

## RESEARCH ARTICLE

# Influence of abiotic drivers on 1-year seedling survival of six mangrove species in Southeast Asia

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Establishment and survival of plant species in systems with dominant environmental drivers (i.e. factors that exert disproportionate control over species establishment and survival) is often thought to be dominated by one master variable. In forested wetlands such as mangroves, hydrology is typically considered the dominant limiting driver. At the same time, light is a major driver of plant community dynamics, with some of the best understood plant life-history tradeoffs related to fast growth under high-light conditions versus survival under low-light conditions. Yet light is given relatively limited consideration in mangrove research compared to other drivers. Understanding the relative importance of abiotic drivers for seedling survival is crucial for effective management and restoration of mangrove ecosystems. Despite increasing global efforts to plant mangrove propagules at elevations appropriate for the hydrologic conditions needed at early life history stages, restoration efforts report low survival of planted propagules. Although many studies have made considerable progress to characterize the abiotic limitations of mangrove propagule establishment, fewer studies have addressed multiple abiotic drivers that limit the survival of the established seedling stage. We characterized the light and inundation conditions of more than 900 naturally established mangrove seedlings and monitored the survival of more than 2,800 seedlings (including 16 species) located on a species-rich island in tropical Southeast Asia for 1 year. Our findings suggest that light has a stronger effect than hydrology on survival following seedling establishment. We provide a conceptual visualization of shifts in the drivers of mangrove survival/loss throughout ontogeny.

**Key words:** *Avicennia*, *Bruguiera*, *Ceriops*, hydrology, light, *Rhizophora*

## Implications for Practice

- Restoration practitioners should consider the influence of multiple environmental drivers, even in systems with a single dominant driver.
- Empirical research on species-specific tolerance thresholds is needed for multiple abiotic drivers, particularly for early to intermediate stages, to inform restoration guidelines.
- An understanding of natural recruitment rates and conditions is needed to gauge expectations for survivorship of restoration plantings.

## Introduction

Mangroves are coastal forests characterized by flood- and salt-tolerant viviparous trees and are greatly valued for their provision of important ecosystem services and functions, including carbon sequestration (Barbier et al. 2011), fishery habitat (Faunce & Serafy 2006), timber production, erosion control, wave attenuation (Lee et al. 2014), and support of human livelihoods and nutrition (Walters 2008). Over the past century, mangrove systems have been degraded and significant areas have been lost due to human development and deforestation

(Gilman et al. 2008). Globally, more than 35% of mangrove area has been lost since 1980 (Valiela et al. 2001; FAO 2007) and mangroves continue to be lost at a rate of 0.3–0.8% since 2000, with highest rates of loss concentrated in Southeast Asia (Hamilton & Casey 2016; Friess et al. 2019; Goldberg et al. 2020). Combined efforts from improved monitoring, conservation, and restoration have decreased the rate of mangrove loss in recent years, but mangroves remain threatened (Friess

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et al. 2020), providing impetus for increased restoration and conservation efforts.

Efforts to restore vegetation in ecosystems with strong environmental drivers, such as mangrove forests, often focus on tolerance thresholds of initial life stages to a master variable; in wetlands hydrology is typically this master variable. Early mangrove establishment and survival is generally understood to be controlled by dispersal dynamics of hydrochorous propagules (Nettel & Dodd 2007; Van der Stocken et al. 2013, 2019; Yando et al. 2021) and the hydrologic conditions of the propagule's stranding location (Krauss & Allen 2003a; Ye et al. 2005; Chen & Ye 2014). As far back as 1928, Watson used inundation classes to describe the distribution patterns of 17 mangrove species in Malaysia (Watson 1928). Since then, many observational and experimental studies in field and greenhouse settings have worked to examine the demographic response of early mangrove life history stages to different flooding regimes (Delgado et al. 2001; Allen et al. 2003; Krauss et al. 2008). Despite a wealth of research on hydrologic thresholds for species-specific propagule establishment (Kitaya et al. 2002; Monroy-Torres et al. 2015; Jiang et al. 2019; Wang et al. 2019), many mangrove restoration efforts are characterized by poor survival (<20%) of planted propagules (Primavera & Esteban 2008; Kodikara et al. 2017; Wodehouse & Rayment 2019). Planting sites are commonly located in lower intertidal to subtidal zones which are exposed to full sunlight and inundated for prolonged periods of time (Asaeda et al. 2016; Wodehouse & Rayment 2019). Such sites may expose the planted mangrove seedlings to physiological stressors beyond their levels of tolerance at their early life stage (Kamali & Hashim 2011).

A contributing factor to poor restoration outcomes is that planting guidelines are available for few species and life stages only, with dominant focus on a few species that occur in the Americas; thus existing guidelines are partially incomplete (Elster 2000). Additionally, in many restoration plantings the survivorship of planted propagules is not critically examined beyond the initial planting period resulting in repeated failed projects (Primavera & Esteban 2008; Thompson 2018). Mangrove restoration efforts, and our basic understanding of these complex multi-driver ecosystems, would benefit from data on key ecological thresholds at the species level throughout ontogeny (Lewis 2005). Each stage of early mangrove life history can therefore be conceptualized as having a shifting suite of factors influencing survival (Fig. 1). Causes of mortality in mangroves have been explored through many studies; however, the majority of studies that quantify loss attributed to a particular driver focus on the earliest life stages (i.e. propagule dispersal, stranding, and establishment) and the constraining role of hydrology and herbivory on species present in the Atlantic-East Pacific (Fig. 1). We propose a shift toward understanding the roles of multiple drivers at the established seedling stage with an emphasis on broadening the inclusion of species to improve both restoration guidelines and understanding of species' ecology.

Light is a major driver of plant community dynamics, with some of the best understood plant life-history tradeoffs related to the ability to optimize growth and/or reproduction under high-light conditions versus the ability to survive under

low-light conditions (Gilbert et al. 2006). Yet light is given relatively limited consideration in mangrove research compared to other drivers considered more influential. The role of light in mangrove seedling dynamics is complex as light can serve as both a limiting resource and a stressor when received in excess (Ball 2002). Field studies that have explored the role of light (canopy gaps) in mangrove forest regeneration have reached varying conclusions—some found higher seedling establishment and growth in gaps (Sousa et al. 2003a; Whelan 2005), whereas others reported no differences between gaps and non-gaps (Clarke & Allaway 1993; Clarke & Kerrigan 2000). Understanding the influence of light, coupled with hydrology, on natural mangrove survival is vital to understanding natural patterns of forest regeneration and informing future management and restoration practices.

