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Caught in transit: offshore interception of seafaring propagules from seven mangrove species

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Abstract. Many organisms are transported passively and make use of the energy of natural phenomena or other organisms to disperse. However, not all species are equally likely to disperse over long distances. In mangroves, which possess seafaring propagules, it is largely unknown which species are more likely to reach the ocean and contribute to long-distance dispersal. This is because dispersal has been mainly studied under reductionist laboratory conditions and via localized release–recapture experiments. Direct interceptions of propagules at sea have hardly been attempted because of the high labor intensity. Here, we set up a local citizen-science network and engaged local fishermen to collect floating mangrove propagules over a period of 27 months. By comparing the dispersing community of propagules from the local stands in which they were produced, the open water of the bay, and the open ocean beyond the coral reef barrier, we could study the transition between local and long-distance dispersal. The composition of the dispersing community changed from the local stands toward the ocean, suggesting that this transition imposes an important selective filter for leaving the local system. With the exception of three rare species (*Lumnitzera racemosa*, *Pemphis acidula*, and *Xylocarpus moluccensis*), we intercepted dispersing propagules of every mangrove species occurring in the East African region. Most intercepted propagules were produced by *Rhizophora mucronata* and *Ceriops tagal*, followed by *Bruguiera gymnorrhiza* and *Avicennia marina*, which also represent the most abundant species in the nearby mangrove forest. A larger number of propagules were intercepted during the wet season, with fewer propagules recovered during the dry season. Overall, our study indicates that differences in the dispersal capacity of mangrove propagules are not straightforward and that some species may better disperse at local scales within an estuary or embayment, while others might be more suitable for dispersal over longer distances. The presence of such trade-offs may help explain why current attempts to use mangrove traits to predict mangrove species distributions at different scales have remained only moderately successful.

Key words: citizen science; connectivity; fishermen; Gazi Bay; ocean dispersal; release–recapture.

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INTRODUCTION

In light of ongoing environmental change, the ability to disperse to new habitats that provide suitable conditions for growth and reproduction, or to replenish the genetic diversity of a stand, is considered a crucial feature that can help species to survive, particularly when adaptation or acclimation to changing local conditions is ineffective. In this context, correlative models (e.g., niche envelope models) are commonly used to predict future ranges of species under different environmental conditions (Guisan and Zimmermann 2000, Araújo et al. 2005, Wiens et al. 2009).

However, most studies have assumed no or unlimited dispersal (Thomas et al. 2004), mainly because dispersal and colonization potential of species is largely unknown (Record et al. 2013). Recent studies have shown that realistic assumptions of dispersal capacity are needed to increase the biological realism of future predictions of species distributions (Barbet-Massin et al. 2012, Génard and Lescourret 2013) and extinction risk (Urban 2015). To assess variation in dispersal capacity, a variety of methods are used. First of all, relative differences in dispersal capacity can be assessed under simplified conditions in the laboratory (Jongejans et al. 2007, Chang et al. 2008, Van der Stocken et al. 2015*a*, *b*). Additionally, for passively dispersing organisms, models using wind and water current data can help to generate hypotheses about processes that occur at larger spatial and temporal scales (Nathan et al. 2005, Mitarai et al. 2009, Watson et al. 2011, Defne et al. 2016, Grech et al. 2016, Wood et al. 2016). Dispersal and colonization capacity can also be assessed indirectly by looking at patterns of genetic differentiation or shared alleles or haplotypes among populations separated by increasing distances (e.g., Pinsky et al. 2010, Simpson et al. 2014, Kennedy et al. 2016). Finally, a large body of work describes the dispersal trajectories of marked organisms released in the field (e.g., Van der Stocken et al. 2013, Gouagna et al. 2015, Walter et al. 2016). While this work has the advantage of providing realistic information, labor intensity and low recapture rates ensure that the method becomes less feasible over larger temporal and spatial scales (but see, e.g., Steinke and Ward 2003, Inoue et al. 2014).

All these approaches have been used to study the process of dispersal and resulting connectivity patterns in mangroves. This phylogenetically diverse group of trees produces a variety of morphologically contrasting fruits and seeds (here commonly labeled as "propagules") that independently evolved the ability to disperse via ocean currents. However, while data on dispersal ability and landscape connectivity are needed to explain correlations between genetic and geographic distance (Orsini et al. 2013), it is still not known which mangrove propagules are more likely to disperse over long distances. This is because current release–recapture studies are restricted to short-term observations on very local scales of a few kilometers. They do not account for intra- and inter-annual variation and only consider one or a few species released from one up to a handful of localities (e.g., Yamashiro 1961, Breitfuss et al. 2003, Van der Stocken et al. 2013). Additionally, because propagules are typically deposited experimentally, instead of being released naturally from their parent trees, these studies do not account for the natural phenology of abscission (i.e., propagule release; but see McGuinness 1997). An alternative method that sacrifices experimental control over realism is to study natural dispersal dynamics by sampling dispersing assemblages of propagules at different locations in the field. Advantages of this method are that large numbers of propagules of different species can be considered and that it is feasible to assess temporal variation. Drawbacks of this approach are that individual dispersal trajectories of propagules remain unknown and that it would require a lot of manpower to sample the ocean for floating mangrove propagules. It is this major investment in sampling effort that explains why such studies are currently absent.

