

Modelling the effects of climate, predation, and dispersal on the poleward range expansion of black mangrove (*Avicennia germinans*)

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ABSTRACT

Globally, species ranges are shifting in response to climate change. For black mangrove (*Avicennia germinans*), fewer severe freeze events in a warming climate facilitate poleward range expansion into temperate coastal salt marshes, however propagules that disperse into marshes encounter biotic interactions (e.g., predation) that affect their survival and subsequent forest development. To better understand the relative roles of climate, predation, and propagule dispersal in shaping *A. germinans* range expansion, we developed a stage-based population model that tested forest stand establishment and survival under differing scenarios of freeze regime, predation pressure, and propagule dispersal. Predation parameters were developed from a field experiment that tested propagule density-predation intensity relationships for purple marsh crab (*Sesarma reticulatum*), which showed proportional propagule consumption decreased with increased propagule density. Model outcomes demonstrated all measures of mangrove stand development and regeneration decreased with increased freeze and predation intensities, modulated by propagule dispersal density and frequency. Regenerating stands were more likely to recover from freezes under a reduced freeze regime compared to a historical freeze regime, but moderate and high predation intensities hindered stand development and recovery across freeze regimes. Maintaining a regenerating stand generally required recurring dispersal events. While several studies have investigated the individual effects of freezes, predation pressure, and dispersal on mangrove ranges, our model is the first effort of which we are aware that quantifies the combined effects of all three controls. The model can thus serve as a tool for understanding patterns of *A. germinans* range expansion in the Big Bend and other regions under future warming.

1. Introduction

In recent decades, global climate change has driven large-scale changes in species distributions across taxonomic groups in terrestrial and marine ecosystems across all major regions of the world (e.g., Burrows et al., 2011; Chen et al., 2011; Pecl et al., 2017; Walther et al., 2002). Changes primarily occur where warming temperatures support range shifts at poleward and elevational range limits; in the Northern Hemisphere, species boundaries have shifted poleward by an average 6.1 km (or higher in elevation by 6.1 m) per decade (Parmesan, 2006; Parmesan and Yohe, 2003). Yet even as populations of species respond to a changing climate, they do so in the context of biotic interactions and dispersal mechanisms that aid or restrict boundary shifts. Biotic interactions together with environmental conditions define a species' niche space and determine whether species survival exceeds mortality, while dispersal mechanisms determine whether a species can reach

environments within its ecological niche (Boulangeat et al., 2012; Holt, 2009; Hutchinson, 1957; Sexton et al., 2009; Soberon and Peterson, 2005; Wiens, 2011). Accounting for the relative contributions of all three ecological factors is critical for predicting whether species can adjust their ranges to maintain sustainable populations under a changing climate.

One of the most visible examples of a climate-driven range shift is the poleward expansion of mangrove forests (Cavanaugh et al., 2018, 2014; Osland et al., 2018, 2017a, 2013; Saintilan et al., 2014). Mangroves, which are sensitive to freeze events and generally restricted to latitudes with tropical and subtropical climates, have responded to past periods of warming and cooling via range expansion and contraction (Osland et al., 2017a). During the warm climate of the Eocene, *Avicennia* were present in Arctic Siberia above 72° N (Suan et al., 2017), and during the global cooling of the Pleistocene, mangrove populations retreated toward the Equator (Sherrod and McMillan, 1985). Globally,

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latitudinal limits of mangroves are correlated with the winter positions of the 20°C sea surface temperature isotherm (Duke et al., 1998); on a regional scale, frequency and intensity of severe freezes and/or precipitation minima mark range limits (Cavanaugh et al., 2014; Osland et al., 2017b; Saintilan et al., 2014). The occurrence of fewer severe freezes at poleward range limits in recent decades has facilitated mangrove encroachment into temperate coastal regions dominated by salt marsh (Osland et al., 2019, 2013). However, rates at which mangrove forests are expanding vary across regions, suggesting that non-climatic factors such as biotic interactions and propagule dispersal mediate expansion at poleward range limits (Cavanaugh et al., 2018).

Studies of mangrove expansion have focused on encroachment at the interface of established forest and salt marsh (Guo et al., 2013; McKee and Rooth, 2008; Patterson et al., 1993; Rogers et al., 2005; Simpson et al., 2013; Yando et al., 2016). Indeed, the majority of mangrove propagules drop in the immediate vicinity of parent trees, promoting radiating patterns of encroachment into salt marsh adjacent to established forest (Duke, 2001; Sousa et al., 2007). However, mangroves also depend on long-distance dispersal to expand their ranges. Most mangroves produce buoyant propagules capable of traveling far distances, carried by tides, ocean currents, and storm surges to substrate uninhabited by mangroves (Clarke, 1993; Duke et al., 1998; Van der Stocken et al., 2019; Van der Stocken and Menemenlis, 2017). When propagules disperse into salt marsh, biotic interactions ranging from facilitative to competitive between mangrove seedlings and salt marsh plants influence mangrove establishment success (Guo et al., 2013; Lewis and Dunstan, 1975; McKee et al., 2007; McKee and Rooth, 2008; Peterson and Bell, 2012). Propagules and seedlings may also face mild to intense predation and herbivory by salt marsh fauna, restricting mangrove establishment in salt marshes with favorable abiotic conditions (Langston et al., 2017a; Patterson et al., 1997; Peterson and Bell, 2018).