Information about the constraints on mangrove seedling establishment and survival is limited. Much of the existing literature on establishment and early development of mangroves has not quantified tidal inundation in the field (Krauss et al. 2008), whereas recent studies that have quantified hydrology in situ (Oh et al. 2017; Leong et al. 2018) did not quantify light availability. Moreover, research on mangrove ecology is concentrated in a relatively limited number of geographic regions. Thus, basic knowledge of mangrove species' ecology and physiology is still limited across most of the global distribution range of mangroves, particularly in the species-rich mangrove forests of tropical Southeast Asia. Our field-based study aimed to understand the relationship between multiple abiotic drivers (inundation and irradiance) and the survival of naturally established mangrove seedlings on a species-rich island in Southeast Asia. The goals of this study were (1) to characterize natural mangrove forest recruitment and survival; (2) to quantify and compare the abiotic conditions at which mangroves establish and survive; (3) to evaluate how our results fit in the existing body of knowledge on abiotic drivers of mangrove loss; and (4) to enhance our understanding of mangrove ecology at the species-level for understudied species in the Indo-Pacific with the goal of building a blueprint to inform ecosystem management and restoration efforts.

## Methods

### Site Description and Experimental Design

This study was conducted on Pulau Ubin, a small (10.19 km<sup>2</sup>) island located in northeast Singapore (1°23'33.4908"N 103°56'59.0928"E). During our study, temperatures in this region ranged between 26 and 30°C with an annual precipitation of approximately 1,368 mm, with highest rainfall occurring in December/January and June (National Environment Agency 2021). Salinity in the Johor and Singapore Straits ranges between 28 and 32 ppt (Ng & Sivasothi 2001). Pulau Ubin is believed to contain 35 species of true mangroves (Yang et al. 2013). In May 2019, we established 21 transects nested within each of five mangrove forest plots on Pulau Ubin (approximately 4–5 transects per plot) (Fig. 2A). The plot locations were strategically selected to distribute plots throughout the island and capture mangroves with less anthropogenic influence (i.e. not in former aquaculture ponds).

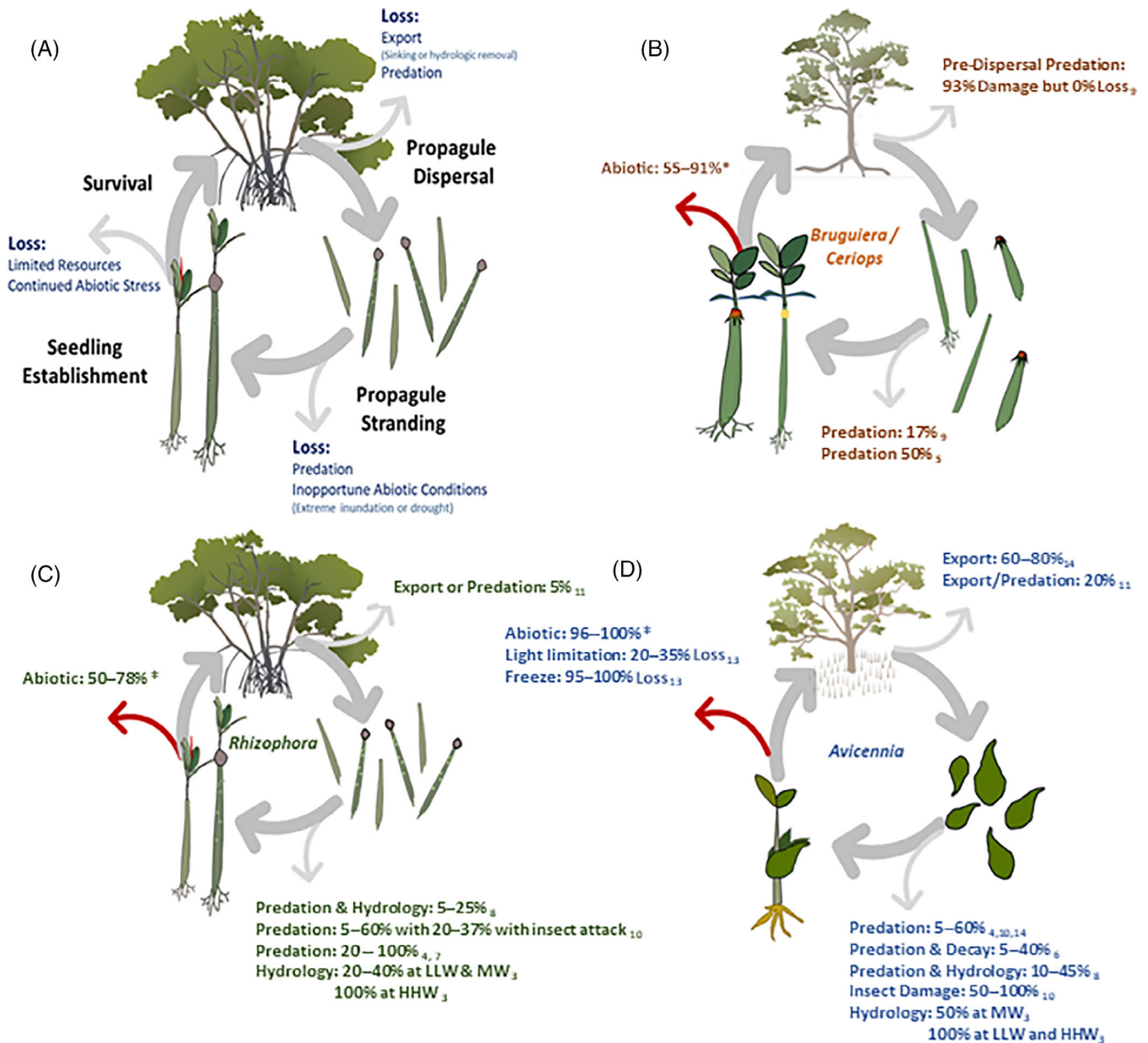


Figure 1. Causes of mangrove loss at multiple life history stages. (A) Conceptual model demonstrating shifts in dominant causes of loss/mortality (blue text) throughout mangrove ontogeny (black text). (B–D) Causes of mangrove loss at multiple early life history stages for four genera determined from field-based observational or experimental studies. Numeric values represent percent loss attributed to each cause by the study (indicated with subscript notation) [1. Robertson 1991; 2. Clarke 1993; 3. Ellison & Farnsworth 1993; 4. McKee 1995; 5. McGuinness 1997; 6. Patterson et al. 1997; 7. Dahdouh-Guebas et al. 1998; 8. Sousa & Mitchell 1999; 9. Krauss & Allen 2003a, 2003b; 10. Sousa et al. 2003b; 11. Sousa et al. 2007; 12. Balke et al. 2011; 13. Pickens et al. 2019; 14. Yando et al. 2021; \* = this study]. Life stage explored in this study is emphasized by the red arrow.

