is particularly common in the marine environment, where ocean currents are the primary means of propagule (i.e. dispersal unit) transport, potentially over hundreds to thousands of kilometers (Kinlan & Gaines, 2003; Nathan *et al.*, 2008; Gillespie *et al.*, 2012).

Large-scale surveys and genetic and modelling approaches have allowed for significant advances in estimating the temporal variation and spatial scale of dispersal and connectivity (gene flow) in coastal and marine taxa (e.g. Cowen & Sponaugle, 2009; Hogan *et al.*, 2012; Le Corre *et al.*, 2015). For example, while some coastal species are capable of transoceanic dispersal by relying on a set of unique adaptations (Sykes & Godley, 1968), a number of studies suggest that the spatial scale of larval transport in nearshore benthic invertebrates and fishes may be limited (Cowen *et al.*, 2000; Jones, Planes & Thorrold, 2005), controlled by ocean

processes such as tides, mesoscale eddies, and fronts (Pineda, Hare & Sponaugle, 2007; Siegel *et al.*, 2008; Condie & Condie, 2016). Besides the role of physical (external) factors, other studies have focused on biological (internal) factors that govern dispersal and connectivity, such as the timing of reproduction (Carson *et al.*, 2010), fecundity (Castorani *et al.*, 2017), and body size (Villarino *et al.*, 2018). Identifying these factors is important to understanding population and species persistence and to align conservation and management strategies with ecological processes (e.g. Gaines, Gaylord & Largier, 2003; Treml & Halpin, 2012). Surprisingly, while dispersal mechanisms and integrated dispersal frameworks are being explored in coastal and marine fauna such as seagrass and corals (e.g. Orth, Harwell & Inglis, 2006; McMahan *et al.*, 2014; Treml *et al.*, 2015; Grech *et al.*, 2016), this has not been attempted for mangroves.

Mangroves comprise a group of terrestrially derived coastal shoreline plants suggested to have evolved around the Tethys Sea during the late Cretaceous to Paleocene–Eocene (Ellison, Farnsworth & Merkt, 1999). Recently, Guo *et al.* (2017) reported a post-Cretaceous–Paleogene boundary divergence of the mangrove clade from the terrestrial lineage within Rhizophoraceae. The mangrove ferns of the genus *Acrostichum* may have evolved and diverged from a terrestrial lineage in the late Cretaceous and are suggested to be among the oldest members of the mangrove ecosystem (Zhang *et al.*, 2016). Today, the mangrove ecosystem is predominantly found at tropical and subtropical latitudes, extending to temperate regions, with the extreme range limits at 32.28° N (Bermuda) and 38.45° S (East Australia) (Spalding, Kainuma & Collins, 2010). Growing along rivers and shores, mangroves have evolved traits to disperse by river and ocean currents, allowing for wide, transoceanic ranges in many species. Members of genera such as *Rhizophora* and *Avicennia* are found almost throughout the entire mangrove range. Ellison *et al.* (1999) concluded that modern ranges of mangroves result almost exclusively from vicariance events (followed by *in situ* speciation). However, since mangrove propagules are water-borne and ocean-surface currents connect regions globally on decadal time scales (Jönsson & Watson, 2016), dispersal can be expected also to shape these

ranges. Contemporary ocean-surface currents, for example, might transport propagules across entire ocean basins (directly or in a stepping-stone manner) (Van der Stocken *et al.*, 2019). If oceanic dispersal allows for long-distance transport, what then constrains mangrove species within their range limits? The latitude of mangrove range limits varies strongly among regions and has been associated with climatic factors (Quisthoudt *et al.*, 2012; Osland *et al.*, 2017; Cavanaugh *et al.*, 2018), geomorphological characteristics (Ellison, 2009), as well as oceanographic conditions and factors such as dispersal limitation (Soares *et al.*, 2012) or combinations of these (e.g. Ximenes *et al.*, 2018).

Despite the socio-ecological importance of mangroves for coastal protection, carbon sequestration (Donato *et al.*, 2011; Alongi, 2014; Atwood *et al.*, 2017), and wood and fish resources (Lee *et al.*, 2014), they are threatened by anthropogenic disturbances such as pollution and oil spills (Duke, 2016), over-exploitation for fuel and construction wood, urbanization, as well as conversion to aquaculture and agriculture (UNEP, 2014; Richards & Friess, 2016; Thomas *et al.*, 2017). This has resulted in increasingly fragmented and degraded mangrove forests globally (Hamilton & Casey, 2016) – thus reducing connectivity – but it remains to be studied to what extent this affects population persistence. Climate change will pose additional threats such as sea-level rise, changes in regional precipitation and temperature regimes, and the increased frequency and intensity of climate phenomena such as those generated by the El Niño Southern Oscillation (Gilman *et al.*, 2008; Krauss *et al.*, 2014; Alongi, 2015; Lovelock *et al.*, 2015, 2017; Ward *et al.*, 2016; Osland *et al.*, 2018). The potential of mangroves to adjust their phenotype to new conditions *via* acclimation and local adaptation is largely unknown. This is because responses to current environmental changes may be slow and experimentally testing responses of mangrove species to anticipated future conditions is practically challenging for this type of habitat (Ward *et al.*, 2016). Therefore, keeping track of changes in habitat suitability *via* dispersal and establishment in new areas with suitable conditions may be essential for mangrove populations and species to survive in the long term (Rogers, Saintilan & Heijnis, 2005; Cavanaugh *et al.*, 2014; Saintilan *et al.*, 2014; Osland *et al.*, 2017). Empirical dispersal kernels can be used to estimate the likelihood of dispersal events and the spatial scale of connectivity. However, even extremely rare long-distance dispersal (LDD) events become likely over time scales of decades and centuries (Jönsson & Watson, 2016). Despite the rarity of LDD, its importance in shaping the distribution of species has been underscored repeatedly (Cain, Milligan & Strand, 2000; Levin *et al.*, 2003; Soons & Ozinga, 2005; Trakhtenbrot *et al.*, 2005; Nathan, 2006; Ronce, 2007; Clobert *et al.*, 2012). Similarly, taxon-specific traits such as fecundity, the timing of propagule release, and propagule traits such as buoyancy and longevity, have been shown to affect dispersal and connectivity patterns (Cowen, Paris & Srinivasan, 2006; Carson *et al.*, 2010; McMahon *et al.*, 2014; Villarino *et al.*, 2018).

The present review aims to synthesize current knowledge and identify knowledge gaps on dispersal in mangroves across the various stages of the dispersal process (Fig. 1), by assembling available empirical data. We start by outlining all factors and processes that are known to modulate successful dispersal of mangrove propagules at different spatial scales in a general framework that splits the dispersal process into three main compartments: emigration, transfer, and immigration. We deliberately avoid exhaustive discussion of the biotic and abiotic conditions involved in propagule establishment, as these have been addressed extensively in previous reviews (Krauss *et al.*, 2008; Friess *et al.*, 2012). Based on this review, a baseline for a research agenda and field campaigns including oceanic surveys, with new, targeted questions emerges. The focus in this review is on mangroves, yet the general framework of dispersal is potentially applicable to other systems comprising ocean-dispersed organisms such as corals and seagrass. We note that while each of these systems is characterized by marine dispersal, their dispersal patterns and potential to adapt to future change may be different, given that the reproductive seasonality and fecundity in marine organisms have been linked to different environmental signals such as wind speed (van Woesik, 2010), sea surface temperature (Keith *et al.*, 2016), lunar phases (Shimose *et al.*, 2017), and moonlight intensity (Gorbunov & Falkowski, 2002), and the fact that active animal larvae have a greater mobility (e.g. behavioural traits such as vertical migration; Pineda *et al.*, 2007) than passive mangrove propagules which are buoyant and generally remain on the ocean surface.

II. A GENERAL FRAMEWORK OF MANGROVE DISPERSAL

Generally, dispersal can be represented by three stages (Bowler & Benton, 2005) (Fig. 1). The first stage, emigration, comprises the departure of propagules from the parental mangrove stand. Phenology (i.e. the timing of biological events such as flowering and seed production) controls the production and release of propagules in the field, and hence determines when propagules are available for dispersal. Fecundity is obviously a limiting factor for the number of propagules that are released and controls the abundance of potential emigrants (Castorani *et al.*, 2017). Local establishment (e.g. Balke *et al.*, 2013), predation (e.g. Farnsworth & Ellison, 1997), and propagule retention in the landscape matrix (e.g. Di Nitto *et al.*, 2013; Van der Stocken *et al.*, 2015a) ensure that a large amount of propagules will not leave the parental stand. The second stage, the dispersal or transfer stage, covers the movement of propagules from one site to another. This stage is governed by fluid dynamics with dispersal trajectories being modulated by tides and tidal flow, the effect of near-shore, coastal, and open-ocean currents, as well as wind (Rabinowitz, 1978; Di Nitto *et al.*, 2013; Van der Stocken *et al.*, 2015b). Propagules can disperse within the same population [short-distance dispersal (SDD)], to nearby or distant populations [long-distance dispersal

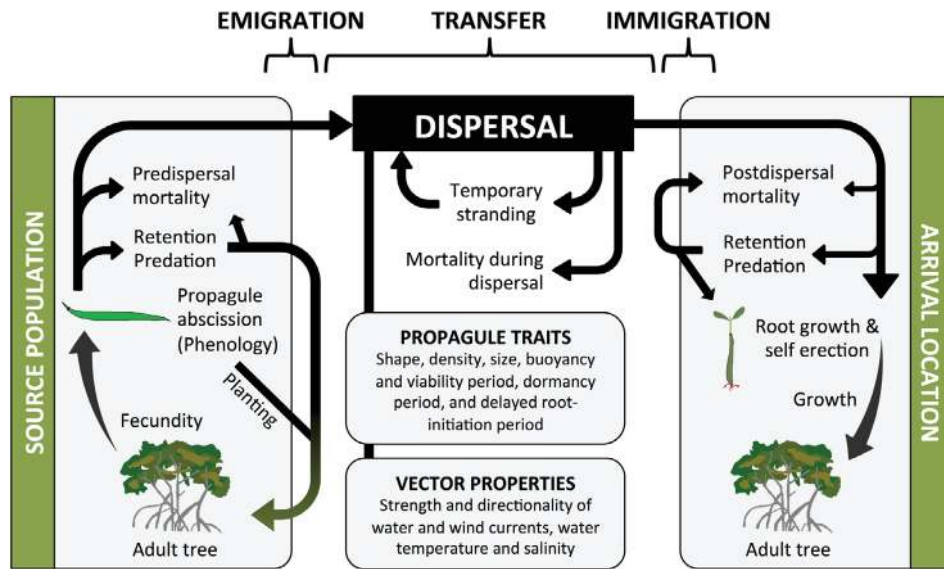


Fig. 1. Mangrove dispersal is determined by a range of factors. Fecundity and predation determine the number of propagules available for dispersal, and in combination with retention in the landscape matrix, the potential number of emigrants. Propagule traits such as buoyancy, viability and dormancy determine the timeframe within which propagules can take root and establish at a suitable location. The site of arrival depends on interactions between propagule traits (size, shape and density), hydrology, and the landscape matrix. While tides and tidal currents can transport propagules within a mangrove stand, the trajectories of propagules reaching open waters will be determined also by near-shore, coastal, and open-ocean currents, as well as by winds in the case of wind-sensitive propagules (e.g. *H. littoralis*). Whether or not a dispersal event is followed by successful establishment and early seedling development will depend on several biotic (e.g. predation, competition) and abiotic (e.g. sediment conditions, temperature, hypoxia, hydrogen sulphide concentrations, salinity, light, nutrients, tides and flooding, sea-level changes) factors. In contrast to long-distance dispersal events, which we here define as dispersal between (nearby or distant) populations, the arrival location is situated within the source population in the case of short-distance dispersal events and ‘emigration’ and ‘immigration’ do not apply. Some factors are influenced by climatic conditions (e.g. phenology) so that climate change is likely to affect dispersal and connectivity patterns. Additional anthropogenic stressors such as clearing can strongly impact the number of propagules available (e.g. fecundity) and the area of suitable habitat. More knowledge about these factors is important to understand better the resilience of mangrove species to various future scenarios of environmental change.

(LDD)], or between a mangrove stand and a new location that lacks established mangroves. Given that water and wind currents vary in time, the actual distance of dispersal and the potential of a stranded propagule to establish in a certain area will depend on the time of propagule release (Van der Stocken, López-Portillo & Koedam, 2017). While water currents represent the standard dispersal vector in mangroves, wind has been shown to influence dispersal trajectories and probably more so for propagules that protrude more from the water (Van der Stocken *et al.*, 2015b). Therefore, emigration of propagules from various species from a particular stand can result in different trajectories. Whether a dispersal event will ultimately result in actual connectivity, i.e. dispersal followed by successful establishment, will depend on post-dispersal processes in the third stage, immigration, following arrival and establishment.

III. DETERMINANTS OF PROPAGULE NUMBERS

Estimating the number of propagules originating from a source requires information on the demography of different

species, which includes the age of maturation, fecundity, and the mortality rate of different life stages. Additionally, to predict dispersal events we need to know the timing of propagule release, the position of the source (parent tree) in the habitat, how release varies over time, and which environmental cues lead to propagule abscission (i.e. controlled natural detachment).

(1) Fecundity

Fecundity determines the abundance of propagules that can be released. As such, it constrains the potential for dispersal and connectivity (Castorani *et al.*, 2017). All else being equal, species with higher fecundity should have a larger number of potential emigrants compared to species with lower fecundity. Thus, higher fecundity is expected to result in a higher number of dispersal events, and an increased probability of LDD (Corlett & Westcott, 2013). In reality, individuals differ in more than just fecundity. A high fecundity might be of little importance if there is a trade-off between the number of propagules and the survival rate of propagules, or when the morphology of the propagule or its establishment strategy favour dispersal over short distances.

High fecundity is a typical terrestrial forest pioneer strategy (Swaine & Whitmore, 1988), and is observed in pioneer mangrove genera such as *Sonneratia* (Lythraceae), *Avicennia* (Acanthaceae), and *Laguncularia* (Combretaceae) (Friess *et al.*, 2012). *Sonneratia* differs from the other mangrove pioneer genera in that it produces fruits that contain a high number (>100) of seeds; these seeds are released once the fruit disintegrates after prolonged immersion in saline or brackish water (Ball & Pidsley, 1995).