This study examined the effects of climate (freeze regime), biotic control (propagule predation), and propagule dispersal on the establishment of *Avicennia germinans* (black mangrove) into salt marsh along the Big Bend coast of Florida, USA (Fig. 1). The Big Bend is a relatively undeveloped region that marks the northernmost limit of *A. germinans* on Florida's west coast. The largest populations of *A. germinans* occur in Cedar Key and Waccasassa Bay and near Anclote Key. Small stands and individuals are scattered in adjacent salt marshes; propagules, seedlings, and saplings can be found in salt marshes several kilometers from larger, regenerating stands. Between 1980 and 2015, mangrove coverage in the Big Bend expanded north by 0.04 km y⁻¹ and has increased by 10–100% within latitudinal zones spanning the region (Giri et al., 2016).

Freeze regime (i.e., freeze severity and frequency) is the climatic control restricting poleward range expansion of *A. germinans* along the Big Bend. Moderate freezes occur most years, generally causing leaf

damage from which trees can recover; on the rare occasion, a moderate freeze may cause low rates of mortality for seedlings, saplings, and young trees (Osland et al., 2015). Severe freeze events cause varying rates of damage and mortality to *A. germinans* populations depending on freeze temperature and frequency (Cavanaugh et al., 2014; Osland et al., 2019, 2013; Osland et al., 2015). All life stages, from propagule to old tree, are vulnerable to severe freezes (Pickens and Hester, 2011). From 1895 to 1996, 17 severe freezes occurred along the coast of the southeastern US, including a set of consecutive severe freezes (multiple severe freezes occurring in two or more consecutive years), which are especially damaging to *A. germinans* populations (Osland et al., 2017a; Stevens et al., 2006). Historically, one set of consecutive severe freezes occurs every hundred years (Stevens et al., 2006). The last set of consecutive severe freezes in the southeast occurred in the 1980s, and coverage of *A. germinans* has increased steadily since (Osland et al., 2013; Stevens et al., 2006).

As *A. germinans* encroaches into temperate salt marshes in the Big Bend, it faces local predation pressure by fauna, namely *Sesarma* species (Grapsidae), which are common and abundant in salt marshes along the eastern and southeastern coasts of the US (Bertness et al., 2009; Subrahmanyam et al., 1976). In previous studies, we found that propagule predation by *S. reticulatum* (purple marsh crab) was the predominant control on *A. germinans* colonization in a Big Bend salt marsh, as well as on islands of freshwater forest converting to salt marsh, when abiotic conditions were favorable and propagule density was low (10 m⁻²; Langston et al., 2017a, 2017b). Propagule predation is routinely documented in mangrove forests in tropical climates as a prevalent biotic control on *Avicennia* populations (Bosire et al., 2005; McGuinness, 1997; Smith et al., 1989; Souza and Sampaio, 2011; Van Nederveelde et al., 2015). However, predation as a biotic control restricting poleward range expansion of *A. germinans* into salt marsh has been largely overlooked.

To help fill this gap, we developed a stage-based population model to evaluate the relative effects of freeze regime, predation, and propagule dispersal on *A. germinans* expansion into salt marshes along the Big Bend, and as a generalizable tool for application elsewhere. While quantifying the relative effects of freezes, predation, and dispersal would be most accurately quantified through field experiments and long-term field observations, these endeavors would require experiments spanning large spatial and temporal scales (100s of kilometers over decades to centuries). Modeling approaches based on both empirical and mechanistic understanding of ecosystem components can be used to gain insight about system dynamics when direct observation and experimentation are unfeasible (e.g., Brown et al., 2013; Gustafson, 2013). For example, models are especially useful for predicting long-term trends such as ecological succession, population growth, and species range shifts in response to large-scale or high intensity drivers of change (e.g., Burton et al., 2010; Langston et al., 2020; Park et al., 2019; Pearlstine et al., 1985). While no model can perfectly capture real-life dynamics, a well-formulated model can be a useful tool for testing hypotheses and predicting outcomes (Jørgensen, 1994).

Numerous models have been used to evaluate environmental factors (e.g., climate, nutrients, light, water resources), or biotic factors (e.g., inter- and intraspecific competition) on population dynamics and distributions of mangroves (Berger and Hildenbrandt, 2000; Chen and Twilley, 1998; Osland et al., 2013; Park et al., 2019; Record et al., 2013). Among the existing population models are two stage-based models developed for other *Avicennia* species (Clarke, 1995; Delgado et al., 1999). However, we are unaware of any modeling efforts that explicitly account for climatic, biotic, and dispersal controls on *A. germinans* establishment. Here we present results of a stage-based model that combines episodic freeze and propagule dispersal events with predation rates informed by field experimentation and life table probabilities for *A. germinans*. Model results demonstrate the interactive effects of freezes, predation, and dispersal on the local establishment of

