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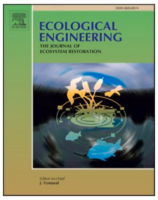

Scalable mangrove rehabilitation: Roots of success for *Rhizophora stylosa* establishment

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ABSTRACT

Large-scale mangrove restoration initiatives have been attempted worldwide but have often suffered from low success rates and high costs. Direct seeding is increasingly used as a viable and cost-effective strategy for achieving restoration at scale for other coastal habitats yet has been little used for mangroves. Planting mangrove propagules instead of saplings can reduce costs and labour associated with the collection, growing out, and re-planting involved in conventional restoration methods. In this study, we document research into direct seeding for mangrove restoration, focussing on early establishment processes and identifying recruitment enhancement strategies that will improve natural recruitment success rates. The elongated propagules produced by *Rhizophoraceae* species can establish by self-planting into the substrate, or after grounding flat as the tide recedes. An aquaria experiment showed that vertically sown (to simulate self-planting) *Rhizophora stylosa* propagules grew significantly longer and more roots than propagules sown horizontally. After 35 days the vertical propagules grew roots 46.3 ± 20.5 mm in length while horizontal propagules grew roots 17.4 ± 16.6 mm in length. A field study showed that specially designed bamboo structures facilitate vertical self-planting, thus enhancing successful establishment. Propagules grounding in a vertical orientation successfully established 52.6 % of the time, whereas propagules grounding horizontally had a 10 % success rate. Results from this study suggest that grounding orientation, and the hypocotyl being embedded into the substrate, prompt root initiation and may lead to *R. stylosa* reaching an establishment threshold quicker than naturally stranding propagules. As such we propose that direct seed planting represents a viable alternative for large-scale restoration of Rhizophora.

1. Introduction

The extensive impact of human activities on natural ecosystems globally, and the resulting need for large-scale ecological restoration, is widely acknowledged. Yet significant uncertainty remains over the most effective frameworks and approaches to achieving restoration goals of key forest habitats. (Lázaro-González et al., 2023). The global decline in mangrove habitat over the last 50 years is well-documented (Bunting et al., 2022; Polidoro et al., 2010; Thomas et al., 2017), and although an increased focus on conservation and slowing rates of decline offer hope (Goldberg et al., 2020; Lovelock et al., 2022), the scale of the issue remains concerning. Moreover, intensifying climate change has driven renewed interest in recovering lost mangrove ecosystems for coastal protection and carbon sequestration. However, despite sustained efforts at achieving successful large-scale mangrove restoration, there is yet no universally accepted approach. Large-scale projects often involve prohibitive costs and complex planning or governance issues (Lovelock et al., 2022), and past project failures due to improper site selection (Primavera and Esteban, 2008), lack of consideration for hydrology (Kodikara et al., 2017) or lack of ecological planning (Kamali and Hashim, 2011) may contribute to a more risk averse approach to scaling up restoration. Identifying cost-effective solutions is critical for reducing the risk associated with the large-scale restoration projects required to achieve global restoration targets (Lovelock et al., 2022).

Reviews of previous successes and failures in the management of keystone coastal species has led, in many cases, to a shift towards seed-based restoration and Nature-based Solutions (NbS) approaches as preferred strategies for restoring and preserving the future of key coastal ecosystems (Kettenring and Tarsa, 2020; van Bijsterveldt et al., 2022; Vanderklift et al., 2020). The question of whether direct seeding or

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Abbreviations: ODP, obligate dispersal period; EMR, Ecological Mangrove Rehabilitation; NbS, Nature-based Solutions.

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planting seedlings is a more effective method in achieving global restoration targets is just as pertinent in the context of mangrove rehabilitation as it is in terrestrial environments (Lázaro-González et al., 2023). Planting nursery-reared saplings generally offers faster growth and establishment, whereas direct seeding is easier to conduct, offers more flexibility, and is more cost-effective. Direct seeding has, however, received surprisingly little attention in the context of mangrove restoration, despite the fact that the traditional plantation approach has suffered from low survival rates of the planted saplings, and the high costs involved in producing and planting nursery-raised seedlings. As such, there is a need for more cost-effective mangrove restoration measures, and a continued focus on efforts that encourage natural recruitment (Vanderklift et al., 2020). This has led to the emergence of Ecological Mangrove Restoration (EMR), which prioritises removing barriers or limits to natural seedling establishment (van Bijsterveldt et al., 2022) and facilitating the natural process of recruitment and establishment, through an understanding of the natural hydrodynamics of the local area (Lewis III, 2005; Zimmer et al., 2022). Improper understanding of the hydrology of mangroves, and the role that microtopography plays in the distribution of mangrove habitat, has led to failures in management of mangrove restoration projects (Lewis III, 2005). The identification of effective restoration methods which focus on increasing the successful establishment of individual plants will improve efficiencies and reduce costs of restoration at scale, and lies at the heart of the concept of 'precision forest restoration' (Castro et al., 2021).

The persistence and expansion of mangrove populations is dependent on the establishment success of their propagules, and root development is, in turn, key to their successful establishment (Balke et al., 2011; Krauss et al., 2008). Despite the availability of literature on these processes, there is still a lack of understanding on the mechanistic processes involved in mangrove seedlings establishing on bare tidal flats (Balke et al., 2011). Adult mangroves develop complex root systems in response to a range of environmental drivers and stressors, as they exist in a challenging environment of high temperatures, varying salinity, hypoxia, and extreme hydrodynamic conditions (Srikanth et al., 2016). For new propagules, establishing roots opportunely and effectively is key to their ability to withstand the hydrodynamic forces that they will be subject to shortly after grounding (Balke et al., 2011; Gillis et al., 2019; Rabinowitz, 1978). Balke et al. (2011) demonstrated that distinct root development thresholds exist for *Avicennia alba* seedlings, a pioneer species, in order for successful establishment to occur. While exact triggers for root initiation remain poorly understood (Van der Stocken et al., 2019), grounding and contact with soil has been demonstrated to initiate root formation for some mangrove species (Robert et al., 2015). Expanding our understanding of mangrove adaptations, including the factors affecting early root development and establishment of key species, is critical to improving mangrove management strategies.