Few studies have quantified the number of propagules per plant in the field. This is most likely due to the labour intensity of acquiring such data and the difficulty of reliably extrapolating tree-specific counts to the stand level, given that such counts may vary greatly among individual trees. Clarke (1992) reported counts between 422 and 5210 propagules annually per tree for *Avicennia marina* (Forssk.) Vierh. stands in south-eastern Australia, with an estimated annual average realized fecundity (i.e. potential fecundity minus losses during development) of ca. 247 viable propagules per tree. Dahdouh-Guebas *et al.* (1998) observed over 500 mature propagules hanging per tree for *Ceriops tagal* (Perr.) C.B. Robinson in Gazi Bay (Kenya). However, fecundity is likely to vary with tree age, with older trees producing more flower buds than younger ones (Clarke, 1992), and it has been found that propagule production is higher for trees in larger mangrove stands as compared to trees in smaller stands (Hermansen, Minchinton & Ayre, 2017). The latter is particularly relevant in the context of habitat fragmentation, directing conservation efforts towards the largest possible stands. Additionally, as light levels may influence the assimilation and growth of mangrove seedlings (Krauss & Allen, 2003; López-Hoffman *et al.*, 2006), it would be worth investigating whether gradients in fecundity exist from the forest edge to the forest interior, depending on light availability.

Besides interspecific differences, net population propagule production may be significantly affected by other factors such as freshwater input, drought length, nutrient influx (Amarasinghe & Balasubramaniam, 1992), herbivory rates (Anderson & Lee, 1995), and pre-abscission propagule predation (Clarke, 1995), or in relation to climatic variables such as mean daily air temperature (Duke, 1990). Other authors have suggested that variations in fecundity may also relate to the type of mangrove system. For example, riverine mangrove forests have been reported as more productive than fringing forests, since the inflow of rivers enhances the availability of nutrients (Chale, 1996). Furthermore, fecundity may exhibit important inter-annual variation, and the rate of propagule production can be modulated by natural disturbances such as tropical cyclones. For example, following the 2004 hurricane Charley in Florida (USA), it was found that propagule production and seedling recruitment in *Rhizophora mangle* L. dropped significantly (Proffitt, Milbrandt & Travis, 2006), while Alleman & Hester (2011) reported a greater number of propagules for *Avicennia germinans* L. trees along the Louisiana coast in the years following hurricanes Katrina (23 August 2005) and Gustav (1 September 2008).

Fecundity may also be determined by pollination. This is shown for example by disturbance through fragmentation of mangroves in urban contexts where pollination can be limiting (Wee, Low & Webb, 2015; Hermansen *et al.*, 2017). The evidence for mangrove pollination processes in the literature is restricted. Amazingly, Hermansen *et al.* (2014) found that the exotic honeybee was the only effective pollinator in a temperate mangrove area in Australia, stressing the need to understand mangrove pollination and its relation to fecundity better. Additionally, identifying pollinators and understanding the mutualistic networks of which they are part is also useful to predict the response of ecosystems and their functioning to processes such as species invasions and climate change. In a study on the Mariana islands Guam and Saipan, for example, Mortensen, Dupont & Olesen (2008) investigated flower visitation, seed set, and germination in the bird-pollinated mangrove species *Bruguiera gymnorhiza* (L.) Lamk., and documented how the effects of a high density of the invasive brown tree snake (*Boiga irregularis*) on Guam had cascaded through the entire ecosystem. In contrast to high numbers of native birds on the island of Saipan with nearly no snakes, the researchers found that flower-visitation rates by birds were zero on Guam, and had resulted in significantly lower seedling recruitment.

While the multiple drivers of mangrove fecundity require further investigation, observed variation in fecundity in the main mangrove genera can, at least partly, be explained by an evolutionary trade-off between the number of propagules produced and the individual propagule size (Alleman & Hester, 2011). *Rhizophora* spp. trees (Rhizophoraceae) may exhibit relatively low fecundity due to high investment in tree and propagule biomass. For example, Amarasinghe & Balasubramaniam (1992) found that *Rhizophora mucronata* Lamk. trees produce a lower biomass of reproductive parts than *A. marina* trees located within the same estuary. It is interesting to note that the (partial) photosynthetic autonomy of the growing large-sized propagules (e.g. up to 50–70 cm long in the Rhizophoraceae representatives; Smith & Snedaker, 2000) has not been investigated but could alleviate parental investment in storage of carbohydrates in the hypocotyl, analogous to seed filling.

(2) Propagule predation

When predation is sufficiently high it can lead to failed recruitment with fewer viable propagules available for dispersal (Robertson, Giddins & Smith, 1990; Clarke, 1992). Although some studies have reported the consumption of propagules by snails (Smith *et al.*, 1989) and fish (Macnae, 1969), predation has been most commonly attributed to two sources: insect infestation on developing seeds or fruits, and post-abscission damage by grapsid and sesarmid crab herbivory (Robertson *et al.*, 1990; Dahdouh-Guebas *et al.*, 1997; Farnsworth & Ellison, 1997; Cannicci *et al.*, 2008). Pre-abscission propagule predation by burrowing beetles, moth larvae, and crabs is a common phenomenon in mangroves, with an estimated global predation rate of 23%

across species (Farnsworth & Ellison, 1997) but substantial site-specific variation (Table 1).

Predation pressure depends on the composition and density of local predator species or parasite assemblages which are inextricably linked to factors such as tidal elevation, mangrove species composition and intertidal position (see dominance-predation hypothesis; Smith, 1987), root structure and density, and nutritional value of the propagules (McKee, 1995; Farnsworth & Ellison, 1997; Dahdouh-Guebas *et al.*, 2011; Van Nederveelde *et al.*, 2015). In a tracking experiment, De Ryck *et al.* (2012) found no predation on *C. tagal* and *R. mucronata* propagules in the most landward site and the most seaward mangrove fringe in Gazi Bay (Kenya), while predation was higher in the mid-intertidal locations beneath dense mangrove canopy. This can be explained by higher leaf litter and mangrove propagule availability, and hence higher crab densities, following reported evidence for increased predation with crab density (Van Nederveelde *et al.*, 2015). However, this association applies only up to a certain limit above which predation rates may be reduced following increased competition between crabs (Van Nederveelde *et al.*, 2015). By contrast, other propagule-predation studies across the entire intertidal zone show nearly 100% predation by *Neosarmatium africanum* in landward stands dominated by *A. marina* (Dahdouh-Guebas *et al.*, 1997, 1998). The variable predation rates across the aforementioned studies carried out in the same forest might be explained by the heterogeneity of propagule predators across the forest, in part dependent on canopy gaps (Bosire *et al.*, 2005).

The actual impact of predation on propagule survival depends on the amount and type of damage on the propagule (Cannicci *et al.*, 2008). Predation has an impact at two scales. At larger ecosystem scales, crabs have been shown to influence tree density and size, as well as species composition [see Lindquist *et al.* (2009) for a review]. Predation pressure has been suggested as a limiting factor for mangrove species distributions within mangrove stands since mangrove species producing small seeds (e.g. *Avicennia* spp.) that are more susceptible to predation can be excluded from areas where crab densities are too high (Smith, 1987), in conjunction with other physical processes. However, the impact of predation may be species-specific due to the preferences of predators (McKee, 1995). Predation can also influence large-scale macro-ecological patterns, for example by suppressing colonization of suitable habitat as shown in *A. germinans* L. near the northern range limit along Florida's Gulf Coast (Langston, Kaplan & Angelini, 2017). At the individual scale, predation pressure on different mangrove species may impact dispersal by limiting the number of propagules available for emigration. Plant strategies to deal with high predation pressure have been reported previously, such as variation in palatability (Cannicci *et al.*, 2008), and coordinated abscission of large numbers of propagules that can saturate predators (Dahdouh-Guebas *et al.*, 1997). However, in any case, herbivory on establishing propagules in its widest sense (comprising parasitism, propagule predation, or herbivory)

is likely to decrease or annihilate the effective output of dispersers for establishment.

(3) Retention within a mangrove stand

Once a propagule abscises from the parent tree, the spatial distribution of dispersing propagules will be controlled by the interactions between propagule traits (e.g. size, shape, and buoyancy), hydrology, and interactions with the landscape matrix. Mangrove propagules show a wide variety of morphologies (Fig. 2). The size of mangrove propagules ranges from 1 cm in *Lumnitzera* spp. to 70 cm or longer in *R. mucronata* (Tomlinson, 2016). In *Sonneratia* spp., a fruit with a diameter of 1–7 cm can contain seeds of only 0.1–0.2 cm in size (Tomlinson, 2016). Intuitively, smaller propagules would appear to have a higher LDD probability because they are less easily retained among the dense aerial root system during dispersal. Indeed, Sousa *et al.* (2007) found that the larger propagules of *R. mangle* were transported on average 200 and 20 times nearer to the source over a two-week period than the smaller propagules of *Laguncularia racemosa* (L.) Gaertn. f. and *A. germinans*, respectively. Similarly, release–recapture experiments by De Ryck *et al.* (2012) showed that the larger propagules of *R. mucronata* are more likely to become stuck in the root systems of other mangrove trees than are the smaller and thinner propagules of *C. tagal*. Besides propagule size, differences in retention rates may also be due to variations in propagule floating orientation (Van der Stocken *et al.*, 2015a). In addition, root systems attract complex debris, which in turn entangles propagules regardless of their orientation (Sousa *et al.*, 2007). While retention diminishes the fraction of propagules that contribute to LDD, retention is also important for establishment in a bare environment under a tidal regime, like mudflats or sandbanks, and may contribute to the spatial distribution of seedling cohorts (Sousa *et al.*, 2007).

The importance of trapping agents and the effect of barrier density on retention rates has been demonstrated in various studies in the field, under controlled conditions in a flume racetrack (i.e. an engineered channel for conveying water), and using numerical models. For example, Sousa *et al.* (2007) found a strong variation in dispersal distance due to physical barriers such as fallen logs and other emergent substrates that blocked propagule movement. In another dispersal experiment, De Ryck *et al.* (2012) found that in the less densely rooted mangrove fringes, dispersal events covered greater distances, while dispersal distances were shorter in the densely vegetated inner mangroves. Although this may imply a high potential for local rejuvenation, predation was very high, especially on *C. tagal* propagules (up to 90% in the inner mangrove). Similar interactions between propagule traits and barrier density were found in a flume racetrack experiment, where vertical bamboo sticks of varying diameter were used as aerial root mimics to assess retention rates of different mangrove propagule types, considering different root densities and water flow speeds (Van der Stocken *et al.*, 2015a). These experiments showed that dispersal distance decreases with increasing root density,

Table 1. Propagule predation as established for propagules from selected mangrove species. A question mark denotes that the predator species were not mentioned in the respective source. For detailed information on the study site(s), experimental period and the number of propagules considered, the reader is referred to the respective source

| Species | Predation (%) (± S.D., if available) | Main predator species | Location | Reference |
|---------------------------------|--|---|---|-------------------------------------|
| <i>Avicennia alba</i> | 62.5 (± 7.6) | <i>Sesarma</i> spp. | Pulau Kechil, Matang (Malaysia) | Smith <i>et al.</i> (1989) |
| <i>Avicennia marina</i> | 50 (± 40) | ? | Global study (41 sites) | Farnsworth & Ellison (1997) |
| <i>Avicennia marina</i> | 96.0 (± 1.8) | ? | Queensland (Australia) | Smith (1987) |
| <i>Avicennia marina</i> | 65–90.4 | ? | Queensland (Australia) | Robertson <i>et al.</i> (1990) |
| <i>Avicennia marina</i> | 0–100 | <i>Neosarmatium africanum</i> , <i>N. smithii</i> and <i>Perisesarma guttatum</i> | Gazi Bay (Kenya) | Dahdouh-Guebas <i>et al.</i> (1998) |
| <i>Avicennia marina</i> | 51.8 (± 10.9) | <i>Sesarma</i> spp. | Missionary Bay, Hinchinbrook Island, Queensland (Australia) | Smith <i>et al.</i> (1989) |
| <i>Avicennia germinans</i> | 60 (± 8) | <i>Goniopsis cruentata</i> and <i>Ucides cordatus</i> | Twin Cays (Belize) | McKee (1995) |
| <i>Avicennia germinans</i> | 72.0 (± 8.8) | <i>Aratus pisonii</i> and <i>Sesarma curacaoense</i> | Snake Bight, Everglades National Park (Florida) | Smith <i>et al.</i> (1989) |
| <i>Avicennia germinans</i> | 6.0 (± 3) | <i>Aratus pisonii</i> and <i>Sesarma curacaoense</i> | Coot Bay Pond, Everglades National Park (Florida) | Smith <i>et al.</i> (1989) |
| <i>Avicennia officinalis</i> | 46.4 (± 10.8) | <i>Sesarma</i> spp. | Pulau Kechil, Matang (Malaysia) | Smith <i>et al.</i> (1989) |
| <i>Bruguiera cylindrica</i> | 5.2 (± 6.1) | <i>Sesarma</i> spp. | Pulau Kechil, Matang (Malaysia) | Smith <i>et al.</i> (1989) |
| <i>Bruguiera gymnorhiza</i> | 40.0 (± 12.8) | <i>Sesarma</i> spp. | Missionary Bay, Hinchinbrook Island, Queensland (Australia) | Smith <i>et al.</i> (1989) |
| <i>Bruguiera gymnorhiza</i> | 27.5 (± 35) | ? | Global study (41 sites) | Farnsworth & Ellison (1997) |
| <i>Bruguiera gymnorhiza</i> | 59.0 (± 6.4) | ? | Queensland (Australia) | Smith (1987) |
| <i>Bruguiera gymnorhiza</i> | 54.2–80.5 | ? | Queensland (Australia) | Robertson <i>et al.</i> (1990) |
| <i>Bruguiera gymnorhiza</i> | 0–100 | <i>Neosarmatium africanum</i> , <i>N. smithii</i> and <i>Perisesarma guttatum</i> | Gazi Bay (Kenya) | Dahdouh-Guebas <i>et al.</i> (1998) |
| <i>Bruguiera gymnorhiza</i> | 0–100 | <i>Neosarmatium meinerti</i> | Galle-Unawatuna (Sri Lanka) | Dahdouh-Guebas <i>et al.</i> (2011) |
| <i>Bruguiera gymnorhiza</i> | 50 (± 25.2) | <i>Neosarmatium meinerti</i> | Chilaw Lagoon (Sri Lanka) | Dahdouh-Guebas <i>et al.</i> (2011) |
| <i>Ceriops tagal</i> | 24.9 (± 23) | ? | Global study (41 sites) | Farnsworth & Ellison (1997) |
| <i>Ceriops tagal</i> | 71.7 (± 4.3) | <i>Neosarmatium smithii</i> | Queensland (Australia) | Smith (1987) |
| <i>Ceriops tagal</i> | 10.2–12 | ? | Queensland (Australia) | Robertson <i>et al.</i> (1990) |
| <i>Ceriops tagal</i> | 0–100 | ? | Gazi Bay (Kenya) | De Ryck <i>et al.</i> (2012) |
| <i>Ceriops tagal</i> | 0–100 | <i>Neosarmatium africanum</i> , <i>N. smithii</i> and <i>Perisesarma guttatum</i> | Gazi Bay (Kenya) | Dahdouh-Guebas <i>et al.</i> (1998) |
| <i>Heritiera littoralis</i> | 76.4–98 | ? | Queensland (Australia) | Robertson <i>et al.</i> (1990) |
| <i>Laguncularia racemosa</i> | 28 (± 9) | <i>Goniopsis cruentata</i> and <i>Ucides cordatus</i> | Twin Cays (Belize) | McKee (1995) |
| <i>Rhizophora apiculata</i> | 19.8 (± 6.3) | <i>Sesarma</i> spp. | Missionary Bay, Hinchinbrook Island, Queensland (Australia) | Smith <i>et al.</i> (1989) |
| <i>Rhizophora apiculata</i> | 6.3 (± 2) | <i>Sesarma</i> spp. | Pulau Kechil, Matang (Malaysia) | Smith <i>et al.</i> (1989) |
| <i>Rhizophora mangle</i> | 0 | <i>Aratus pisonii</i> and <i>Sesarma curacaoense</i> | Flamingo, Everglades National Park (Florida) | Smith <i>et al.</i> (1989) |
| <i>Rhizophora mangle</i> | 0 | <i>Aratus pisonii</i> and <i>Sesarma curacaoense</i> | Coot Bay Pond, Everglades National Park (Florida) | Smith <i>et al.</i> (1989) |
| <i>Rhizophora mangle</i> | 18 (± 5) | <i>Goniopsis cruentata</i> and <i>Ucides cordatus</i> | Twin Cays (Belize) | McKee (1995) |
| <i>Rhizophora mangle</i> | 100.0 (± 0) | <i>Goniopsis cruentata</i> | Panta de San Blas (Panama) | Smith <i>et al.</i> (1989) |
| <i>Rhizophora mucronata</i> | 33.7 (± 31.2) | ? | Global study (41 sites) | Farnsworth & Ellison (1997) |
| <i>Rhizophora mucronata</i> | 0–100 | <i>Neosarmatium africanum</i> , <i>N. smithii</i> and <i>Perisesarma guttatum</i> | Gazi Bay (Kenya) | Dahdouh-Guebas <i>et al.</i> (1998) |
| <i>Rhizophora mucronata</i> | 0–75 | ? | Gazi Bay (Kenya) | De Ryck <i>et al.</i> (2012) |
| <i>Xylocarpus granatum</i> seed | 22.4 (± 8.6) | ? | Kosrae (Federated States of Micronesia) | Allen <i>et al.</i> (2003) |
| <i>Xylocarpus granatum</i> seed | 77.7–90.7 | ? | Queensland (Australia) | Robertson <i>et al.</i> (1990) |
| <i>Xylocarpus granatum</i> seed | 0–100 | <i>Neosarmatium africanum</i> , <i>N. smithii</i> and <i>Perisesarma guttatum</i> | Gazi Bay (Kenya) | Dahdouh-Guebas <i>et al.</i> (1998) |