Here, we solve the practical problem of sampling the ocean using a citizen-science approach. Making use of a tropical bay as a case study, we engaged local fishermen to collect data on the mangrove propagules they caught in their nets over a time period of almost two years.

The resulting dataset allows for reconstructing spatial and temporal variation in the dispersing community of a natural mangrove forest. By comparing the propagule content of samples collected at different locations in the bay, we investigate how variation in species composition changes when mangrove propagules make their way to the open ocean. Samples were taken over a time period of 27 months in three different parts of Gazi Bay (Kenya): (1) a sheltered inland fishing area close to the forest, (2) a transition zone near the mouth of the bay, and (3) an area outside of the bay beyond the barriers provided by the coral reefs in the Indian Ocean. Based on these data, we reconstruct the distance decay of dispersal for different mangrove propagules and explore whether species that are more abundant in the local mangrove stands are also more abundantly represented in the dispersing community by their propagules. We hypothesize that the species composition of intercepted propagules will change toward the open ocean with better dispersing species becoming relatively more abundant. In these analyses, we control for potential confounding effects of seasonality, as some species are more likely to release their propagules in the wet season (Van der Stocken et al. 2017).

METHODS

Fishing events and gear

This project was inspired by the fact that in regions with mangrove forests, fishermen from small-scale artisanal fisheries often catch mangrove propagules in their nets. Consequently, we decided to capitalize on the inadvertent sampling effort of fishermen to reconstruct spatial and temporal variation in mangrove propagule fluxes. For this, we established a network of fishermen in the area of Gazi Bay, which is situated approximately 46 km south of Mombasa (Kenya). Our research group has a long history of research in this area facilitating the establishment of contacts. During our field campaign in 2012, we taught local fishermen to recognize the propagules of seven mangrove species which were locally not rare (Appendix S1: Table S1) and provided logbooks so they could note the abundance of each of the species present during each of their fishing trips, for hereon referred to as fishing events. In general, fishing events are quite comparable. Local fishermen tow a sock-shaped net from the backside of a small, motorized boat (artisanal fishing). The nets contain floaters, which ensure that only the top two meters of the water column is fished. At the same time, this ensures that floating mangrove propagules are also caught. Overall, the gear and net type used by different fishing boats were very comparable since all fishermen worked for the same fishing company. Based on the area that is covered by their daily fishing activities, we defined three different zones: (1) the innermost part of the bay, bordered by mangrove forest (zone A); (2) an intermediate zone, which can be considered as the transition to the ocean (zone B); and finally, (3) a zone in the Indian Ocean at most 2 km behind the coral reef barriers (zone C; Fig. 1a). Overall, the data covered 246 fishing events spread over a period of 27 months (7 March 2012–6 July 2014).

Mesh size of the nets was 2–2.5 cm. Larger nets were used to fish in the open ocean (70 m long instead of 50 m long and having a width of 9 m instead of 3 m) compared to the other locations. This means that we cannot interpret differences in absolute abundances of propagules between fishing zones to make inferences about relative differences in dispersal potential. For the latter, differences in relative abundance, however, can give relevant information. The duration of fishing activities is variable which will result in some noise in the data, as fishermen do not fish for a fixed amount of time. They fish until they have caught enough fish or have to return to shore for other reasons. Because we could not standardize the duration of individual fishing events in this project, we do not interpret absolute differences in propagule abundance between zones but only the relative abundance of propagules. Additionally, more fishing events are undertaken in zone A during the South-East monsoon period (April–October), as sea conditions in zones B and C can be rough. During the North-East monsoon period (November–March), the sea conditions are calm with increased fishing in zone C. The North-East monsoon period is characterized by a bimodal pattern of rainfall, with a longer (March–July) and a shorter (October–December) rain period.