While all mangrove propagules can remain viable floating at sea for long periods, enabling long-distance dispersal (Tonné et al., 2017), for those that are elongate, gradual changes in propagule density during immersion causes their orientation to change from prone to vertical, which increases the likelihood of grounding, entrapment in mangrove roots and pneumatophores, or self-planting (possibly aided by wave action) within natural depressions in the substrate, thereby facilitating establishment (Robert et al., 2015). Although this initial buoyancy and the ability to delay root initiation and maintain viability, allows the elongate propagules of *Rhizophoraceae* to disperse long distances and colonise new habitats, most recruitment is observed to occur near the propagule's parent tree (McGuinness, 1996) and propagule viability decays significantly with time in the water (Tonné et al., 2017). This emphasises the importance of having nearby sources of propagules when applying an EMR method. Furthermore, as we show below, any method for mangrove rehabilitation involving direct seeding should consider collecting propagules prior to, or as close to, natural abscission to avoid any possible loss in viability and to maximise chances of success and cost efficiency.

Studies examining how *Rhizophoracea* spp. propagules colonise new habitat have suggested that stranding generally occurs in a horizontal position, followed by rooting, and then once anchored, propagules are able to erect themselves (Rabinowitz, 1978). Cheeseman (2012) described how *Rhizophora mangle* propagules that grounded prone had the ability to right themselves, but this may come at an energy, and therefore viability, cost. Cheeseman (2012) also observed that while the hypocotyl's ability to curve upwards was diageotropic rather than phototropic, emerging leaves would rotate towards light. An establishing propagule sprouting leaves has a need to grow quickly and extend its leaves as high as possible to avoid shading from roots and other foliage, and to decrease the time the leaves are submerged during high tide. Seedlings establish more successfully in gaps amongst the canopy rather than under shade (Tomlinson and Cox, 2000). As a result, propagules of *Rhizophora* that ground in a vertical position may have an immediate advantage over a propagule that grounds in a prone position. *Rhizophora* spp. may also establish by falling and inserting themselves into the substrate, however, this success is limited by whether they implant properly, are orientated straight, or land at the right elevation to avoid excessive inundation (Cheeseman, 2012). If vertical self-planting infers increased success rates, self-planting may still be an important recruitment mechanism.

Given the relationship between grounding orientation and recruitment success, the preparation of the substrate requires attention in EMR. Previous EMR projects have trialled the use of artificial structures made with natural materials to support mangrove restoration; using bamboo to create fences to facilitate sedimentation (Lewis III et al., 2019), netted bamboo traps to collect propagules (van Bijsterveldt et al., 2022), and melaleuca fences to protect against erosion and wave energy (Van Cuong et al., 2015).

While traditional sapling-based transplanting suffers from high costs due to nursery-rearing process, and low yields, the reliance of EMR on natural recruitment means that restoration may occur very slowly. Here we also assess a third option, referred to as direct seeding, which involves the direct insertion of new mangrove propagules, into the substrate which can reduce much of the costs associated with conventional collection, rearing, and planting (Castro et al., 2021; Chowdhury et al., 2018). Direct seeding is often disregarded in forest restoration practices due to the risk of low seed germination and establishment rates (Lázaro-González et al., 2023), and seeds can experience low survival due to predation. However, as many species of mangroves produce viviparous seedlings, which germinate on the tree, direct seeding may be a more viable option, providing strategies to improve establishment rates of propagules are identified. Furthermore, direct seeding is generally easier to conduct and less costly and may be a preferred option in certain contexts due to logistical practicalities. One review of planting initiatives across southeast Asia found no significant difference between survival of sown propagules and planted established saplings (Wodehouse and Rayment, 2019), suggesting that the additional effort required to dig up, pot, and grow out saplings is unnecessary to improve success rates. Some form of planting may be beneficial to a restoration project in that it may help facilitate quicker mangrove succession (Wodehouse and Rayment, 2019), providing existing stressors on mangrove habitat are considered. However, differences in effort and costs between planting techniques must also be considered, especially when scaling up rehabilitation. Coupling direct seeding with EMR techniques has not yet been thoroughly examined (van Bijsterveldt et al., 2022), but may help promote more success by removing some of the environmental stressors that limit the success of establishing propagules, such as high wave energy or unsuitable tidal dynamics. It has also been found that inserting *Rhizophora* propagules directly into the substrate decreases predation on propagules and increases survival (Ferreira et al., 2023). Additionally, given the relatively slow timescale for natural mangrove habitat development (Erftemeijer et al., 2017), direct seeding can create immediate tangible results, which may be particularly important for NbS projects supported by industry or local government, where there is a need to demonstrate success early on. The rate of establishment can also impact the long-term success of the project, given that resilience to disturbance increases with habitat maturity.

Direct seeding could be a viable option for large-scale mangrove restoration, especially if success rates are higher compared to natural recruitment. Manual sowing of propagules essentially seeks to replicate the self-planting mechanism at scale. If vertically sown propagules were to demonstrate more successful root establishment compared to horizontally sown propagules, this may support direct seeding as a method. In this study we assess the benefit of sowing propagules vertically, to simulate self-planting, partially inserted into the substrate, by measuring root development of different groups of propagules in a controlled aquaria experiment, and the viability of planting propagules harvested directly from the tree, given that they are properly germinated (Chowdhury et al., 2020). A series of aquaria experiments were established to test the following hypotheses: 1) that vertically sown *R. stylosa* propagules would demonstrate better root growth compared to propagules sown horizontally; 2) that there would be no difference in root development between propagules sown in sand and fine sediment; 3) that propagules collected at the point of maturity would exhibit improved root growth compared to those collected premature or after a period of dispersal.

In addition, the relationship between propagule orientation and recruitment success was investigated in a field study, designed to examine the effectiveness of artificial structures to facilitate self-planting of propagules, and hence whether this would lead to more successful propagule establishment in EMR approaches. The field data allowed the following additional two hypotheses to be tested: 4) that propagules grounding vertically would have a higher chance of successful establishment compared to propagules grounding horizontally; and 5) that specially designed bamboo straw devices (BSDs) deployed in the field would be effective in encouraging the propagules to ground in an orientation more conducive to effective establishment.