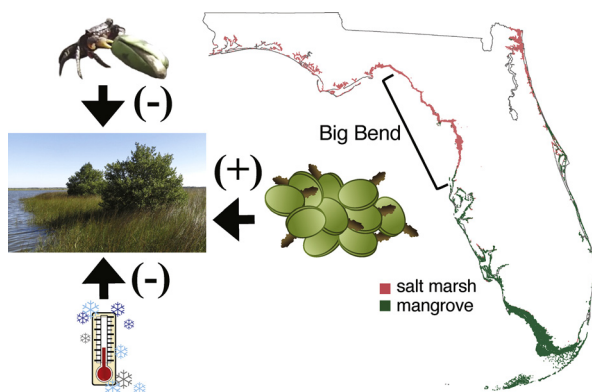


Fig. 1. Freeze events, predation, and dispersal on *Avicennia germinans* expansion into salt marsh at its northern range limit along the Big Bend coast, Florida.

mangrove forests in salt marsh, which can inform regional patterns and rates of poleward mangrove expansion along the Big Bend. Moreover, our model serves as a generalizable tool that can be parameterized to predict regional population responses of other plant species to abiotic and biotic stressors and dispersal mechanisms.

2. Methods

2.1. Field experiment

To parameterize predation in the model, we conducted a field experiment investigating the relationship between propagule dispersal density and predation intensity in salt marshes not adjacent to stands of *A. germinans*. The experiment was conducted in November 2016 in a salt marsh dominated by *Juncus roemarianus* (black needlerush) at the Withlacoochee Gulf Preserve in Yankeetown, FL. Propagules were collected from nearby Cedar Key, FL. We set out propagules in three density treatments (1, 25, and 100 m^{-2}) and recorded propagule mortality from predation for 23 days. Six replicates of each density treatment were randomly placed in a grid of 3×6 plots in the marsh. Each plot consisted of nine 1- m^2 subplots arranged in a square, with the center subplot as the experimental unit and surrounding subplots serving as buffers between the experimental unit and the surrounding marsh matrix (Fig. 2). All propagules in the 1 m^{-2} treatment plots were tethered to the marsh surface using 20 cm strands of monofilament tied to landscape stakes; 10 propagules in each 25 and 100 m^{-2} plots were tethered. The remaining propagules were scattered randomly within the subplots. Only propagules in the center subplots were monitored, and they were marked with an 'x' to distinguish them from propagules in buffer subplots. Propagules were monitored on days 1 through 5, 7, 9, 11, 14, and 23. During monitoring events, we counted all propagules in center subplots and recorded how many were viable (i.e., showed no visible signs of damage or decay). We assumed missing tethered and non-tethered propagules were eaten. To quantify *S. reticulatum* density,

we counted burrows within each center subplot using the description in Bertness et al. (2009).

We conceptually equated propagule dispersal with mast seeding events and evaluated the functional response of *S. reticulatum* to propagule density as described by the Predator Satiation Hypothesis (PSH; Holling, 1959a, 1959b). We hypothesized that *S. reticulatum* behavior would be consistent with a type II functional response, i.e., we expected *S. reticulatum* to consume all propagules when propagule density was low and consume a decreasing portion under increased propagule densities. Data from the non-caged treatment (10 propagules m^{-2}) reported in Langston et al. (2017a) were included in the data analysis as an additional treatment density. We fit type I, II, and III PSH responses to our results using a Levenberg-Marquardt nonlinear least-squares algorithm (Morin, 1999) in R v. 3.4.0 – 3.4.4 (R Core Team, 2018).

2.2. Model

2.2.1. Model structure

We developed a stage-based population model quantifying the combined effects of freeze intensity and frequency, predation intensity, and propagule dispersal density and frequency on *A. germinans* forest stand development. The model tracked densities of seven life stages on an annual time step for 100 years (Fig. 3). As propagules grew into trees, probabilities of remaining in the same life stage, developing into the next life stage, succumbing to miscellaneous causes of mortality, crowding, and propagule production determined rates of stand development, as modified by the effects of freeze regime, predation, and propagule dispersal. The spatial extent of the model was not geographically explicit; rather the model domain represented a generic 100- m^2 area of habitable salt marsh (i.e., low elevation marsh with sufficient precipitation and tidal inundation), allowing us to focus on the relative roles of climate, predation, and dispersal. Freeze regimes reflected the historical regime of the past 100 years and a hypothetical regime of reduced frequency driven by climate warming. Predation was