Vegetation cover

Mangrove tree species in Gazi Bay strongly differ in local vegetation cover. This has been quantified in an earlier study by Neukermans et al. (2008). As a measure of relative cover of each mangrove species, the pixels corresponding to different mangrove species were counted using the intensity level count algorithm included in Photoshop CC 18.0 (2017). For this, we used the mangrove stand map as presented by Neukermans et al. (2008; Fig. 2 therein). This worked well for the most abundant species (*Rhizophora mucronata*, *Ceriops tagal*, *Avicennia marina*, and *Sonneratia alba*). For the other species (*Bruguiera gymnorrhiza*, *Heritiera littoralis*, and *Xylocarpus granatum*), which are known to be rarer and could therefore not be mapped by Neukermans and colleagues from satellite imagery, we conclude that the relative forest cover was negligible. The relative coverage of *R. mucronata*, *C. tagal*, *A. marina*, and *S. alba* in the adjacent

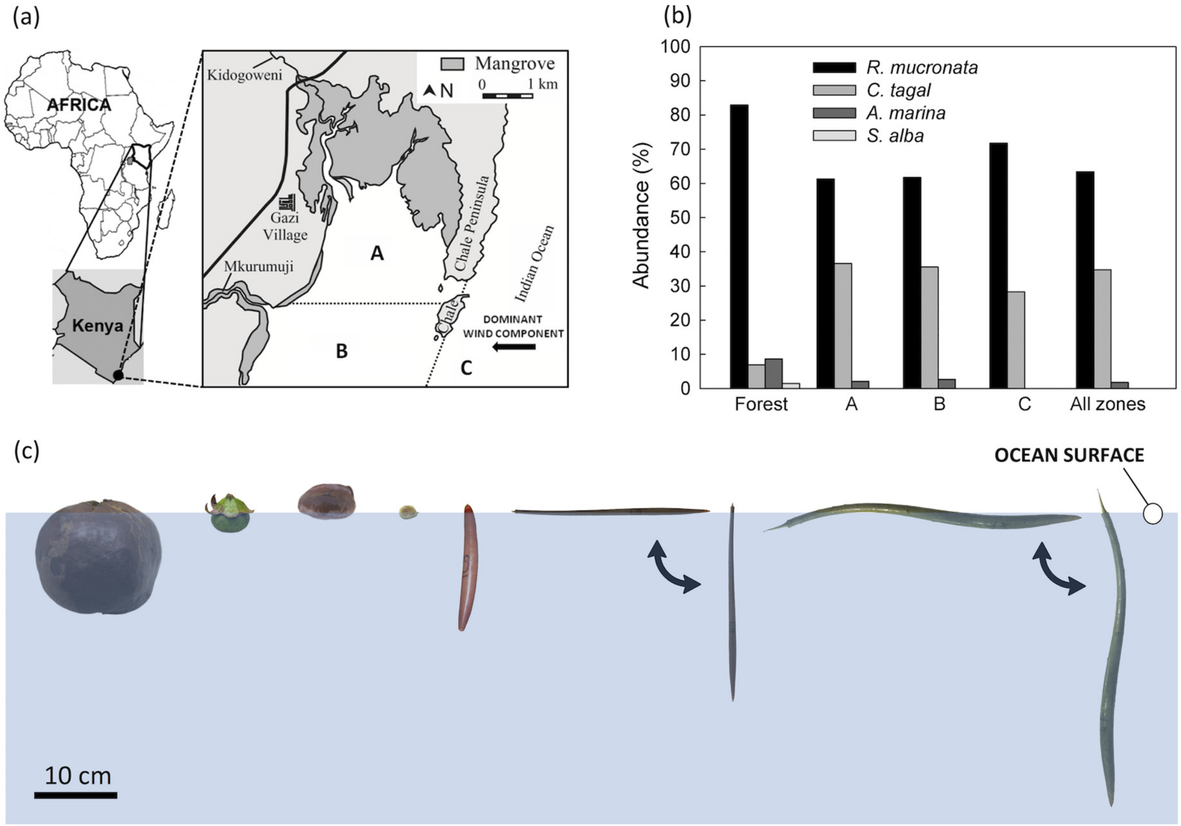

Fig. 1. (a) Map of the study area with the different zones (A, B, C) in which mangrove propagules were captured. (b) Relative abundance of mangrove trees in the forest and recovered propagules in the different fishing zones, for the four most abundant mangrove species considered in this study: *Rhizophora mucronata*, *Ceriops tagal*, *Avicennia marina*, and *Sonneratia alba*. (c) Propagule types of all mangrove species considered in this study, showing their position relative to the water surface while floating. Propagules are from the following mangrove species (left to right): *Xylocarpus granatum* (fruit), *Sonneratia alba* (fruit), *Heritiera littoralis*, *A. marina*, *Bruguiera gymnorrhiza*, *C. tagal*, and *R. mucronata*. For the latter two species, propagules can float either horizontally or vertically, with the potential to shift between these positions (double arrow).

mangrove forest was found to be 82.92% (96,575 pixels), 6.96% (8109 pixels), 8.65% (10,075 pixels), and 1.47% (1706 pixels), respectively (Fig. 1b). All mangrove species present in the area (and in the Western Indian Ocean) produce floating propagules.