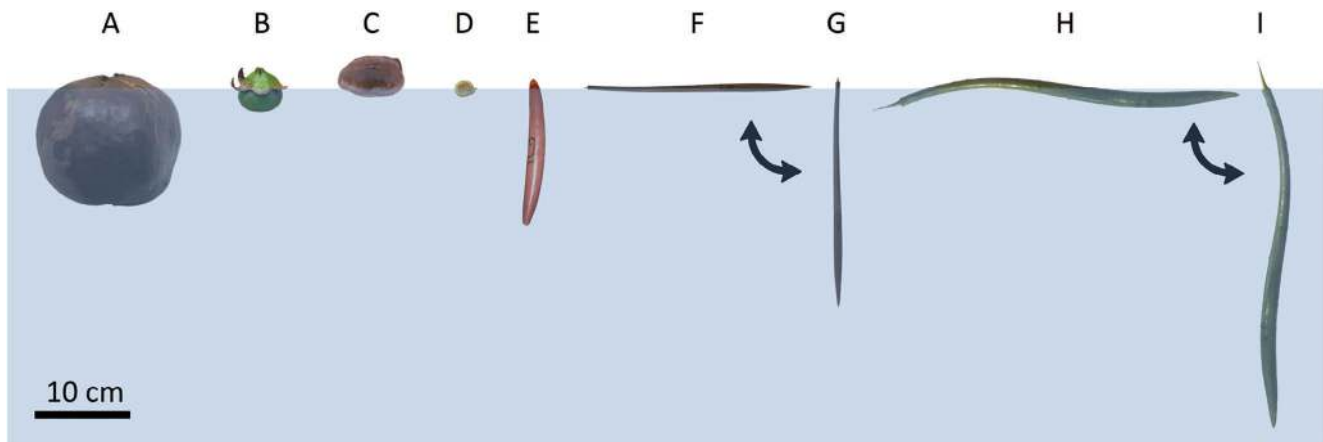


Fig. 2. Propagule types of different mangrove species and their position relative to the water surface while floating. Propagules are from the following mangrove species: *Xylocarpus granatum* (fruit) (A); *Sonneratia alba* (fruit) (B); *Heritiera littoralis* (C); *Avicennia marina* (D); *Bruguiera gymnorrhiza* (E); *Ceriops tagal* floating horizontally (F) and vertically (G); *Rhizophora mucronata* floating horizontally (H) and vertically (I) (after Van der Stocken *et al.*, 2018).

in spite of a continuous directed water flow, as observed also in other hydrochorous plant species (Redbo-Torstensson & Telenius, 1995; Chang *et al.*, 2008; Chambert & James, 2009). Similar results were obtained by Di Nitto *et al.* (2013) who combined a hydrodynamic model with knowledge on the propagule dispersal characteristics of four mangrove species, and using different propagule retention schemes. The authors reported that regardless of the modelling scenarios, SDD was common among all of the species studied (max. 5% LDD), with most propagules being retained within the vegetation. Additionally, field observations suggest that wave action could strongly reduce root retention of propagules (T. Van der Stocken, personal observations), but this remains to be tested formally.

Given the importance of barrier density, propagule transport will also depend on the position of the propagule source (parent tree) in the landscape (Fig. 3A). Within a mangrove stand, for example, the intricate tangled root system of mangrove trees can affect dispersal by constraining propagule movements and the number of propagules reaching open water. Typically, propagules from trees near the edge of the stand or near transport-facilitating channels could be transported over longer distances, facing fewer physical barriers (Breitfuss *et al.*, 2003; Di Nitto *et al.*, 2013). Furthermore, locations differ in elevation and access to tidal water and hence in the depth, duration, and frequency of flooding (Mazda *et al.*, 2005). Although Sousa *et al.* (2007) did not observe a significant effect of tidal elevation on propagule movement, frequent flooding and longer inundation times could increase the probability of propagule transport. Water-depth is important as it determines the potential for free flow. On some occasions for example, water level may reach the canopy (Fig. 3B), especially in seaward stands of short-stature mangroves such as found in arid regions or at the latitudinal limits of mangrove forests. Propagules in the inner forest may then face a dense barrier represented by surrounding tree canopy cover, in

which they can become stuck during transport (T. Van der Stocken, personal observation). As water level changes, barrier density may decrease (Fig. 3C). At low tide, the root system can be exposed or propagule dimensions may exceed the water depth (Fig. 3D), hampering transit. This variation in barrier density will depend on the vertical complexity of the vegetation, including the root system (e.g. pencil roots, peg roots, knee roots, plank roots, prop roots, and stilt roots), and the position within the intertidal area.

High-water events, such as spring and storm tides, have also been shown to facilitate propagule dispersal over vast stretches of salt marsh vegetation (Peterson & Bell, 2012). Yet, if tidal height does not exceed the average height of salt marsh vegetation structures, the latter is likely to hinder propagule dispersal (Peterson & Bell, 2012), depending on vegetation characteristics such as height and stiffness. For example, while propagules of *R. mangle* were found to be equally well retained in patches of the grass *Distichlis spicata* (L.) Greene and the succulent perennial creeper *Sesuvium portulacastrum* (L.), the smaller dispersal units of *A. germinans* and *Laguncularia racemosa* were more retained by the higher and stiffer *D. spicata* grass (McKee, Rooth & Feller, 2007). Quantifying this retention process is of particular importance in understanding the dynamics of mangrove–salt marsh ecotones (Rogers *et al.*, 2005; Rodriguez, Feller & Cavanaugh, 2016).

IV. TEMPORAL COMPONENTS OF DISPERSAL

For mangrove propagules that are successfully exported from a mangrove stand, the dispersal distance and direction will be controlled by the strength and directionality of prevailing dispersal vectors, and the propagules' interaction with the landscape matrix [e.g. retention; see also 'isolation by resistance' (McRae, 2006; Thomas *et al.*, 2015)]. Furthermore, since propagules abscise at particular

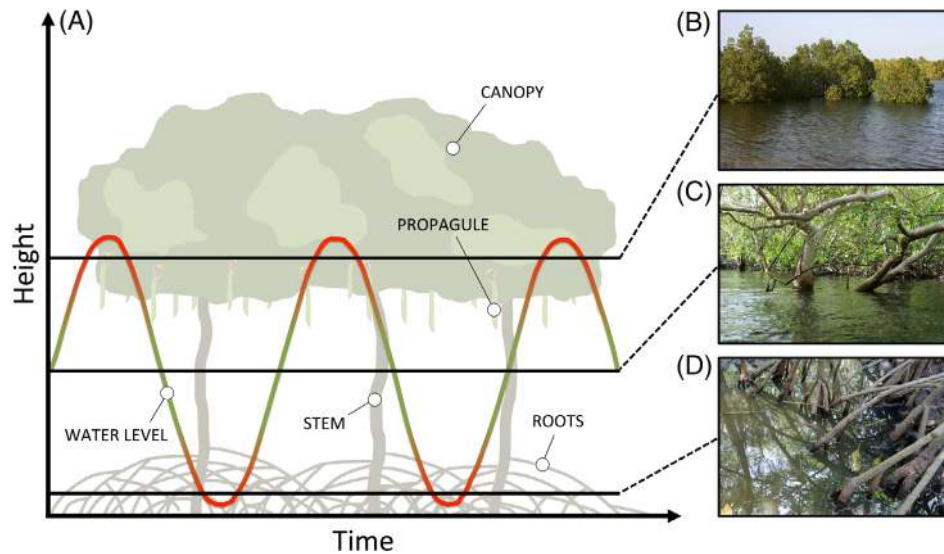


Fig. 3. Schematic illustration of dispersal barrier density variation over a tidal cycle (sinusoidal signal, simplified), using *Rhizophora* as an example case (A). Temporal changes in water level may increase (red) or decrease (green) barrier density and hence the potential for dispersal. Steric hindrance is particularly high when the water level reaches the canopy (B) or when the water level is within the vertical reach of the root structure (D). Steric hindrance is lower in the vertical reach where tree stems present a physical barrier that is less dense (C).

moments in time, and their viability and buoyancy period are finite, there is a constrained timeframe for a propagule to be transported by a vector from its release location to some other location. Here, we review the literature on the determinants that help to identify this timeframe that together with the relevant dispersal vectors determine the spatial scale of mangrove dispersal (see Section VI).

(1) Timing of propagule abscission and release

The timing of propagule abscission determines the moment that propagules become exposed to prevailing dispersal vectors. Nearshore, coastal and ocean currents vary temporally in both strength and directionality. Hence, the timing of propagule abscission can be expected to influence the overall trajectory of propagules as shown also in species with adaptations for dispersal by wind (Greene, 2005; Savage *et al.*, 2010). Duke (1990) suggested that for mangroves the initiation of the reproductive cycle (first appearance of immature buds) is related to day length. This would suggest a shorter peak period and a time shift in propagule production and release with increasing latitude. A meta-analysis of published data with reliable seasonal reports hinted at a latitudinal pattern in propagule release, to be tentatively explained by rainfall patterns worldwide, with *ca.* 70% of reported data on propagule release occurring in association with the wet season (Van der Stocken *et al.*, 2017). Other studies showed that phenology is associated with climatic factors such as rainfall and air temperature (Leach & Burgin, 1985; Saifullah, Khafaji & Mandura, 1989; Duke, 1990; Navarrete & Oliva-Rivera, 2002), soil salinity (Mehlig, 2006), and groundwater salinity (Agraz Hernández *et al.*, 2011). However, due to the complex

environmental determinants that govern phenology in mangroves, the phenology of propagule release can be highly species (Wium-Andersen, 1981; Sasekumar & Loi, 1983) and location specific (Wium-Andersen, 1981; Amarasinghe & Balasubramaniam, 1992), which may explain why no globally applicable insight is available to date. Interestingly, a substantial increase in precocious reproduction and propagule size with increasing latitude has been found at the northern range edge of *R. mangle* in Florida (Dangremond & Feller, 2016). While the consequences of propagule size increase for dispersal are unknown, the authors underscored the potential contribution of this precocious reproduction to rapid population growth and future range expansion northward, and its importance in altering (competitive) species interactions along the mangrove–salt marsh ecotone. Whether this pattern of early reproduction is also prevalent at the leading edge of range expansions on other continents remains unclear.