2. Methods

2.1. Study area and species selection

All aspects of the study were conducted in Gladstone, in the Australian state of Queensland. The laboratory experiment was conducted in the recirculating saltwater mesocosms at CQUniversity's Coastal Marine Ecosystems Research Centre. The field observations were conducted at the Fisherman's Landing living seawall site (Fig. 1), where methods for establishing mangrove habitat along seawalls were trialled in collaboration with Gladstone Ports Corporation. Fisherman's Landing has a partially enclosed tidal waterway in the Gladstone Harbour area with a mature, natural mangrove habitat on one side of the waterway and a constructed rock wall on the opposite side. Sediment was placed alongside sections of the rock wall, fortified by perpendicular rock groynes, to create improved inundation regimes for mangroves recruiting along the rock wall. Each sediment bank covered an area of approximately 8 m × 20 m and were built to an elevation of 3.1 m above lowest astronomical tide (LAT), matching nearby banks where mangrove seedlings had established successfully. Sedimentation rates were observed throughout the study to ensure that fine sediment was accreting.

The species chosen for this study was *R. stylosa*, a common mangrove throughout north-eastern Australia (Duke, 2006). While *Rhizophora* is

Fig. 1. The field component of this study took place in the Port of Gladstone (B) in Queensland, Australia (A). Recruitment trial sites were established along an existing seawall where living seawall designs were being trialled (C). The recruitment trial involved the deployment of the bamboo devices to assess whether they would facilitate the vertical grounding and successful establishment of R. stylosa propagules.

globally dominant genus of mangroves, *R. stylosa* is prevalent throughout much of the tropical Indo-Pacific (Kamruzzaman et al., 2013; Wilson and Saintilan, 2018). At the study site *R. stylosa* dominates the seaward margins of much of the mangrove habitat (Anastasi et al., 2021; Houston et al., 2016). The species was chosen due to its abundance, its widespread distribution, and its ability to rapidly colonise new areas of the coastal zone (van Bijsterveldt et al., 2022). Like many other mangrove species, *R. stylosa* produces fertilised flowers which germinate on the parent tree, developing into viviparous seedlings, or propagules, which are elongate in shape. Their shape makes them much less susceptible to burying by sediment compared to other mangrove species that produce smaller seedlings (Ferreira et al., 2023; van Hespen et al., 2022). As such, this species is an ideal candidate for direct seeding initiatives.

Mangrove propagules have developed several adaptations fundamental to their ability to colonise available substrates, including undergoing an obligate dispersal period (ODP) (Rabinowitz, 1978), initial buoyancy to overcome dispersal obstacles, subsequent changes in density to aid in grounding, maintaining viability for extended periods, and postponing root development until grounding occurs (Robert et al., 2015). The term ODP may be misleading as it suggests that propagules are not immediately viable after abscission and ignores the fact that most successful establishment occurs in the proximity of the parent tree. Moreover, mangrove propagules leave the parent tree ready to be planted into the substrate (Robert et al., 2015), meaning that restoration attempts can occur without the need for expensive and time-consuming nursery-raising periods. The experiments conducted here aimed to examine some of these processes, and test the hypotheses mentioned above, that grounding or partial insertion into the substrate would trigger root initiation, and that timing of collection would affect establishment and root development. It should be noted that many mangroves are viviparous, and as such produce seedlings rather than seeds (Duke et al., 1999), but for distinction from the planting of saplings as a restoration method, the manual planting of propagules is hereafter referred to as direct seeding, and propagules in the aquaria study are described as being sown, rather than planted.

2.2. Collection and sample preparation

For *R. stylosa* in eastern Australia, flowering occurs during the austral summer months, with mature propagules appearing in the months of January and February (Duke et al., 1984), and peak propagule fall commences in March (Duke, 2002; Wilson and Saintilan, 2018). In mangrove surveys in the Gladstone region, flowering was recorded as starting in February and propagules were recorded dropping between February and March (Anastasi et al., 2021) when they were observed in leaf litter traps. Three groups of propagules were collected: 1) mature propagules with a limited dispersal phase (mature); 2) mature propagules with a long dispersal phase (dispersal); and 3) immature propagules with no dispersal phase (immature).

In March 2023, the first group of 144 *R. stylosa* propagules were collected by hand from the nearby mangrove at Fisherman's Landing. To ensure that propagules were mature, collection occurred after observing the mangroves weekly during austral summer (January – March 2023) in anticipation of the propagules dropping, to ensure that propagules were collected as soon as possible after abscission. Propagules that had fallen and become inserted into the substrate, or where root bumps had started to develop, were disregarded for this study, as they were considered to already have had root initiation triggered. Propagules were visually inspected and damaged or unhealthy propagules (e.g., propagules with borer holes) were discarded. In a similar process to previous studies examining root establishment (Balke et al., 2011; Balke et al., 2013; van Hespen et al., 2022), collected propagules were exposed to freshwater before the first mesocosm experiment to encourage germination. Propagules were left floating in tubs of seawater, but with freshwater added to achieve a salinity of approximately 20–25 ppt. However, as will discussed below, this study finds no evidence to support the need for exposure to freshwater for germination, as the propagules collected in 2024 successfully established roots without a freshwater treatment period.

The second group of 48 propagules were collected in April 2023. These propagules were collected by boat, floating in the harbour, rather than washed ashore to avoid propagules that may have grounded and had root initiation triggered. As such, this group can be considered to have undergone a dispersal phase of approximately four to six weeks.

The third group of propagules were collected during the following flowering season in 2024, in a similar fashion to the first group. Firstly, 26 propagules were collected in January 2024, here referred to as the immature group as they were not yet readily shaken from the tree and were still very green in colour, and a subsequent 26 propagules were collected in March 2024, which are referred to as fully mature as they could be easily shaken from the parent tree, as with (Van der Stocken et al., 2015), so were ready to abscise naturally. This second set of 26 were used as a comparison mature group from the same flowering season. A comparison of root development between these two groups was made to determine whether it was required to wait until full maturity before collecting propagules for planting out, or whether immature propagules would still successfully establish roots. This third group of propagules were not subject to a freshwater treatment period prior to the experiment, and instead were sown within 24–28 h of collection, as with Robert et al. (2015). As the purpose of this experiment was to test whether the propagules would still successfully develop roots despite being immature, or not fully germinated, no freshwater soak treatment was applied, and propagules were sown within 48 h of collection. This was the same for the second group of 26 propagules collected at the point of maturity. As seen below, the fact that these propagules still demonstrated healthy root development suggests that a freshwater soak is, in fact, not necessary prior to planting out.