Data analyses

All analyses were performed in R (R Development Core Team 2016, version 3.3.3) using functions from different packages (stats, vegan, and multcomp).

To explore whether the relative abundance of propagules captured in fishing nets (Fig. 1c) reflects the relative coverage of the different mangrove tree species in the nearby mangrove forest, we correlated relative coverage of each species in the forest with its propagule abundance recovered in the different zones using Pearson product-moment correlations (cor.test function). If some species are more likely to disperse over longer distances than others, we expect that their relative contribution to the batches of propagules we intercept will become larger. To test this, we built a generalized linear model with zone and season as categorical predictor variables and the proportion of each species' propagules in each fishing event as a response variable. Season was coded as a categorical variable (wet, i.e., end of March–July and November–December; dry, i.e., August–October and January–early March). We did not further subdivide years into more time periods to avoid unbalance in the number of observations in each level of this categorical variable. We specified a zone × season interaction to test whether the relative abundance of propagules collected at different distances from the coast differs between seasons. Since proportions are bounded between 0 and 100, we specified an appropriate binomial distribution and logit link function when specifying our model. Pairwise Tukey post hoc tests were used to test for differences between zones in dry and wet seasons via the glht function (multcomp package).

A permutational analysis of variance (Anderson 2001) was used to test for differences in community structure of mangrove propagules collected in different zones using relative abundances as responses (adonis function, vegan package). This analysis was performed using both Bray-Curtis and Raup-Crick dissimilarity indices as measures for differences in propagule composition among zones. Bray-Curtis is a classic index that is suitable for testing differences in abundances or relative abundances (compositional dissimilarity) between different sites and can cope with data containing many zeroes. The Raup-Crick index (Raup and Crick 1979) has been recently revalued as a powerful index to test differences in species composition. It is based on deviations from null model expectations and is largely insensitive to differences in richness among pairs of sites and is therefore often used as a relatively unbiased estimate of beta diversity (Chase et al. 2011). To account for potential confounding effects of seasonality on the investigated response, we included season as a predictor, and considered a season × zone interaction in the models to check whether the effects of seasonality could be more pronounced closer to shore. Pairwise comparisons were calculated between different pairs of categories (zones A–B, zones A–C, zones B–C). While adonis tests for differences in average community composition between the different zones (i.e., differences between the centroids), it is also possible that there is no difference in the average composition of a batch of dispersing propagules from fishing events from different zones but that the variation in propagule composition among fishing events (i.e., variation around the centroids) could be larger or smaller depending on the zone in which the collections took place. For instance, with increasing distance from the coast the composition of intercepted propagules could become less variable if it predictably consists of good dispersing species. Such effects were tested using a multivariate homogeneity of variance test (betadisper function; Anderson et al. 2006), again using both Bray-Curtis and Raup-Crick dissimilarities. This analysis is a multivariate extension of the Levene's test and compares distances to centroids in different groups. Pairwise differences in this multivariate dispersion among the three zones were tested using Tukey post hoc tests.

RESULTS

A total of 51,582 propagules were collected over the total duration of the study (Table 1), including propagules of all mangrove species that grow locally in the Gazi Bay mangrove forest (and representative for the Western Indian Ocean) located at the NW end of the bay, with the exception of *Lumnitzera racemosa*, *Pemphis acidula*, and *Xylocarpus moluccensis.*

The number of fishing events in each of the different fishing zones differed amounting 147 in zone A, 49 in zone B, and 50 in zone C. Most propagules were collected in zone A, less in zone B, and least in zone C (Table 1). In all three fishing zones, *Rhizophora mucronata* propagules were most abundant, followed by *Ceriops tagal* and *Bruguiera gymnorrhiza* (Table 1), together representing 97.6% of all recovered propagules. Fewer propagules were recovered for the other species, with 722 and 30 propagules of *Avicennia marina* and *Heritiera littoralis*, respectively, and 9 fruits of *Sonneratia alba*. For *Xylocarpus granatum*, 330 fruits in total were recovered. Overall, the most abundant tree in the adjacent mangrove forest (*R. mucronata*) was also most abundantly represented in the propagules collected at sea (Fig. 1b). While *C. tagal* and *A. marina* have similar tree cover, *C. tagal* was proportionally more represented in the dispersing community. The other, rarer species were rarely collected at sea. Given the low number of species, it is not

Table 1. Number of propagules collected by fishermen in their nets in three different zones of Gazi Bay (Kenya): a sheltered inland fishing area close to the forest (zone A), a transition zone near the mouth of the bay (zone B), and an area outside of the bay beyond the barrier provided by the coral reefs in the Indian Ocean (zone C).