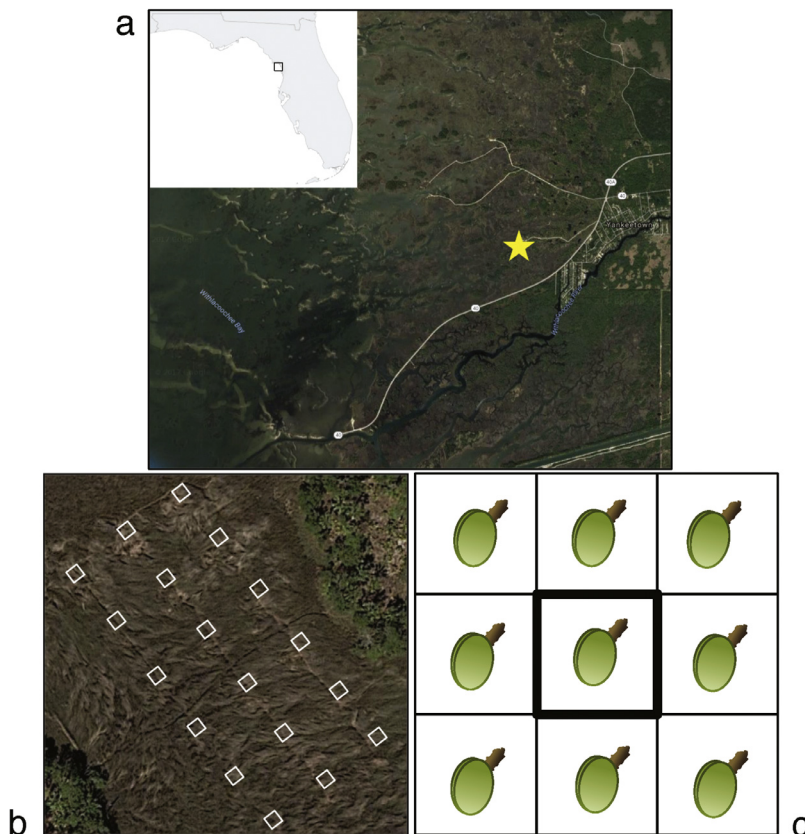


Fig. 2. Field experiment location at a) the Withlacoochee Gulf Preserve in Yankeetown, Florida, and b) layout of the propagule density plots in which density treatments (1, 25 and 100 m^{-2}) were randomized across plots, and c) each plot consisted of a center experimental unit surrounded by eight buffer subplots of the same density.

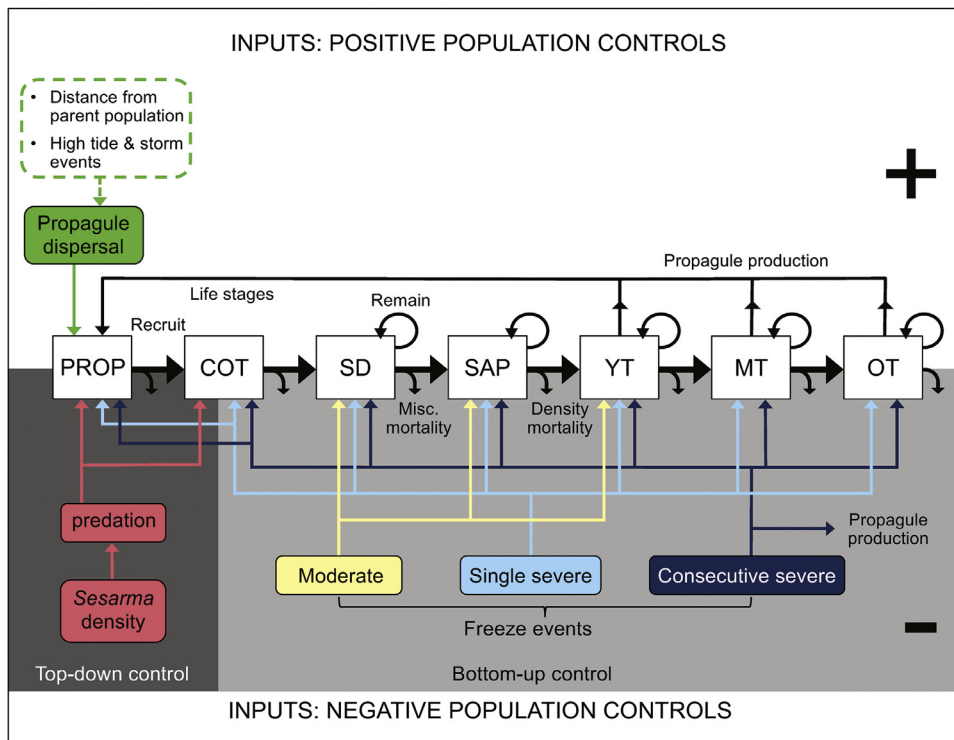


Fig. 3. Model flow diagram showing positive and negative controls on mangrove forest stand development. Populations depend on initial (and sometimes subsequent) propagule dispersal (green box), after which propagules may succumb to predation (pink box) or mature into later life stages (white boxes; PROP: propagule, COT: new seedling with cotyledons, SD: older seedling, SAP: sapling, YT: young tree, MT: mid-age tree, OT: old tree), which are subject to mortality from freeze events.

informed by field data on *S. reticulatum* densities and propagule predation rates. Propagule dispersal densities and frequencies represented variation in dispersal with respect to distance from the parent population and storm-driven dispersal events. The model was developed in R v. 3.4.0 – 3.4.4 (R Core Team, 2018) using the simcol package (Petzoldt and Rinke, 2007).