2.3. Experimental setup

2.3.1. Root development: vertically vs horizontally sown propagules

The aquaria experiments were established to simulate the conditions *R. stylosa* propagules would experience when establishing on upper intertidal sediment substrates, with propagules either placed flat on the substrate or inserted approximately 3 cm into the substrate to simulate self-planting. For this study propagules were inserted to 3 cm as this depth ensured that they would remain upright and was the same depth employed in previous studies examining establishment of propagules of *Rhizophoraceae* spp. (Tomlinson and Cox, 2000; van Hespen et al., 2022). The experiment was conducted in an outdoor mesocosm facility, which comprises of a system of interconnected 1000 L circular flow-through tanks, drawing seawater directly from the adjacent creek. The seawater is filtered through a sand filter, a 20 μm bag filter, recirculated in a header tank through a foam fractionator, and distributed to six 1000 L tanks with a shared sump tank. In the system, salinity is maintained at approximately 35 ppt, temperature is not controlled, and tanks are partially shaded from direct sunlight. Flow rate was maintained at approximately 300 L per hour to ensure that water level remained at a consistent level so that propagules did not become fully submerged, and that sediment remained waterlogged. The flow in the tanks is sufficiently weak that no resuspension of the sediment occurs, but sufficiently turbulent to ensure that conditions are essentially uniform throughout the mesocosm system.

To assess for any difference in successful root establishment between vertically self-planting propagules and propagules grounding horizontally (and therefore whether attempting direct seeding may be effective), an aquaria experiment was set up with propagules of *R. stylosa* either placed flat on top of sediment-filled trays, to replicate a propagule stranding, or inserted 3 cm into the sediment, to simulate self-planting. Thirty-six plastic trays were filled with sediment, and two different sediment types were used to test for any effect sediment composition had on root development. The coarse sand material was comprised of 50 % coarse sand (> 60 μm), 47 % silt (2–60 μm), and 3 % clay (< 2 μm), while the fine sediment material was 12 % coarse sand, 79 % silt, and 9 % clay. The two sediment types are hereafter referred to as "sand" and "fine sediment," respectively.

Six trays were positioned into each of the six mesocosms, with the top of the substrate sitting just above the surface of the water so that the sediment would remain hydrated (Fig. 2), but not fully submerged (to simulate conditions of mangroves recruiting in the upper intertidal zone). In one of the mesocosms eight propagules in each of the six trays were positioned vertically so that the base of their hypocotyl was inserted 3 cm into the substrate, to simulate self-planting. In the remaining trays, four propagules were placed horizontally on the substrate.

After periods of 15, 25 and 35 days, 8 vertical propagules and 8–24 horizontal propagules were removed from each substrate treatment. The number of roots growing on each propagule was recorded, and measurements of the length of each individual root on each propagule were taken. All lengths were measured from the base of the root emanating from the propagule to the tip of that individual root. No branching roots were observed in this study. The measured propagules were then discarded from the experiment, as their root development may have been disrupted by the manual handling.

2.3.2. *Root development: effect of propagule maturity*

A similar procedure was followed to assess for the effects of collection timing on root development, with groups of propagules for this experiment collected: a) prior to maturity, b) at the point of maturity, and c) several weeks after abscission, after having undergone a dispersal phase, as described above. As the results of the initial aquaria experiment revealed that the fine sediment produced better root growth results, for this experiment, only fine sediment substrate was used. For the third group of propagules (collected in 2024) the set of root measurements were only taken once, after 35 days.

2.3.3. *Propagule establishment: effect of grounding orientation*

The field study site was established in January 2023, prior to the known fruiting season for *R. stylosa,* when propagules are expected to germinate and drop from the parent tree (Duke et al., 1984). The bamboo devices trialled here, designed and supplied by Seagrass Technologies Pty Ltd. (mangroves.au), are made from bamboo straw and are entirely biodegradable, designed to eventually rot away after helping mangroves establish and prevent erosion of sediment (Fig. 3).

The BSDs were installed in 36 separate 1 m × 1 m plots across three created sediment banks at the study site, with four devices installed in each plot. The devices were installed by hand, by pushing or digging them into the substrate. There were also plots established with two nursery-reared *R. stylosa* propagules planted ($n = 36$), and plots left just as bare sediment ($n = 36$), as part of a separate study on mangrove restoration techniques and rehabilitation of novel substrate. This living seawall trial allowed us the opportunity to compare how the BSDs would impact orientation and success of establishing *R. stylosa* propagules compared to areas of bare sediment and areas of existing mangrove plant coverage. Monitoring commenced in February 2023 and continued monthly after development of the site. During monitoring, the presence of new *R. stylosa* propagules that had settled was recorded, along with the plot type in which it had grounded, and its orientation - whether it had grounded in a vertical or horizontal orientation. Propagules that grew roots, sprouted leaves, and survived beyond three months were recorded as having established successfully. Propagules that did not grow roots or sprout leaves, or did but then subsequently died, were recorded as unsuccessful. The effectiveness of the BSDs for facilitating self-planting is assessed by comparing the total number of *R. stylosa* propagules retained between the three different plot types and how many in each plot type grounding vertically or horizontally. A comparison was then made between the success rate of vertically grounding propagules and horizontally grounding propagules.

2.4. *Data analysis*

2.4.1. *Root development: vertically vs horizontally sown propagules*

The hypotheses that planting and substrate type have an impact on root metrics (mean root length and total number of roots) was tested with a generalised linear model (GLM). The models were run as negative binomial models, as the data was over dispersed, and were specified as:

$$\text{root length} \sim \text{orientation} \times \text{substrate}.$$

$$\text{root count} \sim \text{orientation} \times \text{substrate}.$$

As data was collected at 15, 25, and 35 days, a separate GLM was conducted on the data from each point in time.

2.4.2. *Root development: effect of propagule maturity*

To assess for difference in root development between propagules collected at the point of maturity and those collected after an obligate dispersal period (six weeks after maturity, referred to as dispersal propagules), a GLM was conducted. The GLM was run as a negative binomial model, as the data was over dispersed, and was specified as:

$$\text{root length} \sim \text{maturity} \times \text{substrate}.$$

Maturity was categorised as either mature (propagules collected at the point of natural abscission) or dispersal (those collected after a period of obligate dispersal), and substrate was either fine sediment or sand.

Where an interaction was discovered, a pairwise comparison was conducted using estimated marginal means (EMMs). A separate GLM was run with data from each point in time where measurements were taken; at 15 days, 25 days, and 35 days.