Zone	*Rhizophora mucronata*	*Ceriops tagal*	*Bruguiera gymnorrhiza*	*Avicennia marina*	*Sonneratia alba*	*Xylocarpus granatum*	*Heritiera littoralis*
Zone A	20,559	12,278	2063	722	9	276	2
Zone B	3234	1861	449	142	0	53	28
Zone C	7101	2797	6	1	0	1	0
Total	30,894	16,936	2518	865	9	330	30
Total (%)	59.89	32.83	4.88	1.68	0.02	0.64	0.06

Notes: The data cover 246 fishing events in total over a period of 27 months (7 March 2012–6 July 2014). Percentages are calculated using the total number of propagules over all zones and species, that is, 51,582 propagules.

surprising that correlations between the relative coverage of a species and relative abundance of its respective propagules collected at sea were not significant. Still, correlation coefficients were high regardless of the fishing zone: zone A ($r = 0.83$, $P = 0.17$), zone B ($r = 0.85$, $P = 0.15$), and zone C ($r = 0.93$, $P = 0.07$).

Overall, our models show that in both the wet and the dry season, zone has an effect on the relative abundance of propagules (Fig. 2). However, a significant season × zone interaction which was found for most species (Table 2) indicates that this pattern changes between seasons. Tukey post hoc test results, illustrated in Fig. 2,

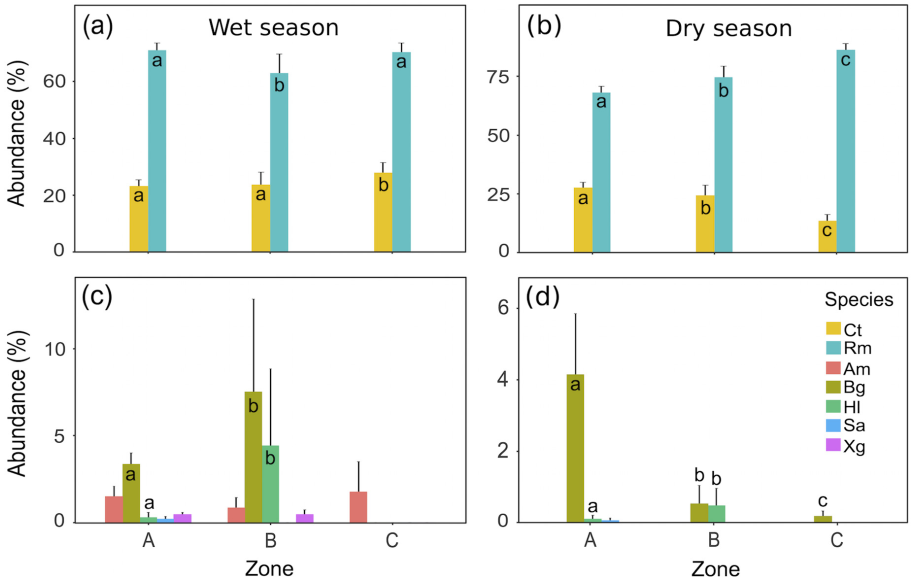

Fig. 2. Means and standard errors of the relative abundance of propagules intercepted during replicate fishing events during the wet and dry seasons (wet, i.e., end of March–July and November–December; dry, i.e., August–October and January–early March), in each of the three fishing zones: the innermost part of the bay, bordered by mangrove forest (zone A); an intermediate zone, which can be considered as the transition to the open sea (zone B); and a zone behind the coral reef barriers in the Indian Ocean (zone C). Different panels (a–d) represent patterns observed for (a, b) the two most abundant species and (c, d) the five rarer species considered in this study. For each species, significant differences ($P < 0.05$) between zones, as tested using Tukey post hoc tests, are indicated using letters. Abbreviations of species names are as follows: *Ceriops tagal* (Ct), *Rhizophora mucronata* (Rm), *Avicennia marina* (Am), *Bruguiera gymnorrhiza* (Bg), *Heritiera littoralis* (Hl), *Sonneratia alba* (Sa), and *Xylocarpus granatum* (Xg).

Table 2. Results from generalized linear models predicting the relative abundance of propagules of seven mangrove species based on the zone in which they were collected and the season during which they were collected.