(2) Propagule buoyancy and viability

Mangrove propagules show a wide range of morphological adaptations to hydrochory including a corky testa (*Sonneratia* spp., *Xylocarpus* spp., and *Nypa fruticans* Wurumb.; see also Das & Ghose, 2003), a fibrous mesocarp (*Heritiera* spp.), aerenchyma tissue within the hypocotyl (*Rhizophora* spp.), fine hairs that trap air bubbles (*Osbornia octodonta* F. Muell. and *Acanthus* spp.), and a pericarp that potentially traps air before it is shed (*Avicennia* spp.) (Saenger, 2002; Tomlinson, 2016). Fine hairs of *Avicennia* propagules often facilitate clumping of propagules, which may also facilitate floating and direct passive movement. These morphological adaptations confer buoyancy and are inextricably linked to a propagule's

floating behaviour. Rabinowitz (1978) reported a gradual change from horizontal floating to vertical floating, and finally sinking, for propagules of *Rhizophora harrisonii*. These floating types have also been observed in *Kandelia candel* (L.) Druce and have been explained by changes in the specific gravity of propagules, being higher for the sinking type than for the floating type (Urasaki, Nehira & Nakagoshi, 1986). Tonné *et al.* (2017) combined anatomical analyses and buoyancy behaviour experiments to demonstrate that propagules of *B. gymnorrhiza*, *C. tagal*, and *R. mucronata* may lose buoyancy over time because the density of the propagule tissue increases. This process progresses from the plumule (embryonic shoot) towards the radicle (embryonic root) and may also change the floating orientation of a propagule from horizontal to vertical, potentially making it less wind-sensitive during dispersal (Van der Stocken *et al.*, 2013, 2015b).

Previous studies show that a substantial variation in buoyancy periods exists across mangrove species, ranging from almost no buoyancy in *Aegiceras corniculatum* (L.) propagules to buoyancy periods of several months for propagules of *Heritiera littoralis* Dryand in Aiton and different *Rhizophora* species (Table 2). The high dispersal potential of *H. littoralis* propagules is mainly due to their very low density and hard woody epicarp (Tomlinson, 2016) and is further acknowledged through the observation that there is no root initiation within 15 weeks of simulated stranding (Clarke, Kerrigan & Westphal, 2001). Due to the long observation periods required, propagule buoyancy periods are more difficult to determine for species in which the propagules retain their buoyancy longer. Consequently, the maximum buoyancy period in species producing propagules with long buoyancy periods is either unknown or based on rough estimations (Table 2). For example, using linear extrapolation, Allen & Krauss (2006) estimated a maximum buoyancy period of 302 days for *R. mangle* propagules, starting from the observation that 83% of the propagules were still buoyant after 63 days in sea water. Although the large propagules of *Rhizophora* species potentially have a long maximum buoyancy period (Clarke *et al.*, 2001; Rabinowitz, 1978), current estimates do not account for the fact that buoyancy characteristics of mangrove propagules are influenced by water salinity, with propagules generally floating for longer under higher salinity conditions (Rabinowitz, 1978; Clarke & Myerscough, 1991; Clarke *et al.*, 2001; Alleman & Hester, 2011). Furthermore, experiments have shown that buoyancy is not an invariable trait (Table 2). Besides the presence of ‘floaters’ (remain floating after shedding their pericarp) and ‘sinkers’ (sink on shedding their pericarp) in *A. marina* (Steinke, 1986) and some Rhizophoraceae species (Tonné *et al.*, 2017), it was found that *A. marina* propagules that sank after shedding their pericarp began to refloat (i.e. lost buoyancy and subsequently regained it) after several days (Clarke & Myerscough, 1991), even when damaged by insect larvae (Minchinton, 2006). The potential to regain buoyancy has also been reported for *A. germinans* propagules, with the ability to regain buoyancy being highest for propagules in full-strength sea water as

compared to propagules in low-salinity water (Alleman & Hester, 2011). Similarly, Rabinowitz (1978) observed that propagules of *R. harrisonii* regained buoyancy after sinking. Although intraspecific variation in dispersal ability may reflect an evolutionary risk-spreading strategy (Pinceel, Vanschoenwinkel & Brendonck, 2013), this link has not yet been investigated for mangroves. Such a strategy may be particularly important given the strong stochastic component of passive dispersal (Lowe & McPeck, 2014). Variation in buoyancy among offspring could ensure that they are likely to be deposited at different distances and in different locations, increasing the probability that at least some will be able to settle and grow. Additionally, while increases in specific gravity with floating time in sea water and repeated exposure to air favour establishment in the intertidal zone (Urasaki *et al.*, 1986), the ability to regain buoyancy could allow for secondary transport after stranding at a potentially unsuitable site. Finally, it would be worth investigating whether selection for prolonged viability in sea water is linked to specific taxa, such as pioneer species that rely on frequent colonization for persistence.

Earlier studies compared the density of propagules with the density of water under naturally occurring salinity and temperature combinations in mangrove systems, to determine buoyancy potential. For example, Tonné *et al.* (2017) estimated that more than 90% of the propagules from *B. gymnorrhiza*, *C. tagal*, and *R. mucronata*, would float immediately after abscission, and along salinity gradients from within-forest to coastal waters. Interestingly, the authors highlighted that heavy rains and evaporation may affect this number by temporally lowering or increasing the water density, and found that the majority of *B. gymnorrhiza* and *C. tagal* propagules in their study remained floating regardless of the surface water salinity conditions, suggesting these species have a high potential to embark on LDD. Propagule buoyancy periods have been used as a proxy for dispersal potential across species (Clarke *et al.*, 2001; Ye *et al.*, 2004; Allen & Krauss, 2006). However, focusing on buoyancy periods without checking for viability is problematic, as non-viable propagules often continue to float even though they can no longer establish and grow. At present, the available data do not allow strong conclusions on whether dispersal and colonization potential are limited by a propagule’s floating or viability period (Table 2), but viability has been suggested to reduce the success of LDD events. For example, Alleman & Hester (2011) reported a strong decrease in viability for *A. germinans* propagules after dispersal periods exceeding 45 days. Similarly, it has been found for *A. germinans* and *R. mangle* that seedling productivity decreases with longer floating durations in sea water, and that seedling establishment was best after one week of floating (Simpson, Osborne & Feller, 2017). While this suggests that the advantage of a long buoyancy period (increasing the potential to colonize remote habitats) might be offset by reduced establishment potential with increased duration at sea, such a trade-off requires further scrutiny.

Table 2. Buoyancy and viability characteristics of propagules from selected mangrove species. Typically, dispersal experiments are conducted using sea water (S), fresh water (F), or river water (R). Salinity values are provided in parentheses when provided in the respective source. Although some studies report minimum, median and mean values for the buoyancy period (BP) and viability period (VP), we here only considered maximum values for these propagule traits. Obligate dispersal period (ODP) refers to the post-abscission period during which a propagule is yet to initiate root growth. For detailed information on the number of propagules considered, the reader is referred to the respective source(s)

| Species | Salinity | Predominant buoyancy pattern | Refloat | BP (days) | Buoyant after reported BP (%) | VP (days) | Viable after reported VP (%) | ODP (days) | Reference |
|-------------------------------|-------------------|------------------------------|---------|------------|-------------------------------|-----------|------------------------------|-----------------|------------------------------|
| <i>Acanthus ilicifolius</i> | S (15 ppt) | Floater | — | — | — | < 11 | — | Table 2 in Ref. | Ye <i>et al.</i> (2004) |
| <i>Aegialitis annulata</i> | F | Sinker | No | 15 | 0 | — | — | — | Clarke <i>et al.</i> (2001) |
| <i>Aegialitis annulata</i> | S | Sinker | No | 15 | 0 | — | — | 10 § | Clarke <i>et al.</i> (2001) |
| <i>Aegiceras corniculatum</i> | F | Sinker | No | 5 | 0 | — | — | — | Clarke <i>et al.</i> (2001) |
| <i>Aegiceras corniculatum</i> | S | Sinker | No | 10 | 0 | — | — | 8 § | Clarke <i>et al.</i> (2001) |
| <i>Avicennia germinans</i> | F | — | Yes | 110 | 40 | ca. 45 | — | < 14 | Alleman & Hester (2011) |
| <i>Avicennia germinans</i> | R (0–8 ppt) | — | — | 25 | — | — | — | — | Delgado <i>et al.</i> (2001) |
| <i>Avicennia germinans</i> | S (18 ppt) | — | Yes | 110 | 30 | ca. 45 | — | < 14 | Alleman & Hester (2011) |
| <i>Avicennia germinans</i> | S (36 ppt) | — | Yes | 110 | 65 | ca. 45 | — | < 14 | Alleman & Hester (2011) |
| <i>Avicennia marina</i> | F | Floater | Yes | 15 | ca. 80 | — | — | — | Clarke <i>et al.</i> (2001) |
| <i>Avicennia marina</i> | S | — | No | A few days | — | 240 | ca. 5 | ca. 7 | Clarke (1993) |
| <i>Avicennia marina</i> | S | Floater | Yes | 15 | 100 | — | — | 4 § | Clarke <i>et al.</i> (2001) |
| <i>Avicennia marina</i> | S | Sinker | No | 2 | 5 to 10 | — | — | — | Clarke & Myerscough (1991) |
| <i>Avicennia marina</i> | S | Sinker | Yes | ca. 6 | ca. 40 | — | — | — | Clarke & Myerscough (1991) |
| <i>Avicennia marina</i> | S (10%) | Sinker | Yes | ca. 6 | ca. 35 | — | — | — | Clarke & Myerscough (1991) |
| <i>Avicennia marina</i> | S (12%) | Sinker | Yes | 2 | ca. 45 | — | — | — | Clarke & Myerscough (1991) |
| <i>Avicennia</i> spp. | F | — | — | — | — | — | — | ca. 14 | Rabinowitz (1978) |
| <i>Avicennia</i> spp. | S | — | No | 82 | Always float | 82 | > 65 | ca. 14 | Rabinowitz (1978) |
| <i>Bruguiera exaristata</i> | F | Floater | No | 15 | ca. 70 | — | — | — | Clarke <i>et al.</i> (2001) |
| <i>Bruguiera exaristata</i> | S | Floater | No | 15 | 95 | — | — | 8 § | Clarke <i>et al.</i> (2001) |
| <i>Bruguiera gymnorhiza</i> | F | Sinker | Yes | 15 | 30 | — | — | — | Clarke <i>et al.</i> (2001) |
| <i>Bruguiera gymnorhiza</i> | S | — | — | 117 | — | — | — | — | Guppy (1906, p. 460) |
| <i>Bruguiera gymnorhiza</i> | S | — | — | 31 | — | 31 | 100 | — | Steele (2006) |
| <i>Bruguiera gymnorhiza</i> | S | Floater | No | 15 | 60 | — | — | 14 § | Clarke <i>et al.</i> (2001) |
| <i>Bruguiera parviflora</i> | F | Sinker | No | 15 | 0 | — | — | — | Clarke <i>et al.</i> (2001) |
| <i>Bruguiera parviflora</i> | S | Sinker | No | 15 | 20 | — | — | 8 § | Clarke <i>et al.</i> (2001) |
| <i>Bruguiera sexangula</i> | S (34.6–35.1 ppt) | — | — | 60 / 67* | 10 / 0* | 63 | — | — | Allen & Krauss (2006) |
| <i>Ceriops australis</i> | F | Floater | — | — | — | — | — | — | Clarke <i>et al.</i> (2001) |
| <i>Ceriops australis</i> | S | Floater | — | — | — | — | — | 8 § | Clarke <i>et al.</i> (2001) |
| <i>Ceriops decandra</i> | F | Floater | Yes | 15 | 75 | — | — | — | Clarke <i>et al.</i> (2001) |
| <i>Ceriops decandra</i> | S | Floater | No | 15 | 80 | — | — | 8 § | Clarke <i>et al.</i> (2001) |
| <i>Ceriops tagal</i> | F | Floater | No | 15 | 85 | — | — | — | Clarke <i>et al.</i> (2001) |
| <i>Ceriops tagal</i> | S | Floater | No | 15 | 95 | — | — | 14 § | Clarke <i>et al.</i> (2001) |
| <i>Cynometra iripa</i> | F | Floater | No | 15 | 100 | — | — | — | Clarke <i>et al.</i> (2001) |
| <i>Cynometra iripa</i> | S | Floater | No | 15 | 100 | — | — | 23 § | Clarke <i>et al.</i> (2001) |
| <i>Excoecaria agallocha</i> | S | — | — | 208 | — | 208 | 35 | — | Steele (2006) |

Table 2. Continued

| Species | Salinity | Predominant buoyancy pattern | Refloat | BP (days) | Buoyant after reported BP (%) | VP (days) | Viable after reported VP (%) | ODP (days) | Reference |
|-------------------------------|-------------------|------------------------------|---------|-----------|-------------------------------|-----------|------------------------------|-----------------|------------------------------|
| <i>Excoecaria agallocha</i> | S (15 ppt) | Floater | — | — | — | < 7 | — | Table 2 in Ref. | Ye <i>et al.</i> (2004) |
| <i>Heritiera littoralis</i> | F | Floater | No | 15 | 100 | — | — | — | Clarke <i>et al.</i> (2001) |
| <i>Heritiera littoralis</i> | S | — | — | 104 | — | 104 | 5 | — | Steele (2006) |
| <i>Heritiera littoralis</i> | S | Floater | No | 15 | 100 | — | — | 23 § | Clarke <i>et al.</i> (2001) |
| <i>Heritiera littoralis</i> | S (15 ppt) | Floater | — | — | — | > 150 | — | Table 2 in Ref. | Ye <i>et al.</i> (2004) |
| <i>Laguncularia racemosa</i> | F | — | — | 90 | ca. 2 | 90 | ca. 85 | 8 | Rabinowitz (1978) |
| <i>Laguncularia racemosa</i> | R (0–8 ppt) | — | — | 8 | 0 | — | — | — | Delgado <i>et al.</i> (2001) |
| <i>Laguncularia racemosa</i> | S | — | No | 90 | ca. 2 | 90 | ca. 40 | — | Rabinowitz (1978) |
| <i>Lumnitzera littorea</i> | S | — | — | 214 | — | 214 | 10 | — | Steele (2006) |
| <i>Lumnitzera racemosa</i> | F | Sinker | Yes | 15 | 20 | — | — | — | Clarke <i>et al.</i> (2001) |
| <i>Lumnitzera racemosa</i> | S | Sinker | No | 15 | 50 | — | — | > 105 § | Clarke <i>et al.</i> (2001) |
| <i>Lumnitzera racemosa</i> | S (15 ppt) | Sinker | — | — | — | < 20 | — | Table 2 in Ref. | Ye <i>et al.</i> (2004) |
| <i>Pelliciera rhizophorae</i> | F | — | — | 107 | ca. 95 | 107 | 100 | 9 | Rabinowitz (1978) |
| <i>Pelliciera rhizophorae</i> | S | — | Yes | 107 | ca. 40 | 107 | ca. 45 | 30 | Rabinowitz (1978) |
| <i>Rhizophora apiculata</i> | S (35–36 ppt) | — | — | 89 | ca. 1 | 89 | ca. 1 | — | Drexler (2001) |
| <i>Rhizophora harrisonii</i> | F | — | — | 104 | ca. 75 | 104 | 100 | ca. 40 | Rabinowitz (1978) |
| <i>Rhizophora harrisonii</i> | S | — | Yes | 104 | ca. 90 | 104 | 100 | ca. 40 | Rabinowitz (1978) |
| <i>Rhizophora mangle</i> | — | — | — | 240–356 | — | > 365 | — | — | Davis (1940) |
| <i>Rhizophora mangle</i> | S | — | — | ca. 90 | ca. 90 | — | — | — | Ellison (1996) |
| <i>Rhizophora mangle</i> | S | — | — | 120 | 5 | — | — | — | Guppy (1906, p. 459) |
| <i>Rhizophora mangle</i> | S | — | — | 247 | — | 247 | 62 | — | Steele (2006) |
| <i>Rhizophora mangle</i> | S (34.6–35.1 ppt) | — | — | 63 / 302* | > 80 / 0* | 63 | — | — | Allen & Krauss (2006) |
| <i>Rhizophora mucronata</i> | S | — | — | 87 | 60 | — | — | — | Guppy (1906, p. 459) |
| <i>Rhizophora mucronata</i> | S (35–36 ppt) | — | — | 150 | ca. 1 | 150 | ca. 1 | — | Drexler (2001) |
| <i>Rhizophora stylosa</i> | F | Floater | Yes | 15 | 85 | — | — | — | Clarke <i>et al.</i> (2001) |
| <i>Rhizophora stylosa</i> | S | — | — | 75 | — | 75 | 55 | — | Steele (2006) |
| <i>Rhizophora stylosa</i> | S | Floater | No | 15 | 80 | — | — | 14 § | Clarke <i>et al.</i> (2001) |
| <i>Xylocarpus granatum</i> | S | — | — | 60 | — | 60 | 80 | — | Steele (2006) |
| <i>Xylocarpus mekongensis</i> | F | Floater | No | 15 | 100 | — | — | — | Clarke <i>et al.</i> (2001) |
| <i>Xylocarpus mekongensis</i> | S | Floater | No | 15 | 100 | — | — | 4 § | Clarke <i>et al.</i> (2001) |
| <i>Xylocarpus moluccensis</i> | S | — | — | 254 | — | 254 | 20 | — | Steele (2006) |