Transects ran perpendicularly from the direction of inundation and spanned the width of the mangrove forest. Each transect was measured and demarked, with 0 m representing the transitional point between the mangrove's edge and mudflat/water, indicated by the most water-ward mangrove (including adults, saplings, and seedlings). Transects ran inland from the 0-m point and ended at the last mangrove tree (excluding mangrove associates) (height  $\geq 1.0$  m or DBH  $> 5.0$  cm) at the terrestrial side of the transect. Thus, each transect was different in total length. Abiotic

conditions (inundation and light) were measured every 2-m along each transect to characterize the general abiotic conditions of the landscape (methods described in detail below).

### Mangrove Sampling

All mangrove seedlings located within 5 m on either side of the transect (10 m total width) were counted, identified to species, and characterized in terms of their position along the transect

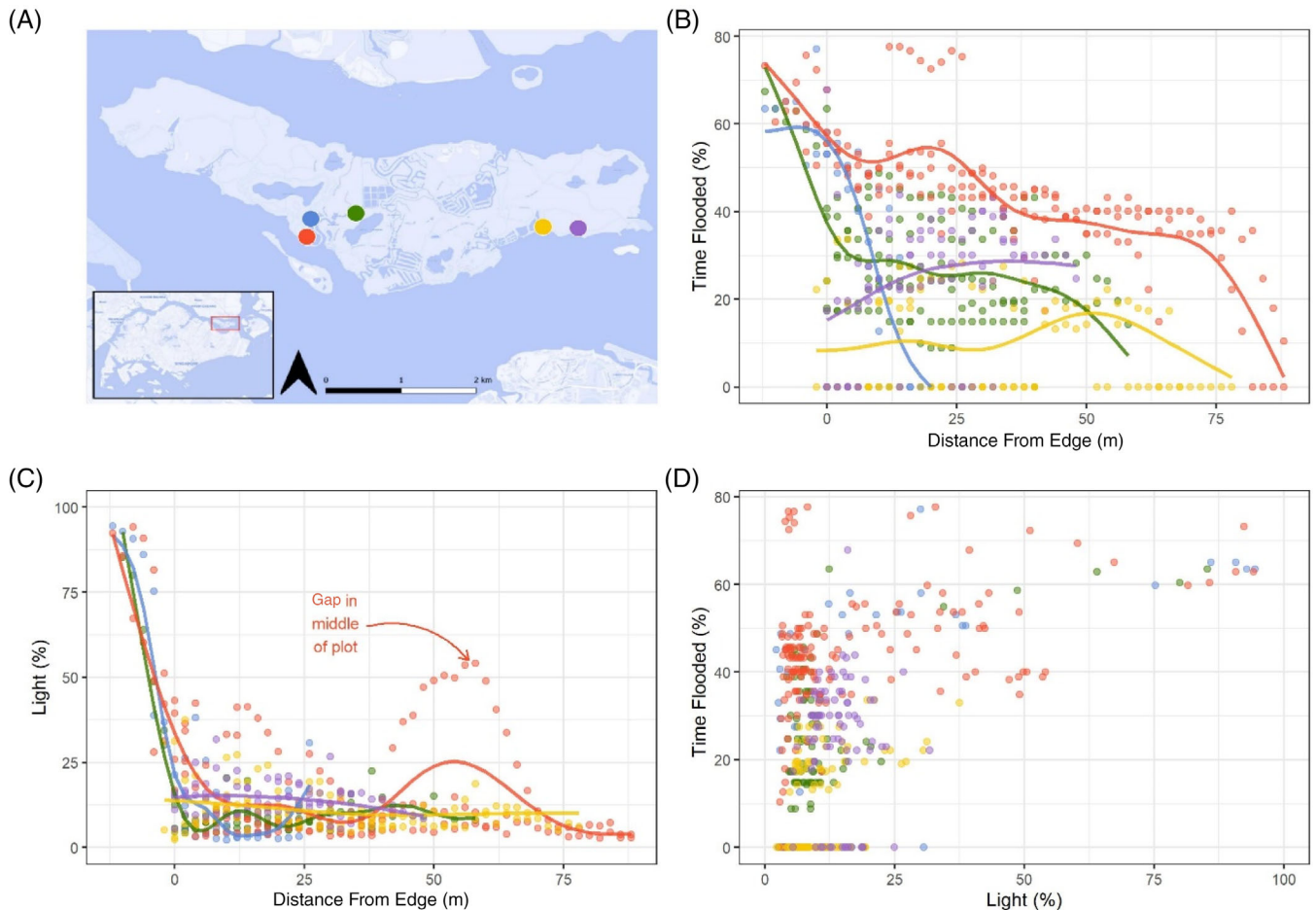


Figure 2. Spatial variation in abiotic conditions among and within plots. (A) Map of Pulau Ubin with field sampling plot locations; (B) inundation (percent time flooded) and (C) light (percent of total above-canopy light) plotted against distance from the shoreline (with 0 m being the end closest to the shoreline or water); and (D) inundation plotted against light levels. Points in (C) and (D) represent sampling locations at every 2 m along the transects. Color coding indicates sites, corresponding to the map in panel (A). To illustrate plot level patterns, smoothed trend lines were fitted per plot, with transects as random variable, using the `gamm4` function of `gamm4` package (Wood & Scheipel 2020). Note that transects differed in total length as the transects traversed the width of the mangrove forest.