Species	Model	df	χ^2	P
Rhizophora mucronata	Zone	2	200.7	<0.0001***
	Season	1	40.8	<0.0001***
	Zone × season	1	235.7	<0.0001***
Ceriops tagal	Zone	2	78.1	<0.0001***
	Season	1	0.07	0.8
	Zone × season	1	194.1	<0.0001***
Avicennia marina	Zone	2	6.94	0.03*
	Season	1	233.7	<0.0001***
	Zone × season	1	0	1
Sonneratia alba	Zone	2	18.73	<0.0001***
	Season	1	5.48	0.02*
	Zone × season	1	0	1
Bruguiera gymnorrhiza	Zone	2	256.5	<0.0001***
	Season	1	15.87	<0.0001***
	Zone × season	1	184.93	<0.0001***
Xylocarpus granatum	Zone	2	16.67	0.0002***
	Season	1	61.12	<0.0001***
	Zone × season	1	0	1
Heritiera littoralis	Zone	2	237.76	<0.0001***
	Season	1	96.92	<0.0001***
	Zone × season	1	4.37	0.11

$^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

support these patterns. Only for the less abundant species *S. alba* and *X. granatum*, no significant differences between groups could be supported by the conservative Tukey post hoc test that was used.

Multivariate analyses support significant differences in community composition captured by the relative abundance of species between zones (adonis; Bray-Curtis: $r^2 = 0.028$, $P = 0.013$; Raup-Crick: $r^2 = 0.037$, $P = 0.002$). Pairwise comparisons showed that community structure differed between zones A and C (adonis; Bray-Curtis: $P = 0.009$; Raup-Crick: $P = 0.002$), but not between zones A and B (adonis; Bray-Curtis: $P = 0.436$; Raup-Crick, $P = 0.245$) and zones B and C (adonis; Bray-Curtis, $P = 0.046$; Raup-Crick, $P = 0.168$). There was no significant difference in community composition between seasons (adonis; Bray-Curtis: $r^2 = 0.005$, $P = 0.27$; Raup-Crick: $r^2 = 0.008$, $P = 0.157$), except when comparing zones B and C (adonis; Bray-Curtis, $P = 0.012$; Raup-Crick, $P = 0.047$). The interaction zone × season was found to have a significant effect when using the Bray-Curtis dissimilarity index ($P = 0.038$), but not when using Raup-Crick ($P = 0.27$).

Besides differences in average community composition (centroids), there were also significant differences in the variation in community composition (distances to centroids) between fishing zones (betadisper; Bray-Curtis: $F_{2,\ 243} = 3.491$, $P = 0.032$; Raup-Crick: $F_{2,\ 243} = 9.963$, $P < 0.0001$). A complete overview of Tukey post hoc pairwise comparisons of community composition between zones is given in Appendix S2: Table S2.

DISCUSSION

Over a time period of more than two years, we monitored the composition of mangrove propagules retrieved by fishermen that were active in different parts of a tropical bay with a nearby mangrove forest. This was done to reconstruct variation in dispersal of different mangrove species and to explore which species may be more likely to embark on long-distance dispersal. We found that different communities of propagules were intercepted at different distances from the mangrove forest, but that this pattern differed between the dry and rainy seasons.

Propagule abundance, vegetation cover, and the importance of fecundity

We intercepted propagules from all mangrove species that grow locally in the Gazi Bay mangrove forest (and that are representative for the Western Indian Ocean), with the exception of *Lumnitzera racemosa*, *Pemphis acidula*, and *Xylocarpus moluccensis*. The absence of propagules from these three species can be explained by the fact that they are rare in the study area so that the number of propagules available for dispersal is low. In Gazi, a few *P. acidula* individuals grow on the supralittoral dunes. This, combined with the small size of the fruits, renders its interception impossible with the approach used in this study. Also for *L. racemosa*, low abundance in our study area (*personal observation*) and its presence in the higher intertidal landward sites may reduce the potential of propagules to reach the ocean. Furthermore, their small-sized propagules (~12–20 mm long) make them less likely to be retained in fishing nets. The local *X. moluccensis* distribution consists of a few small individuals at the bay's open shore and a small patch of trees deep in the northern part of the forest.