—, no data available; §, averaged over different salinity treatments; *, extrapolated.

(3) Propagule dormancy period and delayed root initiation

Apart from the maximum buoyancy period, mangrove propagules may exhibit a minimum dispersal period or so-called obligate dispersal period (ODP). This ODP represents the period after abscission during which a propagule is not yet able to initiate root growth or to germinate (for seeds) (Rabinowitz, 1978). However, as propagules do and should not necessarily disperse during this period, ODP is a rather unfortunate and misleading term. It seems that many propagules do not readily root after abscission unless (self-) planted in suitable conditions. As such they can be considered dormant until triggered for rooting. This mechanism of delayed germination or rooting by means of dormancy, or a process that is similar to

dormancy, may increase the dispersal potential of propagules by postponing establishment. Additionally, variation in ODP among propagules could potentially represent an evolutionary risk-spreading strategy, ensuring that at least a fraction of propagules can grow to reproduce (Childs, Metcalf & Rees, 2010). In contrast to conservative risk spreading, where the ODP of all descendants would be the same or constrained within narrow limits, the diversified bet-hedging strategy (investing in several strategies with offspring differing in ODP) may be more successful in mangroves, especially when considering the costs associated with dispersal (Bonte *et al.*, 2012). Establishment too close to the parent tree may increase competition for nutrients, while dispersal over large distances increases the chance of loss during transit or arriving at a site that is unsuitable for establishment.

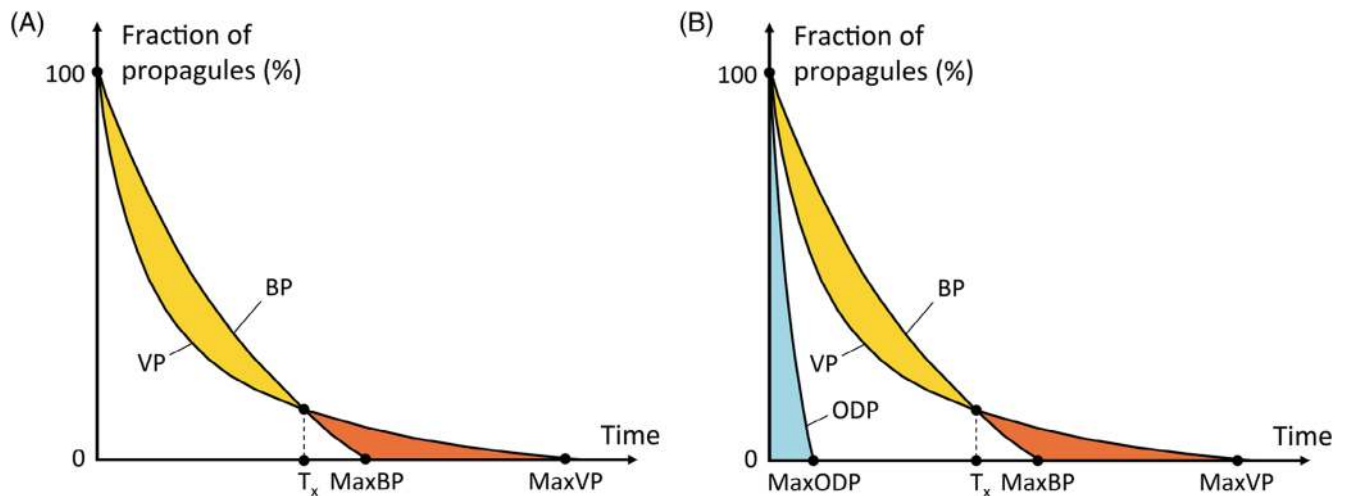


Fig. 4. (A) Conceptual figure showing the fraction of propagules that may contribute to successful dispersal (white surface area), depending on the fraction of propagules that have a certain viability period (VP) and buoyancy period (BP), and the maximum viability and buoyancy period (MaxVP, MaxBP). We note that the VP and BP curves may be reversed or of a different form, depending also on the species. Ideally, in terms of long-distance dispersal (LDD) potential, both curves coincide and are protracted in time. The relative position of the curves also determines the fraction of propagules that are still buoyant but are no longer viable (yellow), and the fraction of propagules that sink (with potential refloating) while still viable (orange). T_x represents a potential moment in time of rapid decrease in the number of propagules that may contribute to successful dispersal. (B) If ‘viability’ becomes the ‘capacity to root’, the (maximum) obligate dispersal period [(Max)ODP] should be considered (blue) and may have different shapes.

ODP has been variably quantified experimentally. For example, previous studies have considered the time until the growth of the first root of 1 mm as the ODP, irrespective of the fact that the propagules were floating (the first 15 days of the experiment) or planted (after 15 days) (Clarke *et al.*, 2001). On the contrary, for *Laguncularia racemosa*, Rabinowitz (1978) made the important distinction between ODP and the minimum time required for root initiation following ODP and after stranding. Rooting of mangrove propagules upon stranding is probably not triggered by temperature, humidity or light (duration) differences, since at the moment of touching ground these are not substantially different from conditions experienced during dispersal. The cues that effectively cause propagules of various species to initiate rooting after dispersal remain unknown, although may possibly be linked to hypoxia or thigmotropism. On the contrary, root development of propagules might be delayed by water turbulence and tidal action (e.g. McMillan, 1971; Patterson, McKee & Mendelsohn, 1997; Delgado *et al.*, 2001), extending the actual dispersal period. Future attempts to extend ODP data may help to identify the timeframe in which dispersal and establishment can occur. Additionally, knowledge on variation in ODP among species can shed new light on the evolution of dispersal in mangroves and the role of risk-spreading strategies (Cohen, 1966) in mediating population persistence and expansion in mangroves.

(4) Temporal window for dispersal

The combination of ODP, maximum buoyancy period, and the variation in the decay of propagule viability over

time results in a limited although often protracted window of opportunity during which propagule dispersal could – but not necessarily will – lead to successful establishment in a new site (Fig. 4). This temporal window for a potential successful dispersal outcome begins at the end of the ODP and extends until the end of the maximum viability period, provided that the buoyancy period was sufficiently long to allow for stranding in a suitable locality. When the loss of viability is negligible, e.g. in floodplain plants with long seed-dormancy periods, the buoyancy period will be the most important determinant of dispersal distance (Edwards, Wyatt & Sharitz, 1994). Maximum buoyancy period might be defined as the moment that surface floating ends, as propagule density increases and the propagule may disappear gradually in the water column. Quantifying the temporal window for dispersal could help explain the variation in realised dispersal distances of mangrove propagules from the same and from different species, and patterns of connectivity. Dispersal events that terminate at a suitable destination within this timeframe may result in connectivity between sites, as the deposited propagules are viable and could initiate establishment.

V. ESTABLISHMENT AT THE STRANDING SITE

Typically, only coastal intertidal areas qualify as suitable areas for mangrove establishment. Yet, even if a propagule manages to strand in such a locality, strong spatial heterogeneity in local conditions may act as an important

filter for establishment. For example, in contrast to the low-energy coastal habitats where mangroves occur, high-energy intertidal habitats such as sandy beaches or rocky coastlines have a low probability of establishment. In addition, several biotic (e.g. predation, competition) and abiotic (e.g. sediment conditions, temperature, hypoxia, hydrogen sulphide concentrations, salinity, light, nutrients, tides and flooding, sea-level changes) factors can influence establishment and early development of seedlings (Delgado *et al.*, 2001; Krauss *et al.*, 2008; Friess *et al.*, 2012). Coastal high-energy hydrodynamics (wind, waves) were shown to reduce growth and survival of planted seedlings in a temperate Australian mangrove near the latitudinal limit of the sole species present, *A. marina* (Forsk.) Vierh. var. *australasica* (Walp.) Moldenke (Hurst, Pope & Quinn, 2015; Hurst, 2018). This also affected natural regeneration after clearfelling, possibly through changes of mudflat elevation and inundation regime. General requirements for all species include: a relatively calm period free of strong currents to allow for settlement; time for the development of sufficient roots which are long enough to withstand tidal and wave action; and even longer roots to outlive removal of sediment around the seedling due to mixing or erosion of the upper sediment layer (Balke *et al.*, 2011). In addition, stranded propagules must tolerate high salinity (Jayatissa *et al.*, 2008) and overcome herbivory (Delgado *et al.*, 2001), and, if other mangrove propagules or trees or other types of vegetation are present, they must be able to tolerate competition for light and resources with con- and heterospecifics. Propagules and seedlings of pioneer species, such as *Avicennia* spp., *Sonneratia* spp. and *Laguncularia racemosa*, possess traits to facilitate establishment including the lack of seed dormancy, high tolerance to salinity and regular inundation, as well as resistance to wave action (Friess *et al.*, 2012). Kodikara *et al.* (2017) have shown that under experimental conditions the success rates of early establishment (first 15–20 weeks) in six mangrove species were higher under low or moderate salinity conditions. Similarly, *A. germinans* and *Lumnitzera racemosa* Willd. were found to survive and grow well at low and medium salinity, but only poorly at high salinity levels (Dangremond, Feller & Sousa, 2015). The same authors reported reduced growth rates for *R. mangle* and a particularly high sensitivity of *P. rhizophorae* to high salinity.

The presence of salt marshes and mangrove, or even mangrove remnants, can facilitate mangrove propagule trapping and establishment (Cunha-Lignon *et al.*, 2009a,b, 2011; Hurst *et al.*, 2015; Peterson & Bell, 2015; Hurst, 2018). Near the latitudinal limits of mangroves, both communities coexist and compete in an apparent vacillation (Saintilan & Williams, 1999; Saintilan & Wilton, 2001; Rogers *et al.*, 2005; Stevens, Fox & Montague, 2006; McKee & Rooth, 2008; Hurst, 2018). Recent studies have reported changes in the distribution of mangroves and salt marsh, and found that the poleward range expansion of mangroves often takes place at the expense of salt marsh (Osland *et al.*, 2013; Saintilan *et al.*, 2014; Armitage *et al.*, 2015). The rate of mangrove establishment in salt marsh may be an important

determinant of which type of habitat will dominate the coasts in the temperate–subtropical zones of the future, and holds important implications for ecosystem structure and functioning. In New Zealand, mangrove expansion has led to a societal debate and discord about possible removal, in view of shifting ecosystem services (Dencer-Brown *et al.*, 2018).

VI. SPATIAL SCALE OF DISPERSAL AND METHODOLOGICAL APPROACHES

Mangrove propagule transport has been investigated using different methods and techniques. Each of these methodologies has provided dispersal data at different spatial scales, ranging from within-stand propagule transport to transoceanic dispersal and connectivity. As discussed previously, dispersal and the spatial scale of propagule transport depend on a wide range of biotic and abiotic factors, each having a different role and varying spatial and temporal characteristics. Tidal inundation times and frequency, for example, will change over the course of a tidal cycle and, depending on surface elevation, affect the potential for propagule transport and LDD. Hence, propagules in the seaward edge of a mangrove forest and in areas adjacent to tidal creeks may have a higher chance to embark on LDD than propagules in sites on the landward margin, as these areas are flooded for longer and more frequently. It should be noted that while this may be intuitively appealing, the action of currents and resulting dispersal fluxes may not be a simple function of distance to the ocean in all mangrove forests, considering differences in topographic features and coastal dynamics. When considering inundation classes (number of flooding times per month) the position in the intertidal zone will define whether or not a propagule has time to anchor (a matter of about five days in several Rhizophoraceae; N. Koedam, personal observations), requiring an inundation-free period (Balke *et al.*, 2011).

Propagules that are not planted directly into the muddy soil near the parent tree or are not retained locally can reach open water and be transported onwards by nearshore, coastal and open-ocean currents. Nearshore hydrodynamics tend to be more complex than open-ocean flow, controlled primarily by factors such as coastal morphology, bathymetric variability, tides, wind forcing, and freshwater discharge (Pineda, Hare & Sponaugle, 2007). Indeed, nearshore currents can be temporally dynamic, strongly non-linear, and spatially complicated, and have been shown to result in complex dispersal and connectivity patterns (Siegel *et al.*, 2008) and a population genetic structure that cannot be explained by traditional and straightforward isolation-by-distance models (White *et al.*, 2010; Thomas *et al.*, 2015). In addition, oceanic features such as tidal ellipses and meso- and submesoscale eddies have the potential to retain propagules (Condie & Condie, 2016; Van der Stocken & Menemenlis, 2017) and limit the spatial scale of propagule transport (Pineda *et al.*,

2007), while frontal zones between mesoscale eddies might create pathways for biological transport as hypothesized by Hancke, Roberts & Ternon (2014).