2.2.2. State variables

The model included densities of seven life stages of *A. germinans*: propagule, seedling with cotyledons, seedling without cotyledons, sapling, young tree, mid-age tree, and old tree (Fig 3; Table 1). These life stages followed those used in a population model of *A. marina* developed by Clarke (1995). Propagules either dispersed into the model domain or were produced by trees that developed within the model population over time. Seedlings with cotyledons represented newly established seedlings with attached cotyledons; based on field observations, viable propagules that settle onto substrate reach this stage within the same year. Seedlings without cotyledons represented a later seedling stage that can persist for multiple time steps. Saplings represented individuals that developed from seedlings but had not reached reproductive maturity. Young, mid-age, and old trees produced propagules. Life stages were defined by differences in annual probabilities of developing into the next life stage (recruiting), remaining in the same life stage (remaining), mortality, density maxima, and propagule production rather than by size (i.e., height, biomass).

2.2.3. Life-stage probabilities

Because stage-based models for *A. germinans* are absent in the literature, we developed life stage probabilities using stage-based models for *A. marina* and *A. bicolor* (Clarke, 1995; Delgado et al., 1999). We modified probabilities from these studies based on field observations from previous studies on *A. germinans* and to create separate probabilities of mortality from freeze events and predation. Changes in life stage densities were calculated for each time step using the general equation:

$$\frac{dx_i}{dt} = x_i r_i + x_{i-1} m_{i-1} \tag{1}$$

Where x_i is the population density of life stage, i , r_i is the probability of individuals remaining in that life stage, x_{i-1} is the population density of the previous life stage, and m_{i-1} is the probability of individuals from the previous life stage recruiting to the next life stage. No propagules or seedling with cotyledons from the previous time step remained in the next; they either recruited to the next life stage or died. Propagules recruited to seedlings with cotyledons during the same time step in which they dispersed into the model domain or were produced by trees in the model population. The probability of mortality from miscellaneous causes (i.e., causes other than crowding, freezes, or predation) was the difference of $1 - (r_i + m_{i-1})$. Miscellaneous causes of mortality accounted for rot, desiccation, uprooting, herbivory on older seedlings, saplings, and trees, competition with salt marsh plants, and local disturbances such as lightning. Because we assumed the model domain represented favorable conditions for establishment, mortality from miscellaneous causes was relatively low (Table 1). This category also included propagule loss from dispersal out of the model domain. Mortality probabilities from crowding (i.e., density maxima), freeze events, and predation were applied after first applying Eq. 1.

2.2.4. Density maxima

Density maxima were applied to all life stages except propagules to account for mortality from crowding and shading (Table 1). Seedling densities of *Avicennia* species range from 140 to 330 m⁻² (Jimenez et al., 1985). We set a maximum density of 150 m⁻²; 100 m⁻² for seedlings with cotyledons and 50 m⁻² for seedlings without cotyledons, assuming the density threshold would be higher for younger seedlings. Maximum density for saplings was 0.34 m⁻², consistent with the mean sapling density from a 6-year study of *A. bicolor* (Delgado et al., 1999). We set a maximum tree density of 0.21 m⁻². Tree density data for *A. germinans* stands in the southeastern US are lacking in the literature; hence, our estimate is similar to tree densities reported for *A. germinans*-dominated stands in French Guiana, which ranged from 0.05-0.2 m⁻² (Proisy et al., 2000). We divided tree density equally among tree stages (0.07 m⁻² for young, mid-age, and old trees). However, total tree density did not exceed 0.1 m⁻² in our model simulations, consistent with the density at which *A. marina* trees

Table 1
Model parameters for life-stage probabilities, density maxima, propagule density, predation, and freeze events

Life-stage Probabilities & Density Maxima						
Life stage	Remaining	Recruiting	Misc. mortality	Maximum density (m^{-2})	References	
Propagule	0	0.9	0.1	N/A	Clarke, 1995; Delgado et al., 1999; Jimenez et al., 1985; Langston et al., 2017a	
Seedling (cot)	0	0.9	0.1	100		
Seedling	0.8	0.041	0.159	50		
Sapling	0.825	0.02	0.155	0.34		
Young tree	0.94	0.01	0.05	0.07		
Mid-age tree	0.967	0.014	0.019	0.07		
Old tree	0.991	N/A	0.009	0.07		
Propagule Production						
Young tree	Mid-age tree		Old tree			
0-100	0-3000		0-5300			Clarke, 1992
Propagule Dispersal						
Density (m^{-2})	Frequency (y^{-1})					
	Single dispersal	Low				High
1	0.01	0.1	1	N/A		
10	0.01	0.1	1			
100	0.01	0.1	1			
Predation						
	None	Low	Moderate	High	Predation coefficient	
Crab:Propagule	0:1	0.1:1	0.5:1	1:1	Field experiment (this study); Langston et al., 2017a	
Propagule mortality	0	0.366	0.898	0.990		
Seedling (cot) mortality	0	0.204	0.680	0.898		
Freeze Regimes						
Regime	# Moderatefreezes	# Severefreezes	# Consecutive severe sets			
None	0	0	0	Osland et al., 2017a; Stevens et al., 2006		
Reduced	8	8	0			
Historical	15	14	1			
Freeze Mortality						
Life stage	Moderatefreezes	Severefreezes	Consecutive severe sets			
Propagule	N/A	N/A	N/A			
Seedling (cot)	N/A	0.5	0.98			
Seedling	0.075	0.5	0.98			
Sapling	0.15	0.2	0.98			
Young tree	0.08	0.12	0.98			
Mid-age tree	N/A	0.12	0.98			
Old tree	N/A	0.12	0.98			

stabilized in the stage-based model by Clarke (1995).