(e.g. distance from mudflat to mangrove transition). Each seedling was tagged with an individual ID number (applied by tying a small piece of labeled vinyl flagging tape to the main stem of the seedling). Vinyl tape was selected instead of aluminum forestry tags to reduce tag weight and hydrologic drag on the seedlings. Seedlings were defined as any plant with at least one leaf present (excluding under-developed propagules) and  $\leq 1$  m tall as per Krauss et al. (2008), except for *Rhizophora mucronata* seedlings for which we accepted plants  $\leq 1.5$  m tall as the propagules of this species are large (30–50 cm). The first census of seedlings was conducted in June/July 2019. All species identified were confirmed to be present on the island by Yang et al. (2013). Seedling species identification can be complicated for closely related species at young life stages. Of particular note, we had difficulty differentiating between *Ceriops tagal* and *Ceriops zippeliana* seedlings so the two species were combined as a genus for analysis.

Along each transect, a subset of the surveyed seedlings was selected for further characterization of inundation duration and

light at the individual seedling position. To select seedlings for this subset, each transect was divided into three equal sections, and up to 10 individuals of every species were selected from each section using a random number generator (for a total of  $\leq 30$  individuals per species per transect). Inundation was calculated as percent time the soil surface was flooded in 2019. Inundation (percent time flooded) of random points and seedling locations was determined by comparing the water depth of the seedling's location at a given date/time to the nearest tide chart datum (Tanjong Changi) (MPA 2020) and applying that relationship for the point throughout the full year (averaged from water depth estimated for every 15 minutes). If the point measured was not inundated at the time of survey, the point was revisited at a higher tide stage to ensure an accurate measurement was collected. Some points were never inundated (0% time flooded), many being higher elevation sections of the forest or mud mounds created by mud lobsters. Though the technique employed is not as accurate as using an on-site water level gauge (i.e. we may have missed characterizing extreme high-water

events or under/over quantified low-frequency flooding locations [ $<10\%$  flooding]), we are confident in the relative flooding duration results. We used digital hemispherical photography and WinSCANOPY (Regent Instruments, Inc.) software to obtain data on light availability. Light availability was calculated as the proportion of total (direct and diffuse) sun light (i.e. total site factor, or %TSF) at the given point relative to open sky.

Six months following the initial census (December 2019–January 2020), all transects were re-surveyed. All seedlings tagged in the initial census were recorded as alive or dead/missing and newly recruited seedlings were tagged with an individual ID number, identified to species, and their position along the transect was recorded. If a tag could not be located, the seedling was searched for using the approximate location noted from the first survey. If an unmarked seedling was located, we confirmed it was not a previously established seedling with a missing tag before counting it as a new recruit. In three transects, there were patches with an extremely high density of new seedlings. In these cases, the segments of the transect that overlapped with those patches were sub-sampled with three  $1 \times 1$ -m quadrats on either side of the transect (leaving 1 m of space between each quadrat), at every 2 m along the transect, to obtain an average seedling density (approximately 30% of the length of those transects). A third census was completed in June–July 2020 to determine the survival of seedlings from both the original and second census. Adult mangroves (height  $> 1.0$  m and DBH  $> 5.0$  cm) within our seedling transects were also identified to species and characterized in terms of position in the transect.

**Data Analysis**

To visualize how seedling establishment and survival varied along the light and inundation gradients, we first modeled, per transect, the relationship between each of these two abiotic predictor variables and distance along the transect using locally weighted least squares (loess) regression. To do this, we combined the data from the subset of seedlings and random points with data on light and inundation and used the regression functions to predict inundation and light for the seedlings of the full dataset. We then divided both abiotic gradients in 10% intervals (bins) and calculated the percentage of the total number of seedlings and the percent of seedlings that survived over 6 months in each bin.

Next, survival was modeled for the subset of seedlings for which light and inundation data were collected for the six most abundant species (each with more than 60 individuals in the first census): *Avicennia alba*, *Bruguiera cylindrica*, *Bruguiera gymnorhiza*, *Ceriops* spp., *Rhizophora apiculata*, and *Rhizophora mucronata*. Seedling survival to 1 year was modeled as a function of light, inundation, a light  $\times$  inundation interaction term, and species using a binomial (with logit link) generalized linear model. We modeled the same full model and all nested models for each species separately using a binomial (with logit link) generalized linear model. We ranked these models based on AIC and selected the top model (lowest AIC) and all other models within two  $\Delta$ AIC units (Burnham & Anderson 2002). We then used likelihood ratio tests to test if the selected model(s) with higher number of variables fitted the data significantly better than the selected model(s) with fewer variables. Model assumptions were checked using diagnostic plots. All analyses were conducted

**Table 1.** Species abbreviation, conservation status in Singapore, and initial seedling abundance and survival of those individuals over time. Census 1 seedlings were initially surveyed in summer 2019 ( $T_0$ ) and followed for 1 year ( $T_1 = 6$  months,  $T_2 = 12$  months). Census 2 seedlings were new recruits at  $T_1$  and were followed for 6 months (to  $T_2$ ). Blank rows indicate that species was not observed during the indicated census. Conservation status is based Yang et al. (2013), status may have changed since. Conservation status as per Yang et al. (2013) is defined as follows: NC = not classified/common, vulnerable = species that occur in one or a few areas ( $<1,000$ ), endangered = species that occur in low numbers ( $<250$ ), and critically endangered = species that occur in very low numbers ( $<50$ ). \*Indicates potential error in species identification, so the genus was combined for statistical analyses.

Species Abbreviation	Species	Conservation Status in Singapore	Census 1 Seedlings				Census 2 Recruits		
			$N(T_0)$	$N(T_1)$	$N(T_2)$	Survival (%) ( $T_0$ – $T_2$ )	$N(T_1)$	$N(T_2)$	Survival (%) ( $T_1$ – $T_2$ )
AVAL	<i>Avicennia alba</i>	NC	153	15	7	4	1,379	14	1
AVOF	<i>Avicennia officinalis</i>	NC	40	1	0	0	334	1	0.2
AVRU	<i>Avicennia rumphiana</i>	NC	8	0	0	0			
BRCY	<i>Bruguiera cylindrica</i>	NC	1,626	621	160	10	877	91	10
BRGY	<i>Bruguiera gymnorhiza</i>	NC	117	67	53	47	26	7	27
CETA	<i>Ceriops tagal</i> *	Vulnerable	47	19	13	28	14	3	21
CEZI	<i>Ceriops zippeliana</i> *	Endangered	38	7	1	2	14	1	7
EXAG	<i>Excoecaria agallocha</i>	NC					1	0	0
RHAP	<i>Rhizophora apiculata</i>	NC	228	145	114	50	238	26	11
RHMU	<i>Rhizophora mucronata</i>	NC	226	106	50	22	30	16	53
RHST	<i>Rhizophora stylosa</i>	Vulnerable	40	18	12	30	11	4	36
SCHY	<i>Scyphiphora hydrophyllacea</i>	NC	1	0	0	0			
SOAL	<i>Sonneratia alba</i>	NC	1	1	0	0	2	0	0
SOCA	<i>Sonneratia caseolaris</i>	Critically endangered	2	0	0	0			
XYGR	<i>Xylocarpus granatum</i>	NC	1	1	1	100			
XYMO	<i>Xylocarpus moluccensis</i>	Endangered	12	7	3	25	7	3	42