Although near- and alongshore dispersal is likely to dominate mangrove propagule transport, large-scale gyre systems and the eastern and western boundary currents may allow for dispersal across ocean basins as observed from genetic studies (see Section VI.2) and numerical models (see Section VI.3). Horizontal dimensions of the oceans range from 5000 to 15,000 km (Talley *et al.*, 2011). However, typical ocean surface current speeds range from 10 to 80 cm s⁻¹ ensuring that even these great distances can be crossed in matters of months (Nathan *et al.*, 2008; Gillespie *et al.*, 2012). In addition, based on a recent study on tsunami-driven dispersal between Japan and North America (Carlton *et al.*, 2017), it is sensible to assume that similar mechanisms including long-distance rafting, for example *via* tumbled mangrove trees (Svavarsson, Osore & Olafsson, 2002), could have played a role in LDD across ocean basins. The importance of mechanisms such as rafting as a means of LDD has been highlighted to explain the distributional range of the mangrove wood-borer *Sphaeroma terebrans* Bate (Baratti, Filippelli & Messina, 2011). In some parts of the world, LDD can also be facilitated by tropical storms that may transport propagules over extensive distances, both inland and beyond the current range limits. Today, this is the case in North America (Gulf of Mexico and Atlantic coasts) where propagule production coincides with the hurricane season and *prior* to winter temperature extremes. Finally, depending on the species, the spatial scale of dispersal, particularly for species producing wind-sensitive propagules (e.g. *H. littoralis*), may be influenced directly by prevailing winds (Van der Stocken *et al.*, 2013, 2015b). Since the directionality and strength of these dispersal vectors is temporally variable (e.g. Sasaki *et al.*, 2014; Callies *et al.*, 2015), so will be the trajectories of dispersing propagules, depending on the very moment that they enter the water.

Reconstructing dispersal patterns of mangrove propagules has been attempted since the early 1960s. However, due to limitations of available methodologies (see also Nathan *et al.*, 2003), the spatial scale of mangrove propagule dispersal and particularly the frequency of LDD remain controversial and largely unquantified (Table 3). In this section, we discuss the methodological approaches that have been considered (Fig. 5) to acquire qualitative and quantitative data on the pattern and extent of mangrove propagule dispersal, and discuss their potential strength and the implications of their nature on the results that they generate.

(1) Release–recapture experiments

Release–recapture techniques have been used frequently over recent decades (Yamashiro, 1961; Chan & Husin, 1985; Komiyama, Chimchome & Kongsangchai, 1992; McGuinness, 1997; Breitfuss, Connolly & Dale, 2003; Sousa *et al.*, 2007; De Ryck *et al.*, 2012; Van der Stocken *et al.*, 2013; Ngeve *et al.*, 2017a). They are the most basic yet robust means and probably the most labour-intensive way to investigate

the movement of individual propagules and evaluate potential connectivity between sites. Although large-scale release–recapture experiments have been conducted (Steinke & Ward 2003), the applicability of this method is generally restricted to local and demographic time scales (Kool, Moilanen & Treml, 2013), yielding data on dispersal distance and direction only for propagules that strand within a few tens of meters up to several kilometers from the release location (Table 3). The probability of successful recapture typically declines with increasing distance, as the number of longer distance dispersers is generally smaller and the search area increases quadratically with increasing distance (search radius). Indeed, in many animal and plant species, including mangroves, the probability density function of dispersal distance is leptokurtic (Harper, 1977; Komiyama *et al.*, 1992; Portnoy & Willson, 1993; McGuinness, 1997; Cain *et al.*, 2000; Nathan & Muller-Landau, 2000; Levin *et al.*, 2003; Geng *et al.*, 2008), with a pronounced peak representing frequent dispersal at or close to the parent's location, followed by a quick decline at intermediate distances and an elongated tail capturing sporadic dispersal over long distances. For the mangrove species *K. candel* (L.) Druce, for example, Yamashiro (1961) found that most of the marked propagules did not disperse farther than 50 m, while Komiyama *et al.* (1992) found that 68% of the 300 propagules released in a mangrove forest in southern Thailand dispersed no farther than 300 m, with a maximum observed dispersal distance of 1210 m. It should be noted that due to the above-mentioned scale-related drawbacks of this method, the fate of an important portion of propagules is generally unknown, and propagules that disperse to the open sea are nearly certainly excluded from the data. In some cases recaptured propagules may represent about 50% of the original batch (<3 km; Van der Stocken *et al.*, 2013) and sometimes no more than 15% (Yamashiro, 1961). Additionally, recovery rates are likely to also decrease over time. For example, in a release–recapture experiment near Punta Galeta on the Caribbean coast of Panama, Sousa *et al.* (2007) recovered more than 80% and over 60% of *Avicennia* propagules after 2 and 4 weeks, respectively. Propagule disappearances in this kind of study can also be due to sinking and predation by herbivorous crabs (see Section III.2).

Given the spatial variation in retention and predation, and important aspects such as proximity of the release site to open waters, propagule recovery rates are case specific. For example, Van der Stocken *et al.* (2013) reported that for different propagule releases along a tidal creek, the percentage of recaptured *C. tagal* propagules was only half of that for *R. mucronata* propagules, and percentages varied strongly for propagules released at different sites. While release–recapture techniques generally result in incomplete and potentially biased dispersal data, this method has the important advantage of accounting for the complexity inherent to natural systems such as tidal dynamics, landscape structure, and predation pressure. Although propagules are collected and deposited experimentally in many cases (e.g. De

Table 3. Dispersal distance values reported for propagules from selected mangrove species and methods used to obtain these values. Different methodological approaches were used to measure dispersal in mangroves, each allowing information to be obtained at different spatial scales. Typically, the applicability of release–recapture (R) experiments is restricted to the landscape scale (10^2 – 10^3 m; but see Steinke & Ward, 2003), while phylogenetic and population genetic studies (G), and dispersal simulation models (M) allow studying dispersal and connectivity at landscape (10^2 – 10^3 m), regional (10^3 – 10^5 m), and biogeographic (10^5 – 10^7 m) spatial scales

| Species or Ecosystem | Dispersal distance | Methodological approach | Specific method | Reference |
|------------------------------|---|-------------------------|---|--------------------------------------|
| <i>Avicennia germinans</i> | Transatlantic | G | Amplified fragment length polymorphism molecular analysis | Dodd <i>et al.</i> (2002) |
| <i>Avicennia germinans</i> | Transatlantic | G | Internal transcribed spacers region sequences, chloroplast DNA, and amplified fragment length polymorphisms of genomic DNA | Nettel & Dodd (2007) |
| <i>Avicennia germinans</i> | Transatlantic | G | Nuclear and chloroplast DNA markers | Mori <i>et al.</i> (2015) |
| <i>Avicennia germinans</i> | Seldom more than 10 m, mostly less than a couple of meters. | R | Marked propagules released at different tidal elevations along different transects and searched for 1, 5, 14, 19, and 28 days after release | Sousa <i>et al.</i> (2007) |
| <i>Avicennia germinans</i> | Transatlantic | G | Microsatellite analysis, and chloroplast and nuclear sequences analyses | Cerón-Souza <i>et al.</i> (2015) |
| <i>Avicennia marina</i> | ≤ 3 km; a few recoveries at 5 km, 12 km, and 24 km; max. 700 km | R | Drift cards with similar buoyancy as propagules of <i>Avicennia marina</i> dropped from an aircraft into the sea | Steinke & Ward (2003) |
| <i>Avicennia marina</i> | Multiple kilometers | R | Observations of stranded propagules on beaches | Gunn & Dennis (1973) |
| <i>Avicennia marina</i> | Close to the parent tree parent; some >20 km; max. 50 km | R | Observations of stranded propagules on beaches and inferences from buoyancy data | Clarke & Myerscough (1991) |
| <i>Avicennia marina</i> | Most <1 km; very few >10 km | R | Marked propagules released at seaward edge of forest stand <i>prior</i> to high tide | Clarke (1993) |
| <i>Avicennia marina</i> | Up to 60 m | R | Marked propagules released on saltmarsh-mangrove interface at 3 runnelled saltmarshes, 6 h prior to predicted highest high tide, and searched for after high tide | Breitfuss <i>et al.</i> (2003) |
| <i>Avicennia officinalis</i> | Short-distance dispersal | M | Combining a hydrodynamic model with knowledge on traits relevant for simulation of species-specific propagule dispersal; the model includes different schemes of retention by vegetation; semi-enclosed lagoon system | Di Nitto <i>et al.</i> (2013) |
| <i>Ceriops tagal</i> | 76% ≤ 1 m; 91% ≤ 3 m | R | Propagules marked while still attached to trees and observed over a period of 6 months | McGuinness (1997) |
| <i>Ceriops tagal</i> | Max. 146 m | R | Marked propagules released in different plots along two intertidal transects, 5 days prior to spring tide, and searched for during a period of 2 weeks and again after 5 months | De Ryck <i>et al.</i> (2012) |
| <i>Ceriops tagal</i> | Short-distance dispersal | M | Combining a hydrodynamic model with knowledge on traits relevant for simulation of species-specific propagule dispersal; the model includes different schemes of retention by vegetation; semi-enclosed lagoon system | Di Nitto <i>et al.</i> (2013) |
| <i>Ceriops tagal</i> | Max. 2958 m | R | Marked propagules released in a creek near the beginning of the ebb tide, 3 days after spring tide, and searched for 12 h after release | Van der Stocken <i>et al.</i> (2013) |

Table 3. Continued

| Species or Ecosystem | Dispersal distance | Methodological approach | Specific method | Reference |
|------------------------------|---|-------------------------|---|---------------------------------------|
| <i>Ceriops tagal</i> | < 50 m; max. 320 m | R | Marked propagules released near spring tide in four different plots along an intertidal transect, and searched for at 1, 2, and 4 days after release | Van der Stocken <i>et al.</i> (2015a) |
| <i>Kandelia candel</i> | 9.4 ± 13.8 m (SD) | G | Combined application of highly polymorphic nuclear and chloroplast simple sequence repeat markers | Geng <i>et al.</i> (2008) |
| <i>Kandelia candel</i> | 18.6 m | M | Modified two-component normal model composed of two kinds of normal distribution with short and long variances | Geng <i>et al.</i> (2008) |
| <i>Kandelia candel</i> | Near release location, some reached outer bay | R | Marked propagules released at the rising tide and near the beginning of the ebb tide | Urasaki <i>et al.</i> (1986) |
| <i>Kandelia candel</i> | ≤ 50 m | R | Marked propagules released at different tidal elevations and monitoring during 30 days after release | Yamashiro (1961) |
| <i>Laguncularia racemosa</i> | Some >85 m | R | Marked propagules released at different tidal elevations along different transects and searched for 1, 6, and 14 days after release | Sousa <i>et al.</i> (2007) |
| <i>Rhizophora</i> spp. | Transatlantic, transpacific and trans-Indian Ocean. | G | Chloroplast and nuclear DNA sequences and genome-wide inter-simple sequence repeats (ISSR) markers | Lo <i>et al.</i> (2014) |
| <i>Rhizophora</i> spp. | Transatlantic, transpacific | G | Chloroplast DNA and nuclear microsatellite analysis on 36 populations across the Atlantic East Pacific and South Pacific | Takayama <i>et al.</i> (2013) |
| <i>Rhizophora apiculata</i> | Extensive distances | R | Based on longevity data | Drexler (2001) |
| <i>Rhizophora apiculata</i> | Short-distance dispersal | M | Combining a hydrodynamic model with knowledge on traits relevant for simulation of species-specific propagule dispersal; the model includes different schemes of retention by vegetation; semi-enclosed lagoon system | Di Nitto <i>et al.</i> (2013) |
| <i>Rhizophora mangle</i> | ≤ 1 km; some >2 km | R | Hand-counting propagules within quadrats on beaches, aerial photographs and satellite imagery classification | Sengupta <i>et al.</i> (2005) |
| <i>Rhizophora mangle</i> | Seldom more than 10 m, mostly less than a couple of meters. | R | Marked propagules released at different tidal elevations along different transects and searched for 1, 5, 14, 19, and 28 days after release | Sousa <i>et al.</i> (2007) |
| <i>Rhizophora mangle</i> | Transatlantic; LDD from East Pacific coast toward the Pacific Islands | G | Microsatellite analysis and chloroplast and nuclear sequences analyses | Cerón-Souza <i>et al.</i> (2015) |
| <i>Rhizophora mucronata</i> | < 20 m; a few >50 m | R | Propagules marked while still attached to trees and dispersal distances recorded at weekly intervals | Chan & Husin (1985) |
| <i>Rhizophora mucronata</i> | 68% < 300 m; max. 1210 m downstream; max. 485 m upstream | R | Marked propagules released in a river stream and on the forest floor, and searched for 1, 4, 12, and 31 days after release | Komiyama <i>et al.</i> (1992) |
| <i>Rhizophora mucronata</i> | Max. 60 m | R | Marked propagules released in different plots along 2 transects, 5 days prior to spring tide, and searched for during a period of 2 weeks and again after 5 months | De Ryck <i>et al.</i> (2012) |

Table 3. Continued

| Species or Ecosystem | Dispersal distance | Methodological approach | Specific method | Reference |
|-----------------------------|--|-------------------------|---|---------------------------------------|
| <i>Rhizophora mucronata</i> | Short-distance dispersal | M | Combining a hydrodynamic model with knowledge on traits relevant for simulation of species-specific propagule dispersal; the model includes different schemes of retention by vegetation; semi-enclosed lagoon | Di Nitto <i>et al.</i> (2013) |
| <i>Rhizophora mucronata</i> | Max. 2783 m | R | Marked propagules released at different locations along a creek, 3 days after spring tide, and searched for 12 h after release | Van der Stocken <i>et al.</i> (2013) |
| <i>Rhizophora mucronata</i> | < 50 m; max. < 150 m | R | Marked propagules released near spring tide in different plots along an intertidal transect, and searched for at 1, 2, and 4 days after release | Van der Stocken <i>et al.</i> (2015a) |
| <i>Rhizophora racemosa</i> | 0–215 km | M | High-resolution, eddy- and tide-resolving numerical ocean model to simulate dispersal trajectories; 3626 modelled trajectories | Ngeve <i>et al.</i> (2017a) |
| <i>Rhizophora racemosa</i> | < 1 km; max. 5 km | R | Release-recapture using 600 mature propagules | Ngeve <i>et al.</i> (2017b) |
| Mangrove | Several hundred of kilometers | M | High-resolution, eddy- and tide-resolving numerical ocean model to simulate dispersal trajectories; floating period of <i>ca.</i> 2.5 months; the model is set up to maximize modelling long-distance dispersal potential. It does not include (intra-forest) retention by vegetation at the release site; order of magnitude of dispersal distances was determined using the distance calculator in Google Earth (great-circle distance) | Van der Stocken & Menemenlis (2017) |
| Mangrove | Along-coast transport, stranding primarily within <50 km; occasions of transoceanic dispersal. | M | High-resolution, eddy- and tide-resolving numerical ocean model to simulate dispersal trajectories; hourly releases over a 1-year period and considering different floating periods ranging between 1 and 12 months; > 36 million modelled trajectories; the model is set up to maximize long-distance dispersal potential and does not include (intra-forest) retention by vegetation at the release site; computation of trajectory path length and great circle distance | Van der Stocken <i>et al.</i> (2019) |

Ryck *et al.*, 2012; Van der Stocken *et al.*, 2013), other studies have accounted for the natural phenology of abscission by marking propagules when still attached to the parent tree (e.g. Chan & Husin, 1985; McGuinness, 1997) or by intercepting dispersing propagules during replicate fishing events over timespans that allow the capture of intra- and inter-annual variation (Van der Stocken *et al.*, 2018).