2.2.5. Freeze regimes

We modeled three regimes of freeze frequency and intensity: historical, reduced, and none (Fig. 3, Table 1). Historical and reduced freeze regimes included moderate, severe, and consecutive severe freeze events, modeled as stochastic events that caused varying rates of mortality across life stages. Only one freeze event occurred in a given time step. Moderate freezes represented events in which temperatures range between 0°C and -6.5°C for under 24 hours (Pickens and Hester, 2011). Though moderate freezes generally cause leaf damage from which individuals can recover, on rare occasions they can cause low rates of mortality for older seedlings and shorter trees, which we assumed to be equivalent to saplings and young trees (Osland et al., 2015; Pickens and Hester, 2011). Severe freezes represented events in which temperatures reach -6.5°C for at least 24 hours, causing mortality to non-propagule life stages and preventing regeneration in the subsequent year (Pickens and Hester, 2011; Stevens et al., 2006). Consecutive severe freezes represented multiple severe freezes occurring in two or more consecutive years. These events caused 98% mortality across all non-propagule life stages consistent with reported mortality

from consecutive freezes along the Big Bend in the 1980s (Montague and Odum, 1997).

The historical freeze regime reflected historical climate conditions along the Big Bend as derived from published studies (Table 1) and included 15 moderate freezes, 14 severe freezes, and a single set of consecutive severe freezes over a period of 100 years. For simplicity, consecutive severe freezes were modeled as a single event occurring in one time step. The reduced freeze regime included 8 moderate and 8 severe freeze events. For both historical and reduced freeze regimes, the timing of freezes was randomized, and ten unique freeze time series were generated for each to evaluate the effects of both freeze intensity and timing on different developmental stages of the forest stand.

2.2.6. Predation

We used the ratio of crabs to propagules as a relative measure of crab density to test different predation intensities ranging from none (0:1), low (0.1:1), moderate (0.5:1), and high (1:1). Using a predator to prey ratio is recommended when evaluating the functional response of a predator, which occurs on short time scales of minutes or hours, and the effect of predation on prey population dynamics, which occurs over years (Arditi and Ginzburg, 1989; Berryman, 1992). Ratios were

Table. 2
Model parameters modified for the sensitivity analysis.

	Sensitivity analysis parameter sets ^a		DM(± 20%)	PM(± 20%)	FM(± 20%)	BC	WC
	MM(± 20%)	PP(± 20%)					
<i>Life-stage mortality</i>							
Propagule	X					-20%	+20%
Seedling (cot)	X					-20%	+20%
Seedling	X					-20%	+20%
Sapling	X					-20%	+20%
Young tree	X					-20%	+20%
Mid-age tree	X					-20%	+20%
Old tree	X					-20%	+20%
<i>Propagule production</i>							
Young tree		X				+20%	-20%
Mid-age tree		X				+20%	-20%
Old tree		X				+20%	-20%
<i>Density maxima</i>							
Seedling (cot)			X			+20%	-20%
Seedling			X			+20%	-20%
Sapling			X			+20%	-20%
Young tree			X			+20%	-20%
Mid-age tree			X			+20%	-20%
Old tree			X			+20%	-20%
<i>Predation mortality</i>							
Propagule				X		-20%	+20%
Seedling (cot)				X		-20%	+20%
<i>Mortality from freezes (for all freeze regimes)</i>							
Propagule					X	-20%	+20%
Seedling (cot)					X	-20%	+20%
Seedling					X	-20%	+20%
Sapling					X	-20%	+20%
Young tree					X	-20%	+20%
Mid-age tree					X	-20%	+20%
Old tree					X	-20%	+20%

^a MM: Miscellaneous mortality; PP: Propagule production; DM: Density maxima; PM: Predation mortality (increased and decreased predation coefficient by 20%); FM: Mortality from freeze intensities (moderate, severe, and set of consecutive severe); BC: Best case scenario; WC: Worst case scenario

calculated from field experiment results and previously collected field data. Propagule mortality probabilities from predation were calculated using a non-linear least squares regression of propagules consumed versus crab to propagule ratios:

$$p_s = 1 - \frac{1}{e^{ax}} \tag{2}$$

where p_s is the probability of propagule mortality from predation by *S. reticulatum*, a is the regression coefficient (predation rate), and x is the ratio of crabs to propagules. Predation intensity was held constant within each predation scenario. During previous field experiments (Langston et al. 2017a and unpublished data) we observed that seedlings with cotyledons were also vulnerable to predation, though less so than propagules. Accordingly, we also applied the predation equation to seedlings with cotyledons using a predation coefficient half that of the predation coefficient used for propagules (Fig. 3).