A *t*-test was used to compare the root measurements (mean root length and total number of roots) for 'immature' and 'mature' propagules (collected in 2024). Data was first checked for normality and homogeneity of variances, and where these criteria were not met a non-

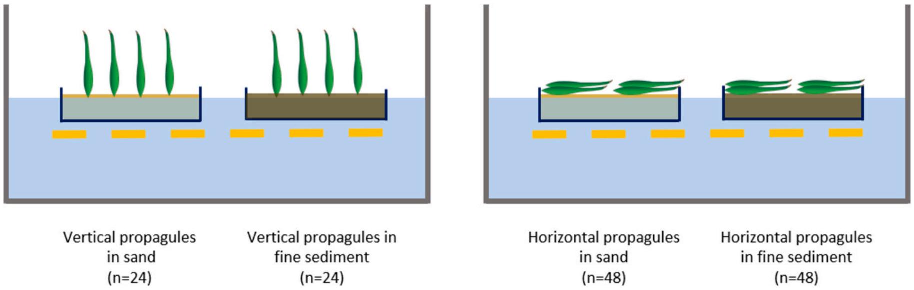

Fig. 2. Experimental setup of sediment trays in the mesocosm tanks. Propagules sown vertically into both sand and fine sediment (left), and propagules sown horizontally onto the same substrates (right).

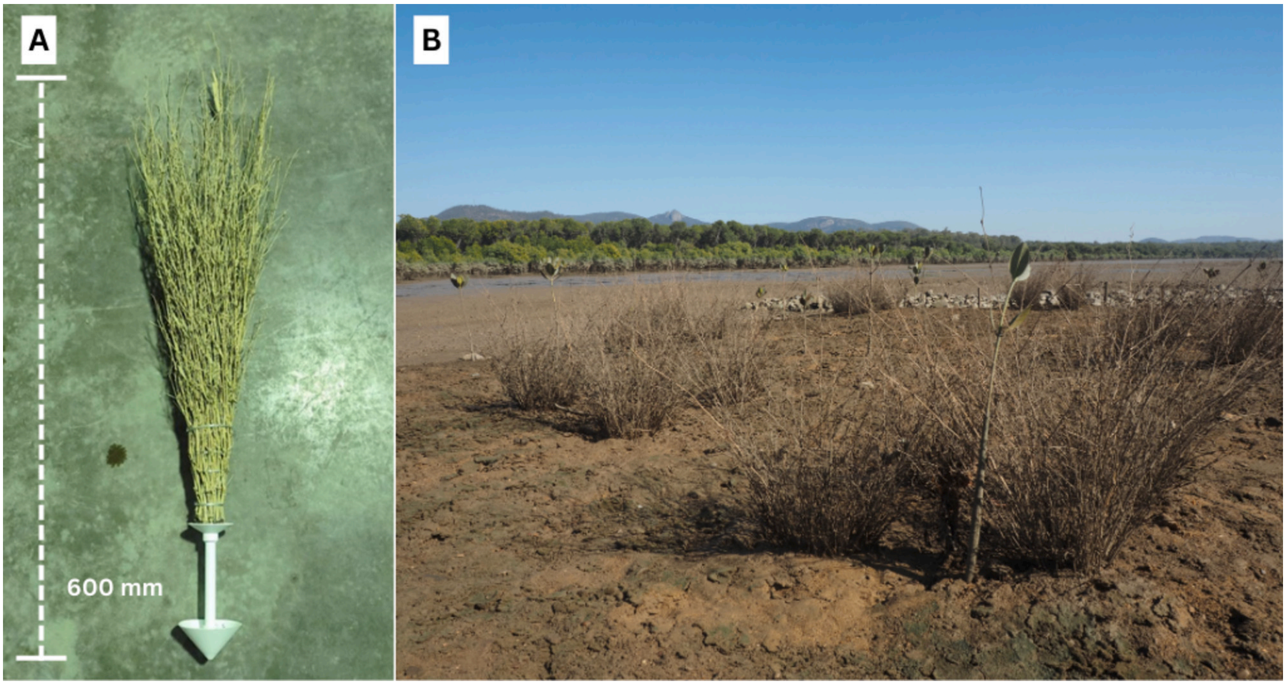

Fig. 3. Bamboo straw devices (A) measure approximately 600 mm in height, including a biodegradable polymer 'plug' that helps anchor it into the substrate. They are installed by hand, by either inserting or digging them into the sediment, and the bamboo branches are held together by a small steel wire which is designed to rust away. Once installed into the substrate they are designed to aid with the establishment of mangroves by entrapping propagules and encouraging vertical self-planting, as seen in situ at the living seawall site (B).

parametric Wilcoxon test was used.

2.4.3. *Propagule establishment: effect of grounding orientation*

For the field study, a Fisher's exact test was used to test for significance in the difference in establishment success between the two groups of recruiting propagules (vertical and horizontal grounded propagules). The Fisher's exact test was used rather than a Chi-Square test because the sample size was relatively small ($n = 39$).

All analyses were performed using R within the RStudio environment (v4.3.3). Data were plotted with *ggplot2* (v3.4.3, (Wickham and Wickham, 2016). Prior to statistical analysis we used the "identify_outlier" function in "rstatix" packages in R (Kassambara, 2021) to check for extreme outliers.

3. Results

3.1. *Root development: vertically vs horizontally sown propagules*

The vertical propagules consistently grew longer and more roots on average compared to the horizontal propagules (Fig. 4). At 15 days vertical propagules had a mean root length of 20.6 ± 9.9 mm whereas horizontal had a mean root length of 2.3 ± 1.4 mm, which the GLM showed to be a significant difference ($p \leq 0.01$). This was also true of propagules recorded at 25 days (37.4 ± 15.6 mm for vertical, and 12.9 ± 12.6 mm for horizontal) and 35 days (46.3 ± 20.5 mm for vertical, and 17.4 ± 16.6 mm for horizontal). The difference in root count grown between vertical and horizontal was also statistically significant for each group (Table 1). There was a significant difference in mean root length between substrate types at 15 days ($p = 0.0004$) with propagules in fine