(2) Phylogenetic and population genetic studies

Genetic studies have been a powerful tool for examining the dispersal patterns of mangroves at various temporal (ecological *versus* evolutionary) and spatial (landscape *versus* biogeographic) scales. Besides palynology and palaeobotany, genetic analyses could be the only available avenue to help reconstruct historical dispersal events. By reconstructing the divergence times, and the location and demography of

ancestral populations of different lineages, recent genetic studies provided evidence for major oceanic dispersal events across the Pacific (Takayama *et al.*, 2013; Lo, Duke & Sun, 2014), Indian (Lo *et al.*, 2014) and Atlantic (Kennedy *et al.*, 2016) oceans. Interestingly, in most cases at a large (biogeographic) scale, the direction of these dispersal events corresponds with that of the presiding ocean currents at the postulated time of dispersal. Particularly, the occurrences and direction of LDD events were consistent with the strength and direction of ocean currents, indicating the important role of the latter in shaping propagule dispersal and ultimately, the patterning of genetic diversity (Kennedy *et al.*, 2017; Hodel *et al.*, 2018). Studies at such large geographic scales are, however, relatively rare (e.g. Takayama *et al.*, 2013; Mori *et al.*, 2015; Li *et al.*, 2016; Wee *et al.*, 2017; He *et al.*, 2018), as they require substantial funding and international

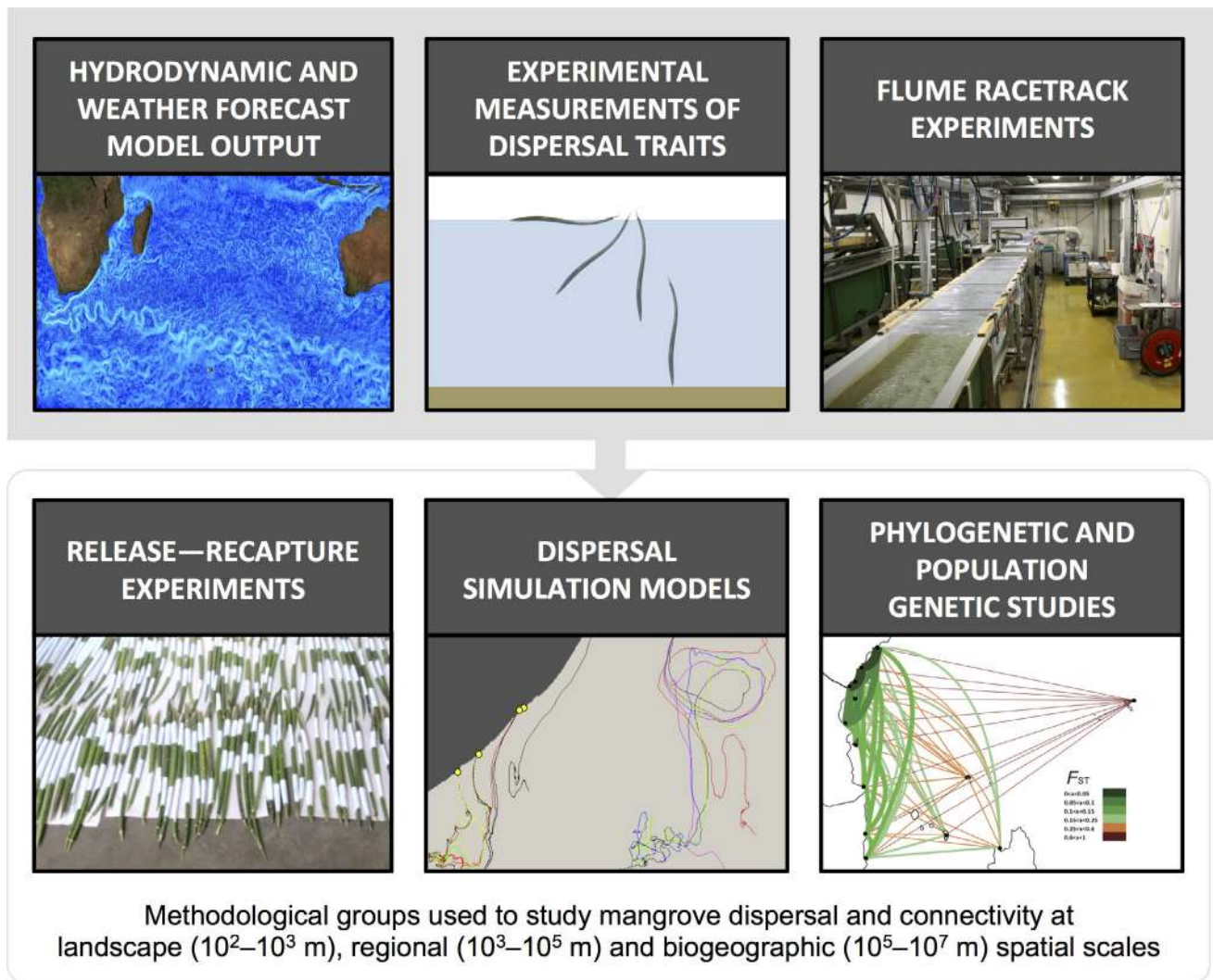


Fig. 5. Methodological approaches used to obtain qualitative and quantitative data on mangrove dispersal and connectivity. Images for ‘hydrodynamic and weather forecast model output’ and ‘dispersal simulation models’ are from Van der Stocken & Menemenlis (2017).

collaboration to support sample collection across countries and high-throughput molecular analyses. Importantly, care should be taken when using depictions or descriptions of large-scale ocean circulation to explain (often fine-scale) genetic information. Maps and descriptive information of large-scale surface ocean currents may be misleading as they fail to capture relevant ocean processes and features such as tides and eddies that may play a role in shaping the complex genetic population structure of coastal marine organisms (White *et al.*, 2010). Indeed, connectivity and spatial gradients in genetic diversity of coastal and marine species along uniform coastlines can be patchy and stochastic due to turbulence and non-linearity in prevailing currents and alongshore variation in habitat quality (Pringle & Wares, 2007; Siegel *et al.*, 2008). Near-shore processes, some taking place at very small spatial scales, may be a filter for access to long-distance processes and thus determine large-scale patterns.

Genetic analyses at both regional and biogeographic scales have been useful in revealing barriers to dispersal (Triest, 2008). In particular, ‘cryptic’ oceanic barriers, such as bifurcating ocean currents (Pil *et al.*, 2011; Mori *et al.*, 2015) and eddies (Wee *et al.*, 2014) may limit dispersal and lead to genetic differentiation across seemingly close populations. Furthermore, as mangroves are coastal vegetation, their present-day genetic structure often harbours the signature of historical vicariance events and dispersal barriers during glacial periods when sea level was low and land masses were exposed. Prominent examples include the Central American Isthmus (CAI; Cerón-Souza *et al.*, 2015), the Malay Peninsula (Yang *et al.*, 2017; He *et al.*, 2018), and Australasia (Wee *et al.*, 2017), all of which were land masses that separated populations that were once connected, with the CAI still acting as a strong dispersal barrier to this day. Therefore, molecular tools allow the identification of land and oceanic barriers that are otherwise difficult to discern, when terrestrial

barriers have disappeared and must be reconstructed, and because oceanic barriers are not static or absolute.

At the smallest geographic scale, genetic analyses showed that dispersal is largely restricted to the parental mangrove stand (up to a few kilometers). Genetic parentage analysis detected pronounced short-distance dispersal in *K. candel*, whereby 81% of seedlings established within 20 m of their parent tree (Geng *et al.*, 2008). An analysis among river basins showed strong isolation by distance in *Rhizophora stylosa* Griff., *B. gymnorrhiza* and *Kandelia obovata* (S., L.), suggesting that inter-population dispersal is restricted to between neighbouring river basins (Islam *et al.*, 2012, 2014). This supported a leptokurtic dispersal kernel in mangroves, whereby most dispersal events occur over short distances, i.e. within the parental mangrove stand. Genetic estimation of migration rates indicated that dispersal could occur bidirectionally within an estuary, due to the opposite effects of river flow currents and incoming tides (Ngeve *et al.*, 2017b). Even at the intermediary geographic scale (hundreds of kilometers), propagule dispersal can be limited to adjacent or neighbouring populations. For example, Binks *et al.* (2018) found that, despite the capacity for LDD, dispersal in *A. marina* is spatially limited and that habitat discontinuities of only several tens of kilometers can disrupt widespread connectivity. Genetic evidence also pointed out that human activities could heavily impact local dispersal. For example, urbanization in mangrove areas may lead to increased pollen limitation and subsequently reduced fecundity in *B. gymnorrhiza* (Wee *et al.*, 2015), highlighting that dispersal patterns change within a human-modified landscape.

Understanding the genetic basis of dispersal, i.e. the genetic architecture and inheritance characteristics of dispersal traits, is important to deduce the potential of a propagule to disperse and to incorporate dispersal evolution into predictive models that forecast species' eco-evolutionary responses to environmental change (Saastamoinen *et al.*, 2018). If at all, the heritability of dispersal-related traits has only been studied for some crop and annual herb species (Saastamoinen *et al.*, 2018). Mangroves could therefore make up an interesting consortium of hydrochorous species to study the heritability of dispersal-related traits, as they offer a wide range of propagule morphologies and dispersal strategies (*K*-oriented, e.g. *R. mucronata*; or *r*-oriented, e.g. *Lumnitzera* spp. and *Avicennia* spp.) adapted to passive dispersal in water.

(3) Dispersal simulation models

Numerical modelling is a widely used approach to study the role of dispersal in ecological and evolutionary processes and to investigate the conservation value of marine areas (Trembl *et al.*, 2008; Coleman *et al.*, 2017). Computational capabilities have increased the potential of using high-resolution ocean simulations that can be used to track particles at increasing spatial and temporal resolutions and scales (Jönsson & Watson, 2016).

Lagrangian particle-tracking models have been employed for a wide range of applications, including trajectory

simulations of oil droplets from oil spills (Paris *et al.*, 2012), near-shore and deep-sea larvae (Siegel *et al.*, 2008; Mitarai *et al.*, 2009; Watson *et al.*, 2011; Young *et al.*, 2012), marine plastics (Lebreton, Greer & Borrero, 2012), and to estimate potential connectivity in coral reefs (James *et al.*, 2002; Cowen *et al.*, 2006; Paris, Chérubin & Cowen, 2007; Trembl *et al.*, 2008; Paris *et al.*, 2013; Wood *et al.*, 2014). For passive mangrove propagule dispersal, this approach has been used to explain the colonization of disused shrimp ponds (Di Nitto *et al.*, 2013), the effect of local dynamics and habitat distributions on the spread of mangroves (Hamilton, Osman & Feller, 2017), population genetic structure (Ngeve *et al.*, 2016), and to study the likely impact of winds on the dispersal trajectories of propagules from different species (Di Nitto *et al.*, 2013; Van der Stocken & Menemenlis, 2017). Recently, a high-resolution, eddy- and tide-resolving numerical ocean model has been used to simulate mangrove propagule dispersal and estimate patterns of connectivity between sites globally (Van der Stocken *et al.*, 2019). In a nutshell, results from this study revealed strong sensitivity of dispersal distance and connectivity patterns to propagule buoyancy periods, high rates of along-coast transport, and support findings from phylogenetic and population genetic studies (see Section VI.2), such as the lack of connectivity between populations on either side of the African and American continents and transoceanic dispersal routes across the Atlantic, Pacific, and Indian oceans.

When using contemporary ocean surface current data, one must consider that “given the capacity [to cross tracts of ocean], there is much that is difficult to understand in the distribution [...]; and it is probable that we shall have to look back behind the means of dispersal to a distant age in the distribution of shore-plants of the mangrove type” (Guppy, 1906, pp. 458–459). Indeed, actual ranges and (meta)population structure may result from palaeocurrents, and present-day distributions may reflect the result of past processes. Reconstructing or assuming direction and strength of palaeocurrents is a challenge and its success will depend on coastal and shelf dynamics under various sea-level fluctuations over a relevant timescale. Ngeve *et al.* (2016) have shown evidence that mangrove genetic population structure in Cameroon could be attributed to (actual and recent) ocean surface current convergence rather than to terrestrial barriers having formed at the Last Glacial Maximum, but conclusions as to the causes and timeframe are not generally valid. Another challenge of developing mangrove dispersal models lies in including the appropriate dispersal processes, needed for reliable evaluations of model output against phylogeographic and population genetic data (see Section VI.2). Ocean currents and propagule traits, for example, vary in time, so that quantifying the spatial scale of dispersal ultimately requires data on the natural phenology of propagule release, as well as propagule buoyancy and viability, each of which alter probabilistic estimates of propagule trajectories and potential connectivity. Additionally, increased data on phenology and better understanding of its temporal variation will

help in making more reliable connectivity estimates under contemporary and future climate scenarios, given that ocean circulation patterns are expected to change (Sen Gupta *et al.*, 2015), likely affecting population persistence, genetic structure, and species distribution (Burrows *et al.*, 2011; Provost *et al.*, 2017). Avoiding the simulation of surplus trajectories (i.e. at moments that propagules are not available) may also reduce computation cost and output data size. Alternatively, dispersal simulation models allow for evaluating the sensitivity of dispersal and connectivity patterns to changes in biological variables such as propagule abscission and buoyancy period, and present a valuable tool for hypothesis testing and formulation (Van der Stocken *et al.*, 2019). Ideally, dispersal models should be paired with climate data and habitat suitability maps. Such an integrated approach will allow simulated stranding locations to be evaluated *in silico* for potential establishment (Hamilton *et al.*, 2017) and improve our understanding of the way climatic and non-climatic factors control global mangrove distributions, abundance, and species richness. For example, while changing temperature and precipitation regimes may expand a species' potential range towards higher latitudes (Saintilan *et al.*, 2014; Osland *et al.*, 2017), unfavourable establishment and ocean conditions (e.g. ocean surface current directionality and temperature, or geomorphological barriers) could limit dispersal to these sites (Soares *et al.*, 2012; Cavanaugh *et al.*, 2018).