2.2.7. Propagule dispersal and production

Propagule density at each time step was calculated as:

$$x_p = p_d + p_y + p_m + p_o \tag{3}$$

where x_p is total propagule density, p_d is the density of propagules dispersing into the model domain, and p_y , p_m , and p_o are propagule densities produced by young, mid-age, and old trees within the model population (Fig. 3). Three scenarios of propagule dispersal density were applied, low (1 m^{-2}), medium (10 m^{-2}), and high (100 m^{-2}), and each was modeled at three dispersal frequencies: once (first time step only), low (10 dispersal events randomly occurring over 100 years), and high (annual dispersal). Low and medium dispersal densities at infrequent frequencies represented propagule delivery by tides and currents from non-adjacent mangrove forests. High dispersal density at infrequent frequencies reflected pulse events, such as storms, which might deliver high densities of propagules to a new location. High frequency, high

density scenarios represented tidal delivery from a neighboring forest in close proximity. Rates of propagule production were based on modeled rates and field measurements of *A. marina* (Clarke, 1995, Clarke, 1992) and varied by tree stage. Propagule production was modeled as a uniform random process during each time step, with old trees able to produce more propagules (≤ 5300) than mid-age trees (≤ 3000), which could produce more than young trees (≤ 100).

2.2.8. Model scenarios

Forest stand development depended on an initial dispersal density of propagules; densities of the other life stages developed over time from propagule dispersal events and propagule production within the population (Fig. 3). Scenarios varied by freeze regime (historical, reduced, no freezes), predation pressure (0, 0.1, 0.5, and 1 crab propagule⁻¹), dispersal frequency (0.01, 0.1, and 1 yr⁻¹), and dispersal density (1, 10, 100 propagules m⁻²) for a total of 108 scenarios (Fig. 3, Table 1). These scenarios represent a broad range of probable conditions in salt marshes along the Big Bend into which propagules could disperse. For each scenario, we developed 10 unique time series of freeze events, generated from a uniform random distribution, for the historical and reduced freeze regimes. For each freeze time series, we ran the model 1000 times, allowing dispersal timing and rates of propagule production to vary stochastically (also based on uniform distributions) according to the frequencies described above. This yielded a total of 1,080,000 simulations (108 scenarios * 10 freeze time series * 1000 dispersal and propagule production time series).

Results for each of the 108 scenarios were summarized using three population metrics: 1) mean probability of a regenerating stand developing (i.e., probability of tree density > 0); 2) mean peak tree density over time (young, mid-age, and old trees combined); and 3) mean number of years with a regenerating stand. This combination of metrics described the probability of a stand sustaining itself via

propagule production, maximum tree density reached over 100 years, and how long a regenerating stand persisted under each modeled scenario, respectively.

2.2.9. Sensitivity analysis

Finally, we conducted a sensitivity analysis (SA) to identify model sensitivity to the 25 parameters summarized in Table 1. Rather than testing the model one parameter at a time, we evaluated model sensitivity by grouping together parameters associated with specific population control processes, including: miscellaneous mortality (MM), propagule production (PP), density maxima (DM), predation mortality (PM), and mortality from freeze intensities (FM), as well as a “best” and “worst” case scenario across parameters (Table 2). For all parameter sets, relevant parameter values within each group were modified $\pm 20\%$ of original values, and all other parameters maintained their original values. The best and worst case parameter sets consisted of simultaneously changing all parameters by 20% to favor or hinder population development, respectively. This approach of “bundling” parameters allowed us to parsimoniously identify the population control processes that had the greatest influence on model results. Model sensitivity was assessed for each primary model output.

3. Results

3.1. Field experiment

Percent of propagules consumed during the field experiment differed between density treatments ($F_{2,15} = 228.2$, p -value < 0.001). As expected, all propagules in 1 m^{-2} plots were consumed, and more propagules in 25 m^{-2} plots were consumed than in 100 m^{-2} plots. Percent of viable propagules decreased over time more slowly at higher propagule densities (Fig. 4a). By day 23, more than half ($55\% \pm 3.7 \text{ SD}$) of propagules in 25 m^{-2} plots and a quarter ($25\% \pm 11.2 \text{ SD}$) of propagules in 100 m^{-2} plots were absent or partially depredated. As expected, the relationship between predation and propagule density was best described by a type II functional response ($r^2 = 0.96$; Fig 4b), However, a type III response, in which peak consumption occurs at an intermediate density, fit nearly as well ($r^2 = 0.95$). A type I response, in which there is no relationship between predation intensity and propagule density, was the poorest fit ($r^2 = 0.72$). Percent of propagules consumed increased rapidly with greater crab to propagule ratios (Fig. 4c); the coefficient from the regression equation that best fit the data was used as the predation coefficient, a , in Eq. 2 to quantify predation intensity in the population model (Table 1).