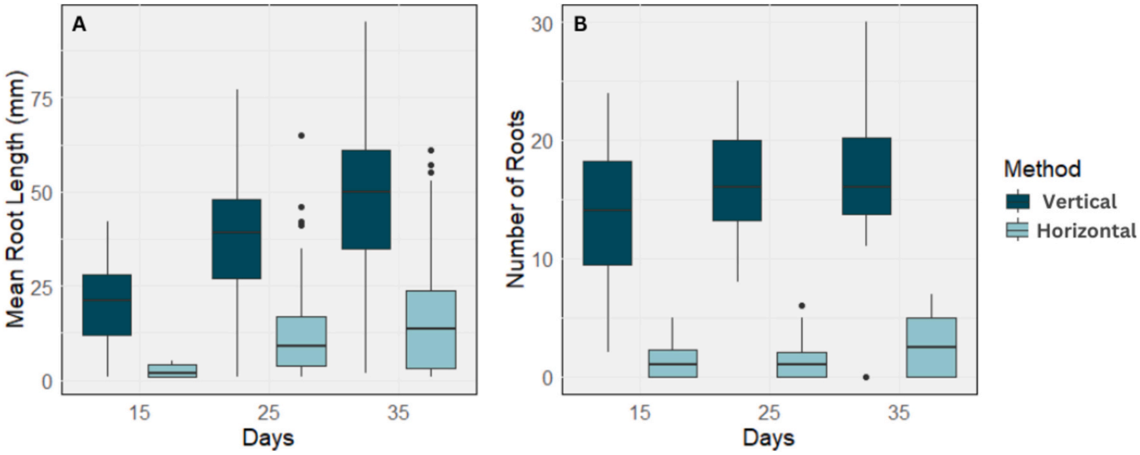

Fig. 4. Mean root length of vertical propagules compared to horizontal propagules at each measurement time (A), and number of roots grown between the two groups at each measurement time (B).

Table 1

GLM results examining effects of orientation (two levels: vertical, horizontal) and substrate type (two levels: fine sediment, sand) on mean root length and total root count of propagules (for 15 days $n = 32$, for 25 days $n = 72$, and for 35 days $n = 40$, $p < 0.05$).

root length ~ orientation × substrate

	15 days				25 days				35 days			
	Est.	SE	stat	p	Est.	SE	stat	p	Est.	SE	stat	p
(Intercept)	3.17	0.06	56.99	**< 2e-16**	3.71	0.05	72.98	**< 2e-16**	3.93	0.06	70.95	**< 2e-16**
orientation	−1.92	0.23	−8.27	**< 2e-16**	−0.94	0.11	−8.57	**< 2e-16**	−0.93	0.13	−7.17	**7.52e-13**
substrate	−0.25	0.07	−3.53	**0.0004**	−0.22	0.07	−3.12	**0.002**	−0.20	0.08	−2.57	**0.01**
maturity * substrate	−0.64	0.35	−1.85	0.06	−0.30	0.16	−1.92	0.055	−0.12	0.18	−0.62	0.53

root count ~ orientation × substrate

	15 days				25 days				35 days			
	Est.	SE	stat	p	Est.	SE	stat	p	Est.	SE	stat	p
(Intercept)	2.36	0.17	14.16	**< 2e-16**	2.74	0.13	20.36	**< 2e-16**	2.77	0.27	10.09	**< 2e-16**
orientation	−2.14	0.38	−5.64	**1.7e-08**	−2.44	0.22	−11.19	**< 2e-16**	−1.82	0.39	−4.67	**3.09e-06**
substrate	0.47	0.23	2.08	**0.04**	0.13	0.19	0.68	0.49	−0.03	0.39	−0.10	0.92
maturity * substrate	−0.13	0.50	−0.26	0.79	−0.13	0.31	−0.42	0.68	0.04	0.55	0.07	0.94

sediment recording a mean root length of 21.7 mm (± 11.7 s.d.) and those in sand recording a mean root length of 16.9 mm (± 10.2 s.d.). There were also differences in mean root length between fine sediment (35.8 ± 18.8 mm) and sand (28.4 ± 16.8 mm) at 25 days, and at 35 days (44.9 ± 23.4 and 36.1 ± 21.6 mm respectively). There was a significant difference in root count between substrate types at 15 days ($p = 0.04$), however, there was no significant difference at 25 or 35 days. There were no significant interactions between treatments.

3.2. Root development: effect of propagule maturity

3.2.1. Mature vs dispersal

Mature propagules recorded a markedly higher mean root length than dispersal propagules at each period at which measurements were taken during the experiment (Fig. 5). Mean root length of mature propagules after 15 days was 20.57 mm (± 9.91 s.d.), whereas for dispersal propagules it was 3.38 mm (± 2.4 s.d.), and the results of the GLM showed that this was significantly different (p < 0.01) (Table 2). The mean root length of mature propagules at 25 days (37.37 mm, ± 15.58 s.d.) was higher than for dispersal propagules (5.19 mm, ± 4.51 s.d.), which was also statistically significant ($p < 0.01$). At 35 days, mean root length of mature propagules was 46.32 mm (± 20.52 s.d.) whereas for dispersal propagules it was 12.10 mm (± 7.88 s.d.), which was statistically significant (p < 0.01). The GLM revealed an interaction between maturity and substrate type at 35 days, but not at 25 or 15 days. Pairwise comparisons of the estimated marginal means showed that at 35 days the mean root length was significantly greater for mature propagules in fine sediment compared to sand (p < 0.01), and that dispersal propagules also exhibited significantly higher root length in fine sediment compared to sand (p < 0.01).

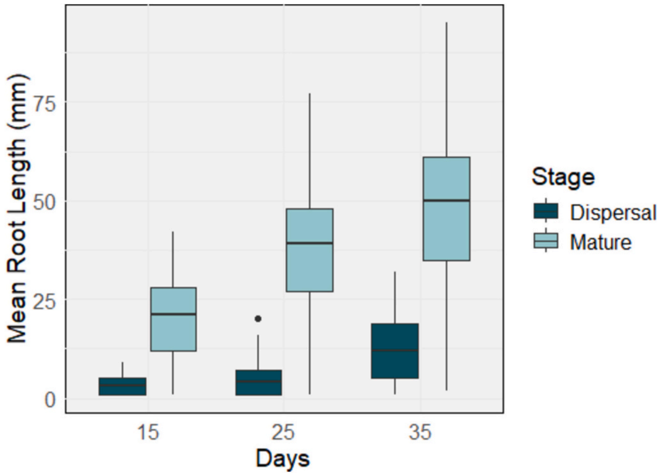

Fig. 5. Mean root length (mm) of propagules collected in 2023 as at 15, 25, and 35 days, showing mature propagules (those collected at the point of natural abscission from the parent tree) with higher mean root length values compared to those collected six weeks later after a dispersal period.