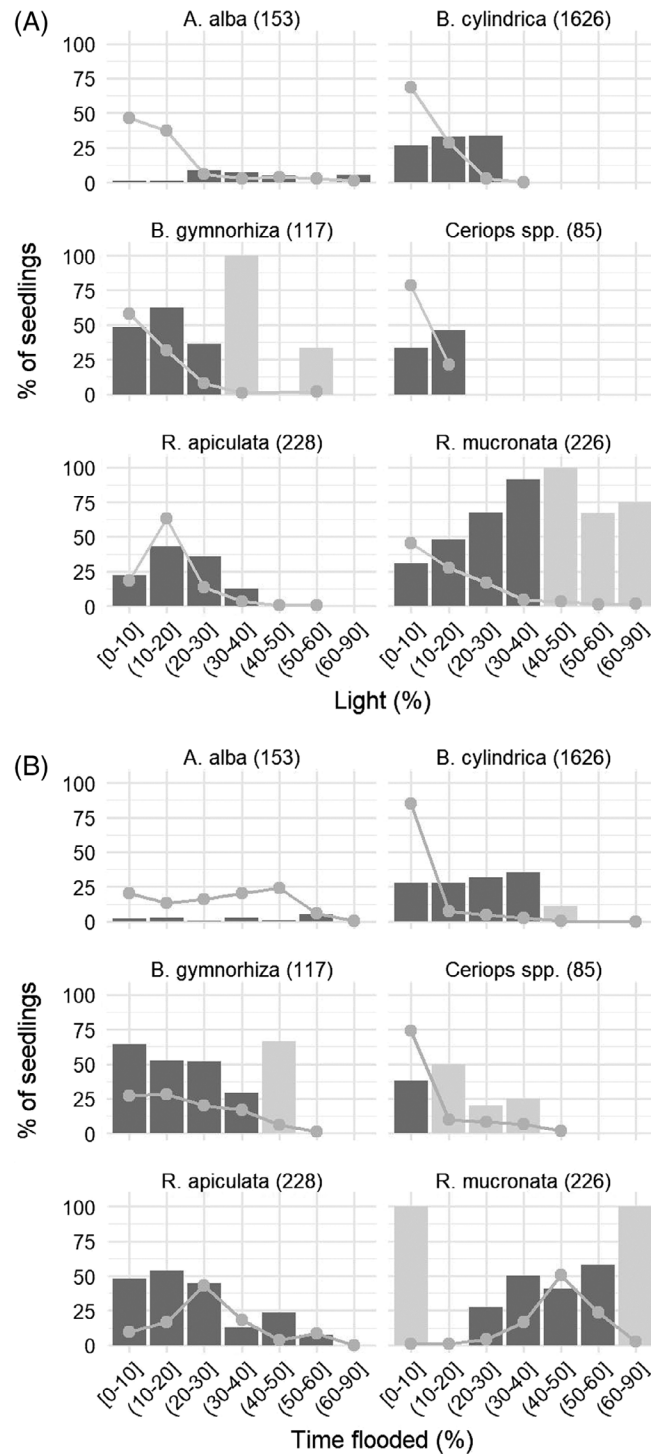


Figure 3. A visualization of seedling establishment and survival along (A) light and (B) flooding gradients. Percent survival was calculated as the percentage of the seedlings in each bin that were still alive after 6 months (bars; light-gray when sample size was less than 10). Dots and lines superimposed on the histogram indicate the percentage of total number of seedlings established in the first census in each abiotic condition bin. Total seedling count per species at the first census is indicated between brackets after the species name. See Method section and Figure S2 for more details.



in R (R Core Team 2020), binomial regression models were fitted using the base R `glm()` function (family = binomial), loess regression, the loess function of the R stats package, and figures were produced using the package `ggplot2` (Wickham 2016).

## Results

### Abiotic Condition

In our study site, both inundation and light availability tended to decrease with distance from the shoreline, but with strong variation among and within plots (Fig. 2B). Micro-topography was particularly irregular in plot 5 due to the abundance of mud lobster mounds. In plot 3, a large forest gap, caused by a storm prior to

the study, contributed to high-light availability in the center of the plot (Fig. 2C). Overall, light and inundation were only weakly positively correlated (Spearman  $r = 0.25, p < 0.0001$ ). Inundation varied most among locations with lower light levels, light levels varied most among lower-elevation locations. Across all sample sites, locations at higher elevations (inundation time  $< 30\%$ ) were always relatively more shaded ( $< 35\%$  light; Fig. 2D).