Most intercepted propagules were produced by *Rhizophora mucronata* and *Ceriops tagal*, followed by *Bruguiera gymnorrhiza* and *Avicennia marina*, which also represent the most abundant species in the nearby mangrove forest. If we correlate vegetation cover with propagule abundance, there seems to be a strong positive association. However, because of the low number of species as independent units in this analysis, this pattern was non-significant. Although tree cover did show a positive trend with propagule abundance, we note that in reality this relationship is more complex. When tree-specific seed production (fecundity) is low, for example, high tree densities may still ensure a high total number of emigrants. Despite fecundity data being limited, observations for the main mangrove genera reflect a possible evolutionary trade-off between the number of propagules produced and the individual propagule size (Alleman and Hester 2011). This could explain why *C. tagal*, producing smaller propagules than *R. mucronata* (*personal observation*), contributed substantially to the recovered propagules relative to its overall abundance in the forest. While *C. tagal* makes up <10% of the forest, it represents more than 30% of recovered propagules. At the same time, based on our field observations in the bay over several years, *C. tagal* trees typically carry very large numbers of propagules compared to the other species, suggesting a higher fecundity (*personal observation*). Similarly, a high fecundity may also explain why *B. gymnorrhiza* contributed almost 5% of the total number of propagules recovered, despite its relative low abundance in the forest (<1%). In addition, the abundance of potential emigrants may be controlled by the proximity to open water given that propagules deposited at the edge of the forest are less likely to get stuck in the maze of roots (Van der Stocken et al. 2015*a*). *Rhizophora mucronata* trees, for example, typically represent the most seaward stands, while *A. marina* trees are found both seaward and landward. Hence, with respect to the total proportion of *A. marina* in the forest, it is clear that some tree stands have no direct access to tidal channels and probably contribute less propagules to the bay.

Differences in dispersal capacity?

A summary of our data suggests that interceptions at different distances from the shore reflect the typical distance decay of dispersal in most species, with most propagules captured close to the mangrove forest (Table 1). While this apparent decrease could be partly explained by the fact that propagules are diluted over much larger areas of water when leaving the bay, it is sensible to assume that the dilution effect will be similar among species. In addition, this pattern might be biased by variation in the length of fishing events that we could not standardize. Therefore, we chose not to draw conclusions from this distance decay pattern and decided to focus on relative proportions of species collected at different distances from the shore to test our hypotheses.

Adonis models revealed that the community composition of dispersing mangrove propagules changes when they are floating from the local mangrove stands in the bay toward the open ocean. In our data, we see that *B. gymnorrhiza* and *A. marina*, although quite abundantly represented in the transition zone in the wet season, contribute next to nothing to the propagule collections in the open sea (zone C). This suggests they may be poorer dispersers than *R. mucronata* and *C. tagal*, of which propagules were abundant in all three zones. The absence of some species in zone C as compared to *R. mucronata* and *C. tagal* may be due to shorter floating periods (Rabinowitz 1978, Tonné et al. 2017) so that the relative abundance of different propagule types could change *en route* to the open ocean. Reported floating periods of *A. marina* (15 d; Clarke et al. 2001) and *B. gymnorrhiza* (31 d; Steele 2006), for example, are shorter than for the large-sized propagules of *R. mucronata* (150 d; Drexler 2001). However, data on maximum floating periods can be misleading, given that most propagules in these studies were still floating at the end of the respective experimental periods. Knowledge on dispersal capacity (and biological connectivity) in general would benefit from long-term floating (and viability) experiments, that is, experiments of which the duration exceeds the maximum floating (and viability) period. Such data would allow for better understanding the relative importance of factors such as floating period, fecundity, and abundance of the species in the forest, as well as distance to the open water.

Steele (2006), for example, reported a floating period of 60 d for *Xylocarpus granatum*, while floating periods of 104 d (Steele 2006) and 150 d (Ye et al. 2004) have been published for *Heritiera littoralis*. Since these are among the longest floating periods currently reported in mangroves, aspects such as tree abundance and tree-specific fecundity, as well as intertidal position (determining hydroperiod and hence potential for dispersal), are more likely to explain why propagules from these species were absent in zone B and zone C. The rarity of these species and their landward position in our study area make it unlikely that high numbers of these propagules would be intercepted. It is unclear to what degree wind forces may have determined the limited number of wind-sensitive *H. littoralis* propagules in our campaign (Van der Stocken et al. 2013, 2015*b*).

While some fruits of *Sonneratia alba* were captured in zone A, these fruits, containing more than 100 tiny seeds, typically disintegrate after prolonged immersion in saline or brackish water (Tomlinson 1986, Ball and Pidsley 1995). As these seeds are too small to be trapped in the fishing nets, we expected that the chance of finding *S. alba* in zone B and zone C was low.