3.2.2. Immature vs mature

The mean root length of immature propagules was 19.15 mm (± 12.91 s.d.), whereas for mature propagules it was 23.61 mm (± 12.86 s.d.), at the end of the 35-day experiment (Fig. 6). A *t*-test showed that this difference is not, however, statistically significant, t (50), = −1.2475 $p = 0.218$.

3.3. Propagule establishment: effect of grounding orientation

In the three months after the field site was installed, a total of 39 *R. stylosa* propagules were recorded as settling at the recruitment trial sites, with 19 grounding in a vertical orientation and 20 grounding horizontally (Table 3). After nine months the group of propagules that settled vertically had a 52.6 % success rate in establishing, compared to a 10 % success rate in the horizontal group. A Fisher's exact test revealed a significant difference between the two groups ($p = 0.0057$), showing that propagules settling in a vertical orientation were more likely to establish successfully.

Of the 19 propagules that grounded in a vertical orientation, 17 of these recruited within the BSD plots (Table 4). In the BSD plots 56.6 % of propagules had grounded vertically, while 33.3 % had grounded horizontally. The very small numbers of recruits found in other plots makes comparison difficult, but at the least a Fisher's exact test revealed no significant difference in the proportion of propagules grounding vertically between plot types ($p = 0.1$).

4. Discussion

This study demonstrates that direct seeding is a viable method for rehabilitation of mangroves with elongate propagules, and hence represent a promissory option for large-scale mangrove forest restoration initiatives. The study has revealed several key aspects influencing the establishment of *R.stylosa* that are relevant for its use in mangrove restoration efforts. Firstly, vertically sown *R. stylosa* propagules develop roots more successfully compared to propagules that ground

Table 2
GLM results examining the effects of propagule maturity (two levels: mature, dispersal) and substrate type (two levels: fine sediment, sand) on difference in mean root length ($n = 48$, significance level $p < 0.05$).

root length ~ maturity × substrate

	15 days				25 days				35 days			
	Est.	SE	stat	p	Est.	SE	stat	p	Est.	SE	stat	p
(Intercept)	1.37	0.11	12.07	**< 2e-16**	1.78	0.13	13.82	**< 2e-16**	2.75	0.06	45.94	**< 2e-16**
maturity	1.79	0.13	14.19	**< 2e-16**	1.95	0.14	14.22	**< 2e-16**	1.18	0.08	15.71	**< 2e-16**
substrate	−0.42	0.19	−2.23	**0.03**	−0.22	0.16	−1.36	0.17	−1.02	0.11	−9.09	**< 2e-16**
maturity * substrate	0.17	0.20	0.85	0.39	0.004	0.18	0.02	0.98	0.82	0.13	6.28	**3.4e-10**

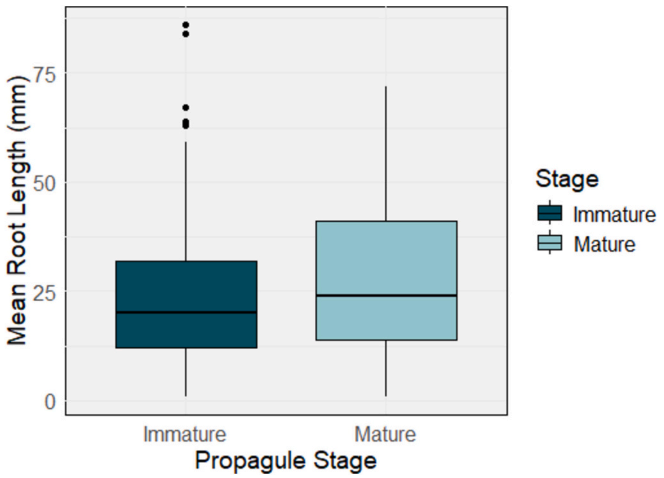

Fig. 6. Mean root length of immature propagules, collected six weeks prior to natural abscission, did not significantly differ from mean root length of mature propagules collected when naturally ready to drop.

Table 3
Contingency table showing the success rates of R. stylosa propagules based on their grounding orientations (vertically and horizontally).

	Total recruits	Successful	Unsuccessful	Success Rate
Grounded vertical	19	10	8	52.6 %
Grounded horizontal	20	2	18	10 %
Combined	39	12	26	

Table 4
Number of R. stylosa propagules that were found in each plot type, whether they grounded vertically (V) or horizontally (H), and their subsequent establishment success rate.

Plot Type	Recruits	V H	Success	Success Rate	Fail
Bamboo	30	17	9	52.94 %	8
		13	2	15.38 %	11
Sapling	6	2	1	50 %	1
		4	0	0 %	4
Sediment	3	0	0	NA	NA
		3	0	0 %	0

horizontally, independently of any other factor. Notably, propagules that were sown vertically had developed more roots and longer roots at each point in time when measurements were taken, compared to propagules that were horizontal on the same substrate. These results give credence to the concept of propagules self-planting as an establishment strategy for *Rhizophoraceae* and illustrates how propagules that self-plant may have an advantage over other propagules by exploiting the window of opportunity to establish before a subsequent high tide may dislodge them again.

Secondly, previous studies on the mechanisms of propagule self-planting have observed their ability to do this in either sand or soft mud (Menezes, 2019), but here we showed that propagules grew slightly longer roots in fine sediment compared to coarse sand. This supports findings from previous studies on root development of *Rhizophora* spp. propagules (Léopold et al., 2024). As such, for EMR approaches hoping to exploit this, the placement of finer sediment, or measures aimed at facilitating the accretion of fine sediment, may result in a small improvement in recruitment success. It should be noted, however, that propagules still successfully grew roots in the coarser material, highlighting the well-documented ability of mangroves to establish in a range of substrate compositions (Jorquia, 2022; Krauss et al., 2014; Léopold et al., 2024). As such, for novel EMR substrates that are likely to be subject to greater levels of wave energy, it may be preferable to use coarser sediment that is better able to resist resuspension. This demonstrates that a range of substrates may still be considered for EMR approaches in different environments.