### Species Abundance and Distribution

A total of 16 mangrove species were encountered, some of which are considered vulnerable, endangered, or critically endangered in Singapore (Table 1). Abundance of established seedlings varied by species and census. The six most abundant

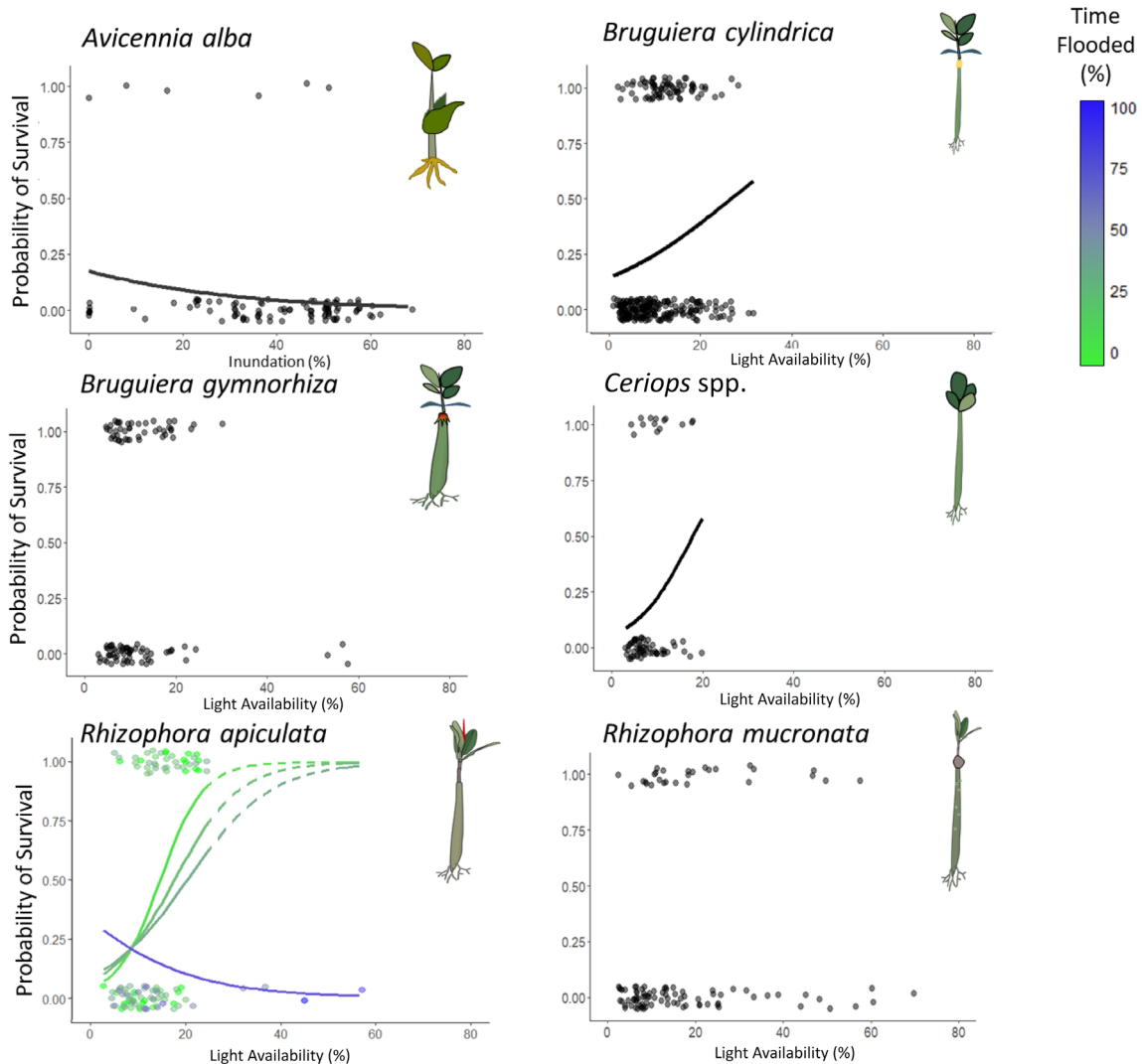


Figure 4. Probability of seedling survival to 1 year modeled as a factor of light availability and/or inundation from binomial survival data (points). The fitted curves shown were obtained from logistic binomial regression for each species separately. Models with lowest AIC per species are shown and only significant models ( $p < 0.05$ ) are shown. If no model was significant, only points are shown. For models with one significant main effect, one line is modeled, and the significant main effect is indicated on the x-axis. For models with either two significant main effects or a significant interaction effect (Table S1), multiple lines are plotted which represent quartiles 1, 2 (median), and 3 of flooding data for each species. For *R. apiculata*, an additional curve representing a higher extreme (75% of the total flooding range) was plotted to demonstrate the significant interaction between flooding and light availability. All lines span the range of observed seedlings. Lines are dotted at light and inundation combinations with fewer than five seedlings at the given light and flooding combination.

species across both censuses were *A. alba*, *B. cylindrica*, *B. gymnorhiza*, *Ceriops* spp., *R. apiculata*, and *R. mucronata* (Table 1). In general, the distribution of established seedlings across and within plots reflected that of conspecific adults, with the exception of *A. alba* which was able to recruit in plots with no conspecific adults present (Fig. S1). The seedlings of most species tended to be found at the lower ends of the light and inundation gradients (i.e. low light levels and limited flooding). Exceptions were the seedlings of the two *Rhizophora* species with peak abundance at mid elevation.

### Species Differences in Survival

Overall seedling survivorship varied by species, with the majority of species having less than 50% survival of naturally established seedlings after the first 6 months, and less than 20% of seedlings after a full year (Table 1). Of the species with an initial abundance of more than 60 individuals, *R. apiculata* (approximately 50%) and *B. gymnorhiza* (approximately 45%) showed the highest survival to 1 year. In contrast, *R. mucronata* (22%), *B. cylindrica* (9.8%), and *A. alba* (4.6%) had much lower survival rates, with multiple additional species showing 0% survival (Table 1). Seedling survival (in the measured subset) differed significantly among species ( $p < 0.001$ ) when accounting for inundation, light and their interaction effect (Table S1).

### Light and Inundation Effects on Survival

The survival of seedlings along the light and inundation gradients varied between species (Figs. 3 & S2). For most species, the median light level of the seedlings that survived (15–25%) was higher than the seedlings that died (8–15%). The exception was *A. alba*, which showed a more even initial distribution and survival across the light gradient (Fig. 3). Establishment and survival along the inundation gradient varied between species, with many species showing greater recruitment and retention at lower flooding levels, and *R. mucronata* showing dominant establishment and survival above 40% time flooded (Fig. 3). The correlation between light and inundation differed among species (Table S1; Fig. 4). The two AIC-selected models ( $\Delta\text{AIC} \leq 2$ ) for *B. cylindrica* and *Ceriops* spp. included light and light + inundation as predictor variables, respectively. However, the latter model did not fit the data significantly better than the former (*B. cylindrica*,  $\text{SD} = 1.44$ ,  $df = 1$ ,  $p = 0.23$ ; *Ceriops* spp.,  $\text{SD} = 1.43$ ,  $df = 1$ ,  $p = 0.23$ ), suggesting seedling survival was mostly driven by light. In case of *A. alba*, among the two AIC-selected models, the full model did not provide a significant improvement over the inundation model ( $\text{SD} = 5.16$ ,  $df = 2$ ,  $p = 0.076$ ). In case of *B. gymnorhiza* or *R. mucronata*, among the top models, none provided a significantly better fit to the data than the intercept-only model (Table S2). Finally, for *R. apiculata*, the only selected model (the second-best models had a  $\Delta\text{AIC} > 9$ ) was the full model, indicating that the seedling survival of this species depended on the interplay of both light and inundation. (Fig. 4). It is important to note that this study only quantified individuals that had naturally established and as a result the sampled seedlings did not cover the full