VII. DISPERSAL AND CLIMATE CHANGE

Mangrove propagule dispersal operates within a long-term, dynamic and uncertain historical and future climate. Mangrove forests will be affected by a range of environmental perturbations related to global climate change, such as changes in ocean circulation, temperature and precipitation patterns, high water events, salinity, greenhouse gas concentrations, and sea-level rise (Gilman *et al.*, 2008; McKee, Rogers & Saintilan, 2012; Alongi, 2015; Ward *et al.*, 2016; Duke *et al.*, 2017). Generally, populations or species may respond to environmental change by going locally or regionally extinct, but they may also be replaced by other genotypes or species that arrive *via* dispersal or respond to these changes through phenotypic plasticity or adaptation (Davis, Shaw & Etter-son, 2005; Jump & Peñuelas, 2005; Chevin, Lande & Mace, 2010). While an increasing amount of evidence shows that rapid evolution is possible in a wide range of plants and animals even over short time scales of a few generations (Carroll *et al.*, 2007), the fact that mangroves have very long generation times might limit the potential for rapid local adaptation to some extent. To what extent dispersal in mangroves can stimulate local genetic diversity and, hence, the potential for local adaptation, remains to be investigated.

Over long time scales, the role of dispersal is illustrated by accumulating evidence of geographical shifts in response to historical and recent climate variability and sea-level rise (e.g. Sherrod & McMillan, 1985; Woodroffe & Gindrod, 1991).

For example, evidence from palynological and chronological data revealed considerable changes in mangrove habitat distribution and species composition along the west coast of India, controlled by hydrological regime shifts in response to sea level and monsoonal rainfall fluctuations in the Late Holocene (Limaye, Kumaran & Padmalal, 2014; also see Ellison, 2008). Similarly, using remote-sensing metrics, recent studies have addressed the matter of range limit sensitivity in mangroves (Osland *et al.*, 2017; Cavanaugh *et al.*, 2018), explaining the poleward expansion at their latitudinal limits along the marsh–mangrove ecotone on multiple continents (Rogers *et al.*, 2005; Osland *et al.*, 2013; Cavanaugh *et al.*, 2014). These changes may be due to the complex interplay of different factors such as land use and hydrology change, variation in sedimentation and erosion patterns (Giri & Long, 2016), but has been associated mainly with temperature-related variables such as a reduced frequency and intensity of extreme freezing events (Cavanaugh *et al.*, 2014, 2015; Saintilan *et al.*, 2014; Osland *et al.*, 2017). Despite the focus on climatic drivers of global mangrove distributions, these studies underscore the importance of quantifying dispersal to assess the likelihood of spatial rescue effects that could reduce potential adverse effects of climate change on mangrove forests. Population genetic data from range-edge mangrove populations generally signal a situation of low diversity and low effective dispersal rates resulting from high environmental pressure, low population sizes and founder effects (Arnaud-Haond *et al.*, 2006), dispersal-limiting ocean currents (Kennedy *et al.*, 2017), and coastal geomorphology (De Ryck *et al.*, 2016).

While climatic factors may primarily result in larger-scale (latitudinal) mangrove expansion and contraction, variations in sea-level rise can be expected to impact mangroves more locally (Lovelock *et al.*, 2015). Increasing sea level can force mangroves to shift their distribution to higher tidal elevations (Krauss *et al.*, 2011; Di Nitto *et al.*, 2014), along with shifting gradients in geophysical factors such as soil salinity, inundation time, and flooding frequency. Landward shifts can be constrained by physical structures from coastal development (Schuerch *et al.*, 2018) and patch features such as salt marsh vegetation at the landward boundaries of mangrove forests. The latter has been shown to control landward propagule dispersal and strongly increase establishment success (Peterson & Bell, 2015).

Propagule transport into the upper inland (across the mangrove–marsh ecotone) can be facilitated by rare high-water events such as spring and storm tides (Sousa *et al.*, 2007; Peterson & Bell, 2012) or the combined action of El Niño events and sea-level rise (López-Medellin *et al.*, 2011). In a rare example of such research, Jiang *et al.* (2014) modelled regime shifts following storm surges in South Florida and concluded that changes in the duration of salinization and propagule delivery may control regime shifts from freshwater marsh to mangroves. This will depend on the severity of the disturbance, which must exceed the system's ecological resilience. Indeed, while Jiang *et al.* (2014) found that the long-term effects of hurricane Wilma (24 October 2005)

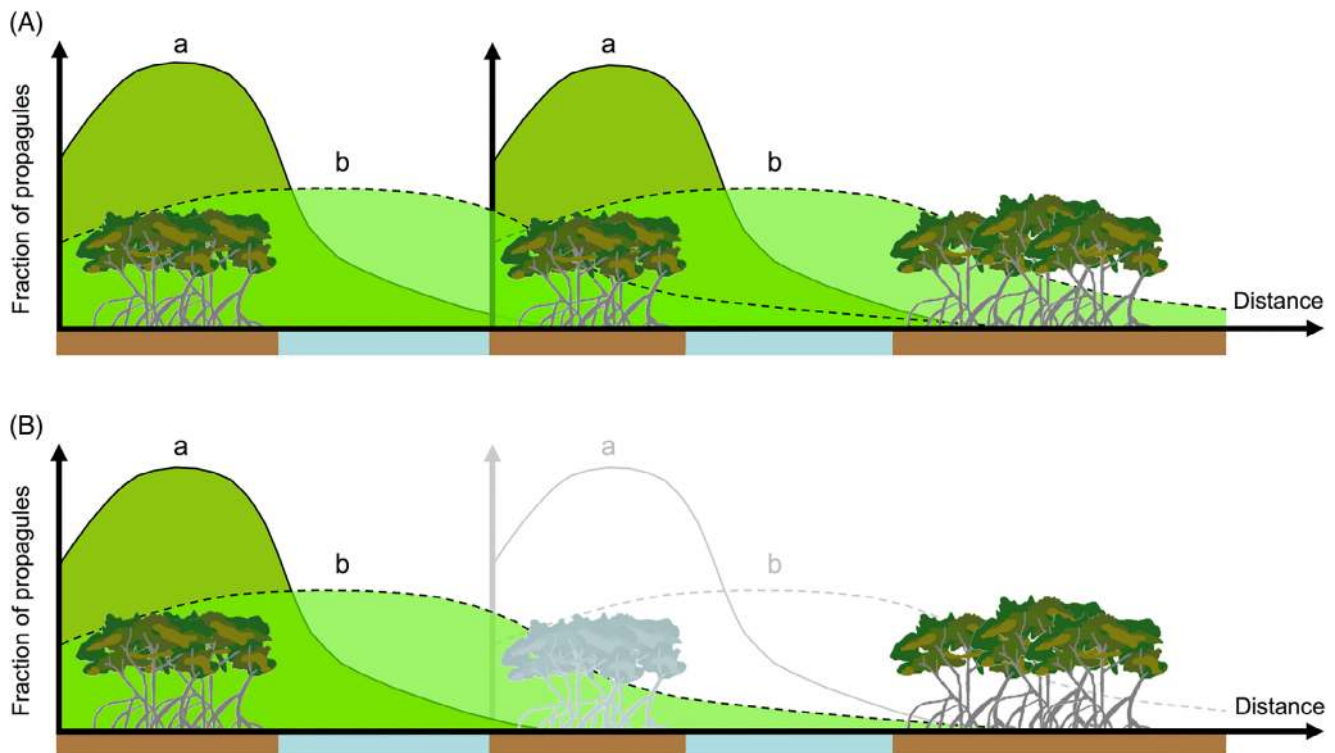


Fig. 6. Indicative propagule (not pollen) dispersal kernels for two mangrove species (a and b) to illustrate the potential impact of mangrove habitat fragmentation and degradation on connectivity and colonization potential (blue: water mass; brown: land). Note that the precise shape of the curves describing the kernels depends on various factors such as strength and symmetry of tidal currents, retention in the system, and buoyancy traits of the propagules. (A) Remote habitat fragments can be connected through a network of populations (stepping stones) within the dispersal range of a species. Species can reach the site on the right, either in a stepping-stone manner (species a) or directly (species b). (B) If changing conditions render the central stand unsuitable for establishment or deforestation strongly reduces the presence of mangroves in this area, species b may become the only species that can reach the habitat on the right, assuming that there are no other established stepping stones.

were too weak to trigger a regime shift, their model results indicated that such shifts are possible following more severe disturbances. This is particularly important in certain regions of the world (e.g. North America) where tropical cyclones play an important role in LDD, and given that the intensity, seasonal occurrence, and region of occurrence of these storms are expected to change upon global warming (e.g. Kossin, Emanuel & Vecchi, 2014; Knutson *et al.*, 2015; Sobel *et al.*, 2016; Murakami *et al.*, 2018). Changes in storminess may affect the process of pulse dispersal and the dynamics of shifting ecotones, transporting propagules far inland, but also beyond the range limits, and potentially reinforcing poleward expansion. Impacts from this type of high-energy disturbance on propagule dispersal, as well as on plant productivity, will likely depend on storm intensity, the position of a mangrove stand relative to the storm track, and other aspects such as the degree of exposure (Hurst *et al.*, 2015; Ward *et al.*, 2016).

Collectively, while the global distribution of mangrove populations over time depends on diverse geomorphological and hydrological processes and gradients (Woodroffe, 2002; Ellison, 2009), and climatic controls such as temperature and precipitation (Duke, Ball & Ellison, 1998; Record *et al.*, 2013; Feher *et al.*, 2017; Osland *et al.*, 2017), the

potential to track changing environmental conditions and colonize suitable habitat ultimately depends on the process of dispersal and the factors that influence propagule transport. Since different mangrove taxa have a different dispersal capacity, the responsiveness to these changes is likely to differ among species. In addition, climatic factors and anthropogenic activities such as deforestation may result in habitat fragmentation and degradation, impacting connectivity and colonization potential (Fig. 6), and alter factors that control dispersal dynamics, such as phenology, fecundity, and retention, but this remains to be quantified.

VIII. CONCLUSIONS

(1) The dispersal framework presented here consolidates knowledge on the physical and biological factors relevant in the process of mangrove dispersal. It brings together the multiple factors that are likely to shape the dispersal trajectories of propagules at local, regional, and global scales, and control temporal variability in dispersal and connectivity patterns.

(2) The quantification of propagule numbers available for dispersal (fecundity) remains challenging, given the inability to observe propagule production in a representative manner and the fact that fecundity varies strongly within and among species, and shows strong spatial and temporal variability. Additionally, as water velocity fields vary over time, the timing of propagule release in combination with the tidal framework and seasonal changes in ocean circulation determine the start of dispersal and the potential site of arrival.

(3) When it comes to the number of propagules available for dispersal, predation and herbivory control the number of potential colonists as a variable fraction of fecundity. Available data indicate that predation rates can be high, removing nearly all propagules in some cases. *In situ* experiments to quantify predation rates are labour-intensive and complex from the point of view that the effects of different environmental parameters (e.g. soil conditions, root density, hydroperiod) as well as the biotic interactions (intraspecific and interspecific competition) may be difficult to distinguish. Also, predation rates vary among mangrove species. Therefore, experiments should aim at identifying simple proxies of predation rates linked to, for example, mangrove tree zonation or latitude, albeit realising that so far the dominance-predation hypothesis has been proven wrong (e.g. McKee, 1995) as frequently as it was proven right (e.g. Smith, 1987), meaning that intertidal position and tree species cannot consistently be linked to predation. Possibly the combination of intertidal elevation (a proxy of presence of certain predatory crabs, e.g. Dahdouh-Guebas *et al.*, 2002) and canopy-gap presence (a proxy of predatory crab clustering *sensu* Bosire *et al.*, 2005) may in turn be a proxy to predict the likelihood of predation.

(4) Data on the buoyancy and viability period of propagules show pronounced variation among and within species. While short buoyancy and viability periods have been recorded in some experiments, other data reveal time spans that support the traces of transoceanic connectivity observed in genetic studies. Buoyancy and viability period of a propagule determine the temporal window available for successful dispersal. To identify the limits of this timeframe, experiments to quantify these propagule traits should be sufficiently long, allowing capture of the average as well as the maximum timeframe for successful dispersal. In combination with data on dispersal-vector properties, this will allow estimations of average and maximum dispersal distances, and simulations of patterns of successful dispersal when combined with habitat suitability maps.

(5) As the spatial and temporal resolution of ocean data increases, numerical dispersal models to simulate and predict mangrove dispersal and connectivity particularly require more data on biological factors such as the phenology of propagule release, propagule viability period and buoyancy periods. Such data should allow meaningful model parameterization and more robust simulations of present-day connectivity and assess changes in connectivity under future scenarios of climate change. In addition, data

from release–recapture experiments and genetic studies can be used to evaluate model output against observations.

(6) Mangroves face a wide variety of natural and anthropogenic threats across much of their range. Connectivity is an important conservation concern because it can facilitate long-term persistence of populations and species. Apart from adaptive (evolutionary) processes allowing persistence under new conditions, successful range shifts of mangrove species depend on dispersal traits and efficiency. This combines many of the above research questions and approaches. Both local dispersal and establishment (as a response to sea-level rise), and LDD and colonization (as a response to changing temperature and rainfall patterns, and changes in the frequency and intensity of storminess), may come into play.

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