Thirdly, the study shows that propagules sown at the point of maturity establish more and longer roots compared to propagules that have dropped from the parent tree and undergone a period of obligate dispersal. This suggests that, while the prolonged viability during floatation has a benefit for colonising new areas, this does come at a high cost in establishment success. The rapid drop-off in viability caused by dispersal should be considered when timing collection for restoration approaches involving direct seeding. Moreover, any loss in viability or root growth from collecting propagules directly from the tree prior to natural abscission was negligible. The propagules collected prior to full maturity did not exhibit a significant difference in root growth compared to those collected at the point of maturity. This has clear implications for the harvesting of propagules for direct seeding restoration – the fact that viable propagules can be obtained across a wide range of maturities significantly reduces the effort and/or cost involved. As the two groups of propagules collected in 2024 (both immature and mature) still successfully developed roots without exposure to freshwater prior to sowing, it suggests that this process is not necessary to trigger germination. This may save substantial effort and timing for large scale restoration approaches using direct seeding methods.

Lastly, the use of structures to promote establishment, such as the BSD described here, could improve results of EMR of *R stylosa*. The results from the field study showed that propagules grounding vertically had a significantly higher success rate in establishing compared to those grounding horizontally, and 17 out of 19 propagules grounding vertically were observed in the BSD plots. However, the small sample size from this study means that further investigation is required to determine definitively whether propagule trapping devices such as these lead to more recruitment and more successful establishment at scale. Ecological mangrove rehabilitation approaches aim to minimise the reliance on costly manual interventions like planting. However, earlier reviews of restoration methods emphasise the importance of proactive strategies to promote mangrove establishment in areas where they are currently absent (Vanderklift et al., 2020), such as on rock seawalls. This may require the use propagules and propagule entrapment devices, such as the BSDs tested in this study.

Although we have concentrated on the propagules of *R. stylosa*, it is likely that the results project to other *Rhizophora* species to some degree, and potentially all mangroves with elongate propagules. Previous studies on root development of other *Rhizophoraceae* species have shown similar results to those found here for *R. sylosa,* that propagules grounding upright exhibit longer root growth (Robert et al., 2015). The production of propagules that are buoyant and elongate - a strategy used by many mangrove species - has the function of improving recruitment success following dispersal by facilitating grounding. As such, it is likely that all mangrove species with elongate propagules may show similar responses to orientation documented here, such as the high rates of recruitment success when inserted directly into the substrate.

Seedling establishment strategies do, however, vary significantly across mangrove species (van Hespen et al., 2022), and even within *Rhizophoraceae* (Robert et al., 2015). While it has been suggested that this self-planting mechanism is a key factor in their establishment, especially for species with elongated propagules (Van Speybroeck, 1992), it may usually occur naturally only when falling from the parent tree (Van der Stocken et al., 2019). Some authors have dismissed the likelihood of self-planting as an effective establishment strategy for *Rhizophora* spp., suggesting that propagules are more likely to self-erect after prone grounding, given the fact that prone grounding is much more common (Rabinowitz, 1978; Tomlinson and Cox, 2000). However, the results from this study suggest otherwise – that the rare cases of insertion are likely to dominate recruitment, compared to the more common case of prone landing. This is especially significant for mangrove rehabilitation projects aiming to exploit the natural adaptations of *Rhizophoracea* to encourage successful establishment, either through direct seeding or EMR approaches that increase the number of propagules settling. As noted above, and in previous reviews of seed-based restoration, the use of mangrove propagules effectively for restoration depends on the species, and the elongate shape of *Rhizophora* spp. propagules, combined with the ease of their collection, makes them a suitable candidate (Vanderklift et al., 2020). Successional, or climax, mangroves such *Rhizophora* spp., may be suitable for direct seeding interventions, whereas pioneer species such as *Avicennia marina* may thrive in harsh conditions even without intervention (Buttarazzi et al., 2024).

We note that rapid root growth, used as the metric to quantify recruitment success, does not guarantee development into a mature mangrove. There is some lack of clarity about what constitutes the threshold for determining whether a propagule has established successfully or not. Although Yun et al. (2022) suggest that a propagule can be considered successfully established if it has firmly rooted and developed at least one leaf, Krauss et al. (2008) offer that if a propagule grows to a sapling of approximately 1 m in height it can be assumed that establishment has occurred successfully. However, at the very least, successful root development is clearly a necessary step in establishment and must be achieved for propagules to overcome the hydrodynamic stressors faced in the intertidal zone. While rapid root growth does not guarantee success, slow root growth almost certainly guarantees failure, either due to hydrodynamics, or to intraspecific competition.

5. Conclusion

The results from this study have significant relevance for mangrove restoration, raising the prospect of achieving large scale mangrove habitat restoration through manual intervention approaches that involve direct seeding of propagules to facilitate root development and rapid establishment of the plant. Although the propagation strategy of mangroves differs significantly from the majority of terrestrial plants, parallels may be found to the active research in forest restoration on the merits of planting versus seeding (Lázaro-González et al., 2023). The difference in root development between vertically and horizontally sown propagules suggests that direct seeding could be a cost-effective, scalable restoration method, compared to relying on natural recruitment. Additionally, the similar root development of immature and mature propagules supports direct seeding by extending the viable collection window.

The study results in a number of recommendations for restoration project managers implementing EMR approaches. Firstly, there is a benefit in minimising the dispersal distance to donor populations, given the significant reduction in viability with ODP. Secondly, more than the type of substrate, the presence of features to encourage vertical grounding could greatly enhance EMR approaches. Propagules of *R. stylosa* were significantly more successful in establishing if they self-planted, or stranded in a vertical orientation, and the rate of vertical planting was greatly increased by adding features to the bare substrate such as the BSDs used in our field trials.

As such, direct or facilitated vertical planting of *R. stylosa* propagules has the potential to yield an enormous benefit in mangrove restoration projects. Furthermore, the possibility to use fresh or even premature propagules harvested directly from the tree and not subject to any prior treatment greatly simplifies the effort involved in seed-based restoration. As a result, we propose that the vertical sowing of tree-harvested propagules can represent a cost-effective method for mangrove restoration targeting *R. stylosa* at scale.

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CRediT authorship contribution statement

Rory Mulloy: Writing – review & editing, Writing – original draft, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Christopher M. Aiken:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Gordon Dwane:** Writing – review & editing, Supervision, Resources, Methodology, Funding acquisition, Conceptualization. **Megan Ellis:** Writing – review & editing. **Emma L. Jackson:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Raw data file is publicly available on Zenodo: https://doi.org/10.5281/zenodo.13901242

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