environmental space defined by the hydrologic and light gradients. Specifically, few seedlings were found in conditions of high-light availability (>20%) and limited inundation time (<30%; Fig. 2). Seedling distributions of individual species covered even smaller portions of both environmental gradients (Fig. 3).

Previous studies, which are predominantly conducted in two genera within the Americas, focus on quantifying rates and identifying causes of mangrove loss prior to seedling establishment (Fig. 1). These studies show seedling establishment is heavily limited by drivers such as predation and hydrology, with loss rates reaching >60% prior to seedling establishment. Our monitoring over 1 year shows that, conservatively, between 50 and 100% of the established seedling cohort may be lost within the time span of 1 year. Our results fill an important data gap in the context of a broader body of knowledge on drivers of mangrove loss, particularly because this work addresses understudied species and life stages while emphasizing the importance of understanding the role of multiple drivers.

### Discussion

Our research suggests that the abiotic heterogeneity at which mangrove seedlings can establish is broader than the conditions at which they survive in the longer term, resulting in low survival of successfully established propagules. Our results indicate that for most species surveyed, light played a more important role in limiting seedling survival beyond the initial establishment phase than hydrology/elevation. The observed greater influence by light compared to hydrology may be partially attributed to the fact that seedlings that successfully establish are already sorted by hydrology, but also that the relative importance of limiting resources may change throughout the life cycle of the plant. We suggest that the influence of hydrology is disproportionately important in the earliest life history stages as propagules disperse, strand, and establish. However, once established, light may become relatively more influential. Our results point to the importance of recognizing that causes of mortality may change at each ontogenetic phase depending on species, geographic location, and interactions with other species.

### Light and Inundation as Drivers in Mangrove Ecosystems

The influence of light availability at multiple ontogenetic stages has been better characterized for mangrove species in the Atlantic-East Pacific than for those in the Indo-West Pacific. For example, although *Rhizophora mangle* can initially establish at all light levels, juvenile survival has been shown to be greater in canopy gaps (Smith et al. 1994; Sousa et al. 2003b; Whelan 2005). This response may be partially driven by changes in the species' morphological and physiological traits throughout ontogeny. Farnsworth and Ellison (1996) found that *R. mangle* trees showed flexibility in light-demanding versus shade-tolerant traits across seedling, sapling and mature tree phases as trees persist in the understory at low-growth rates and grow rapidly upon receiving light. Further, Luna et al. (2019)



found that both *R. mangle* and *Avicennia germinans* seedlings showed the ability to acclimate to full light exposure, but *R. mangle* performed better under low-light (80% shade) conditions. *Avicennia germinans* seedlings in the neo-subtropics exhibited greater growth during early life stages when surrounding canopy was removed (Pickens et al. 2019). In Indonesia, Ulqodry et al. (2014) exposed *R. mucronata* seedlings to various light conditions and observed maximum carbon fixation at approximately 50% light. A study from the Sundarbans found mangrove canopy structure did not influence species richness, but there was a difference in floristic composition, and gaps demonstrated greater seedling density (Azad et al. 2020).

In our study, the influences of inundation and light on seedling survival trends varied by species. Whereas most species exhibited an establishment and survival peak at a given light/inundation level, *A. alba* showed more evenly distributed establishment along the inundation gradient and survival (albeit low survivorship of only seven individuals) along the light gradient. *Avicennia alba*'s divergence from the pattern of other species may suggest that its initial establishment may be less constrained by abiotic drivers. *Avicennia* spp. produce small, buoyant, tear-shaped propagules that establish in sediment only after growing a radicle and roots, which may also be a contributing factor to its broad dispersal and establishment. In contrast, *Cerriops* spp., *Rhizophora* spp., and *Bruguiera* spp. produce elongated, torpedo-shaped propagules that can become lodged in the sediment after falling from the parent tree (though some may travel via hydrochory) (Van Speybroeck 1992). Additionally, *A. alba* seedlings were observed in plot locations where conspecific adults were not present, further suggesting that although propagules of this species are successful in dispersal and initial establishment in a wide range of abiotic conditions, they ultimately experience high mortality and the few that establish into adults are constrained to a much narrower niche.

Although seedling establishment and survival trends were similar for hydrologic conditions, seedling survival tended to occur at slightly higher median light conditions than establishment. Binomial regression allowed us to predict the impact of light on seedling survival under various inundation conditions. Light significantly impacted seedling survival in *B. cylindrica* and *Cerriops* spp., with increased light availability resulting in greater survival. Hydrology impacted survival in *A. alba*; and although apparent propagule production for *A. alba* was high compared to other species, overall survival in surveyed plots was low in the duration of this study. *Rhizophora apiculata* seedlings inundated for short to moderate durations showed a positive relationship between light and survival, but seedlings inundated for longer durations exhibited reduced survival with increasing light. Exposure to additional stress factors such as salinity and inundation during exposure to light is known to increase the potential of photoinhibition (Goh et al. 2012). The differential response to light depending on inundation suggests that photoinhibition may occur in *R. apiculata* seedlings when exposed to longer durations of flooding. Although mangroves have both physiological and morphological mechanisms for avoiding photoinhibition (Krauss et al. 2008), the role of these mechanisms deserves more comparison across more species as well as developmental stages.