Effects of seasonality

It is clear that seasonal variation in propagule production complicates the story of this paper. When we look at propagule abundances for fishing events during the wet and dry seasons, respectively (Fig. 2), we see that *B. gymnorrhiza* and *A. marina* show strong variation in how much they contribute to the propagules in zone C. Propagules from both species are most abundantly found in the ocean during the wet season, which aligns with reported timing of propagule production in both species (Wang'ondu et al. 2010; *personal observation*). In addition, fluvial discharge in the rainy season is higher and increases the potential of propagules to be transported out of the system. For *C. tagal* and *R. mucronata*, our data show that propagules are abundant in both the wet and dry seasons, but with some interesting differences between both species. In the dry season, for example, *R. mucronata* seems to become relatively more abundant in collections in zone C (open ocean) compared to zones A and B, while in *C. tagal* the opposite pattern is found. While this could indicate that *R. mucronata* is a better disperser over long distances than *C. tagal*, this pattern may as well be due to differences in propagule production periods. Propagule production periods for both species have been associated with the wet season (Gwada and Kairo 2001, Wang'ondu et al. 2013), but may be longer in *R. mucronata* than in *C. tagal*, and partly extended into the dry season. Phenological data for the northerly-situated mangrove population in Mida, for example, provide evidence supporting this explanation (see Fig. 3 in Gwada and Kairo 2001). However, phenological patterns may differ inter-annually and between sites, and long-term records for *C. tagal* are currently lacking.

Limitations and perspectives

Our citizen-science network provided a cost- and time-effective way to gather data on dispersing propagule assemblages over a spatial scale that is much larger than the scale of earlier (release–recapture-type) studies. However, a drawback is that the exact origin and the trajectories of the propagules remain unknown. During the wet season months (end of March–July and November–December), the regional ocean circulation is characterized by strong continuous northward flow along the coast, while regional ocean currents during the dry season (August–October and January–early March) are characterized by the southward-flowing Somali Current (Mayorga-Adame et al. 2016). We cannot exclude that differences observed in zone C may in part be explained by the import of propagules from more southerly or more northerly located mangrove populations, such as Mida and Mombasa, situated 130 km and 45 km north (Euclidean distance), respectively, or populations at Wasini or Vanga, situated 30 km and 40 km south, respectively.

However, when all potential underlying determinants are considered (e.g., fecundity, retention, predation, floating period, and viability period), estimating dispersal capacity becomes very complex. For instance, while the potential for long-distance dispersal in *C. tagal* may be favored by a higher fecundity and smaller propagule size (reducing the potential to be retained by physical barriers), *R. mucronata* typically occupies low intertidal zones bordering open water expediting access to the water vector. Additionally, *R. mucronata* produces propagules that are less sensitive to dehydration and predation and initiate root growth more quickly upon stranding (De Ryck et al. 2012, Robert et al. 2015). While it is difficult to assess the combined impact of all these factors on the overall dispersal potential, both species dispersed more or less equally well in our study.

Overall, while this study contributes novel intermediate-scale information on dispersal, it is still difficult to generalize differences in dispersal capacity among species. This is mainly because the long-term viability and buoyancy of propagules under oceanic conditions remain understudied. We corrected for differences in abundance that are prone to a sampling intensity bias in our analyses by using relative abundances to assess relative differences in dispersal capacity. However, it is clear that regardless of the shape of the propagule, longer floating and viability periods, and higher abundance of propagules in the water, promoted by higher fecundity and higher abundance of trees, will always be beneficial for long-distance dispersal. Oceanic dispersal is a process that includes a very strong stochastic element besides the determinism related to the directionality of currents and propagule traits such as floating and viability periods that limit the duration of dispersal trajectories. This stochasticity entails that small changes in trajectories at small spatial scales can lead to large differences in the final dispersal trajectory of a propagule. Hence, the more propagules can leave, the higher the number of trajectories and the more likely unlikely trajectories over very long distances can become. In our study, we intercepted propagules that were on such trajectories, and it was clear that for some species, fewer of these trajectories managed to carry them out of the bay toward the open ocean. In part, this was due to differences in abundance, but the fact that relative contributions from some species dropped with distance does highlight that not all propagules disperse equally well. Overall, our study indicates that differences in the dispersal capacity of mangrove propagules are not straightforward and that the propagules of some species may be more suitable for dispersal at local scales within an estuary or embayment, while others might be more suitable for long-distance dispersal. The presence of such trade-offs has not been confirmed but may help to explain why current attempts to use mangrove traits to predict the distribution of mangrove species at different scales have remained only moderately successful.

It is clear that wider generalizations of interspecific differences in dispersal capacity of mangroves cannot be limited to the reductionist view adopted higher. Differences in fecundity, retention, predation resistance, and floating and viability periods should be accounted for when attempting to accurately model dispersal trajectories of mangrove propagules. In this context, we believe that (release–recapture) experiments at larger spatial scales and over meaningful timespans through citizen-science networks, such as presented in this study, may help to derive estimations that take into account real-life complexity. Except for rare species and species with low access to water, not permitting a conclusive statement, all mangrove species present in the adjacent forest contribute to the seaborne pool with a potential for long-distance dispersal. Knowledge about their dispersal capacity can help to better understand the spatial range dynamics of these wide-ranging coastal species.

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