### Mangrove Loss Throughout Ontogeny

Seed-seedling conflict, caused by habitat heterogeneity, suggests that during an individual plant's life cycle, the seedling stage is the most vulnerable to environmental stressors and has the highest mortality rate (Schupp 1995; Deng et al. 2009). Seed-seedling conflict has been observed in species in a variety of ecosystems, including coastal salt marshes (Deng et al. 2009), bottomland hardwood forests (Battaglia et al. 2000), forest-tundra ecotones (Cranston & Hermanutz 2013), among others. In mangroves, however, loss may be greatest before the plant reaches the seedling phase and dominant threats may change throughout ontogeny. In some mangrove species, 5–60% of propagules may be lost prior to dispersal (Sousa et al. 2003b). After release from the parent tree, a large portion of the remaining propagules (80–100%) may be lost due to export from the system (e.g. lost at sea) during dispersal (Yando et al. 2021). Propagules that strand (settle on land) show high variability regarding further loss due to herbivory, fungal disease, or inopportune abiotic conditions (Sousa & Mitchell 1999; Sousa et al. 2007; Yando et al. 2021). Even propagules that establish as seedlings (i.e. become secured in the sediment and produce radicle/roots and leaves) may not necessarily be located in a location physically suitable for the tree's continued growth and survival to the sapling or adult phase. Continued survival after depletion of the propagule's initial resources depends on suitable environmental conditions. Therefore, the surviving seedling community may not reflect the original seed source or early established propagule community (López-Hoffman et al. 2007).

Though mortality is well understood to be high in mangroves prior to seedling establishment, understanding the multiple dynamics limiting survival and longevity of intermediate life stages have important implications for both the success of human-aided restoration and rehabilitation efforts as well as community composition in mangroves that naturally recover following disturbance. For example, Baldwin et al. (2001) found that the loss of mangrove canopy following a hurricane stimulated seedling recruitment, but whether the recovering community was monospecific (*R. mangle*) or more diverse (*A. germinans*, *Laguncularia racemosa*, and *R. mangle*) depended on whether previously established *R. mangle* seedlings survived the disturbance (i.e. release of advance recruits).

### Future Research and Restoration

International concern over rapid mangrove loss in recent decades has given impetus to improving restoration practices (Ellison 2000; Lee et al. 2019). Historically, mangrove restoration efforts have depended on hand-planting propagules or young seedlings in unvegetated areas in full sun where the vast majority do not survive. Unfortunately, many such restoration plantings have exhibited poor success and low survival of planted seedlings (Elster 2000; Kamali & Hashim 2011; Kodikara et al. 2017). Though restoration efforts exhibiting <20% survival have been described as failures (Primavera & Esteban 2008; Thompson 2018; Wodehouse & Rayment 2019), results from our study sites over 1 year of observation suggest

that naturally established seedlings of many species exhibit similarly low survivorship rates. Ideally, human-assisted restoration should exhibit greater survival than random dispersal, but basic knowledge on the stress tolerance thresholds and ecophysiology is needed for a variety of mangrove species and at multiple life stages, particularly for historically underrepresented species in the Indo-Pacific.

Although planting efforts typically occur in full sun, the majority of surviving seedlings we surveyed occurred at lower light intensities (TSF < 60%). Although practices such as enrichment plantings are rarely employed in mangrove ecosystems, our observations give impetus for further study of planting within the forest canopy to rehabilitate systems with poor recruitment or for sustainable silviculture operations. Previous studies on *Avicennia* spp. and *Bruguiera* spp. found that photosynthetic rates saturate at approximately 40% irradiance (Ball & Critchley 1982; Cheeseman 1991). Inundation may further moderate the effects of light by reducing light availability during leaf inundation or by contributing to physiological stress of the plant (e.g. production of reactive oxygen species) that make the plant susceptible to photoinhibition. The relationship between irradiance, inundation, and photoinhibition in mangrove seedlings deserves further research in both natural and controlled settings, and creative planting approaches such as using shade cloth when planting in full sun and low tidal prism deserve experimentation.

We recommend restoration practitioners adjust expectations for survivorship. The results from our study and the work of others can be used to prioritize planting species and life stages that exhibit greater survivorship after propagule establishment across a suite of abiotic conditions. Although survival of *Avicennia* spp. seedlings was low within the conditions explored in this study, restoration efforts using this genus may be more effective if larger individuals are planted instead of propagules or young seedlings. Conversely, *Rhizophora* spp. exhibited improved survivorship of established propagules, though more attention is needed to understand the suite of local abiotic drivers, particularly inundation in combination with light.

Next, we want to emphasize the importance of long-term monitoring (i.e. monitoring beyond initial planting for several months to years) to accurately assess the survival of restoration plantings or natural recruitment. Mortality is a continuous and complex process at early life history stages, and the relative influence of the suite of environmental drivers may shift throughout a species' ontogeny. Regular survival assessments and adaptive management should be crucial components of restoration planning.

Mangrove research has been predominantly focused on understanding dispersal and establishment dynamics or characterizing spatial dynamics of adult stands. Further, the majority of research quantifying loss rates and identifying causes of loss originates from limited geographic regions and addresses relatively few species, and intermediate ontogenetic stages (seedlings and saplings) remain understudied compared to their propagule and adult counterparts. The high mortality at early life stages, combined with the variability and heterogeneity of abiotic conditions at which seedlings establish, limits data

collection and analysis. Intermediate life stages are intensive to track over time in ground sampling and difficult to capture using remote sensing techniques. Even our study, which specifically focused on early life stages, had limitations due to difficulties of sampling this stage. Because this was an observational study, sampling of light-inundation combinations was uneven across species and the proportion of species was skewed toward common species. While we want to emphasize the utility of observational field efforts, which we still believe can serve as a blueprint for conservation and restoration, sampling efforts need to be increased to obtain adequate number of surviving individuals to inform more robust prediction models for all species. Acknowledging the caveats of this study (limited temporal and spatial scale), our work nonetheless suggests that light, in addition to hydrology, may be an important driver of early mangrove survival and further suggests the relative influence of abiotic drivers shift throughout the life cycle of the plant. Ecological thresholds and planting guidelines are thereby encouraged to consider life history stage in addition to species-level specificity.

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## Supporting Information

The following information may be found in the online version of this article:

**Table S1.** Full summary of statistics for binomial logistic regression models.

**Table S2.** For each species, seedling survival to one year was modeled as a function of light, inundation and the light × inundation interaction term.

**Figure S1.** Density (#/m<sup>2</sup>) of mangrove seedlings (pink) and adults (blue) relative to placement along the transect.

**Figure S2.** Inundation (percent time flooded) and light (percent TSF) conditions for seedlings separated by species and survivorship.