3.2. Model

We first present four selected model runs to illustrate the range of population responses to freezes, predation, and dispersal (Fig. 5). Each example highlights the mean ($\pm 1 \text{ SD}$) results for a single freeze time series driven by stochastic differences in dispersal timing and rates of propagule production across 1000 runs. Figure 5a shows results for a population subjected to a historical freeze regime, no predation, and an initial high-density (100 m^{-2}) dispersal event. The mean population reached a total density of 13.7 m^{-2} (including all life stages) and tree density (young, mid-age, and old) of 0.07 m^{-2} before being decimated by consecutive and individual severe freezes that occurred between years 25 and 30, from which the population did not recover (Fig. 5a). In contrast, a population subjected to a reduced freeze regime and mild predation intensity (0.1 crab:propagule) and supported by infrequent (0.1 y^{-1}), low-density (1 m^{-2}) dispersal events survived all severe freeze events and reached a mean total peak density of 11.2 m^{-2} (including a tree density of 0.05 m^{-2}) by year 100, though with considerable variance in propagule and seedling densities (Fig. 5b). Under a reduced freeze regime and moderate predation intensity (0.5 crab:propagule), a population receiving infrequent, medium-density (10

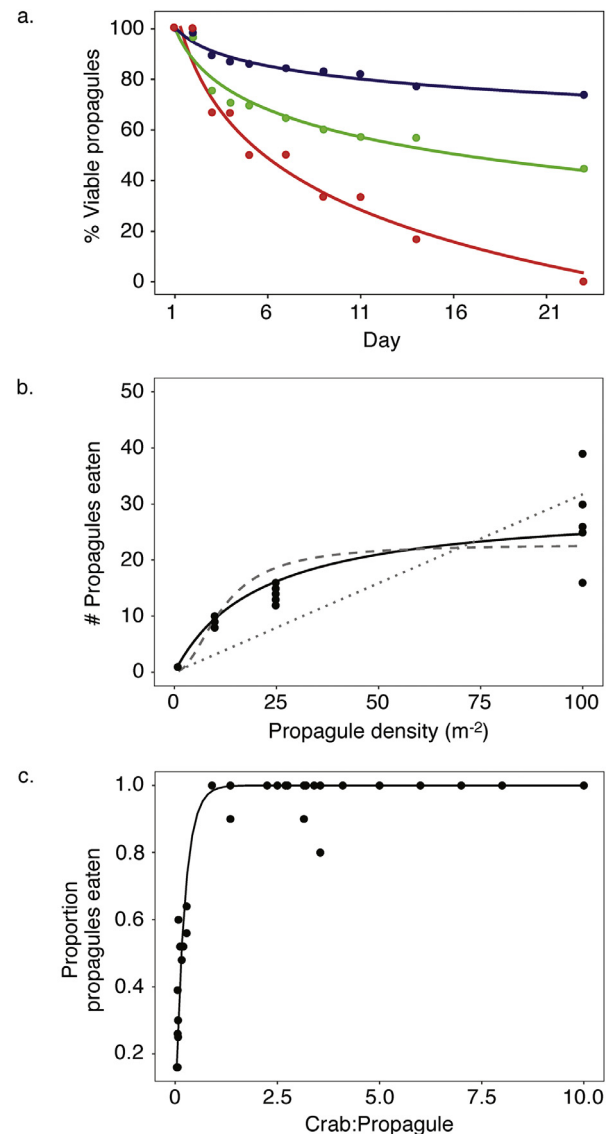


Fig. 4. Results from predation field experiment: a) change in the proportion of viable propagules over time for each density treatment (red: 1 m^{-2} ; green: 25 m^{-2} ; blue: 100 m^{-2}); b) functional response of *Sesarma reticulatum* to propagule density best fit a type II response (solid black line; $r^2 = 0.96$), compared to type I (gray dotted line; $r^2 = 0.72$) or type III (gray dashed line; $r^2 = 0.94$) responses; c) burrow density across propagule density treatments used to parameterize predation intensity (number of crabs per propagule).

m^{-2}) deliveries of propagules had a mean total density of 0.17 m^{-2} and was unable to develop into a regenerating stand (i.e. life-stages did not advance beyond sapling; Fig. 5c). Finally, a population subjected to high predation intensity (1 crab:propagule), no freezes, and annual, high-density (100 m^{-2}) dispersal events developed into a low-density, regenerating stand (peak total density of 1.63 m^{-2} ; tree density 0.05 m^{-2} ; Fig. 5d).

Among all 108 scenarios, 57 always supported the development of a regenerating forest stand (probability = 1), 11 sometimes did ($0 < \text{probability} < 1$), and 40 never did (probability = 0; Fig. 6a). For these scenarios in which regenerating forests always or sometimes developed, peak tree density (Fig. 6b) and mean number of years the stand supported regenerating trees (Fig. 6c) varied with respect to all three controls. Under a historical freeze regime (i.e., bottom three rows in all panels of Fig. 6), 22 out of 36 scenarios could support regenerating stands (Fig. 6a), with likelihoods ranging from very low to 100%. In these regenerating stands, mean peak tree density ranged from 0.008 to

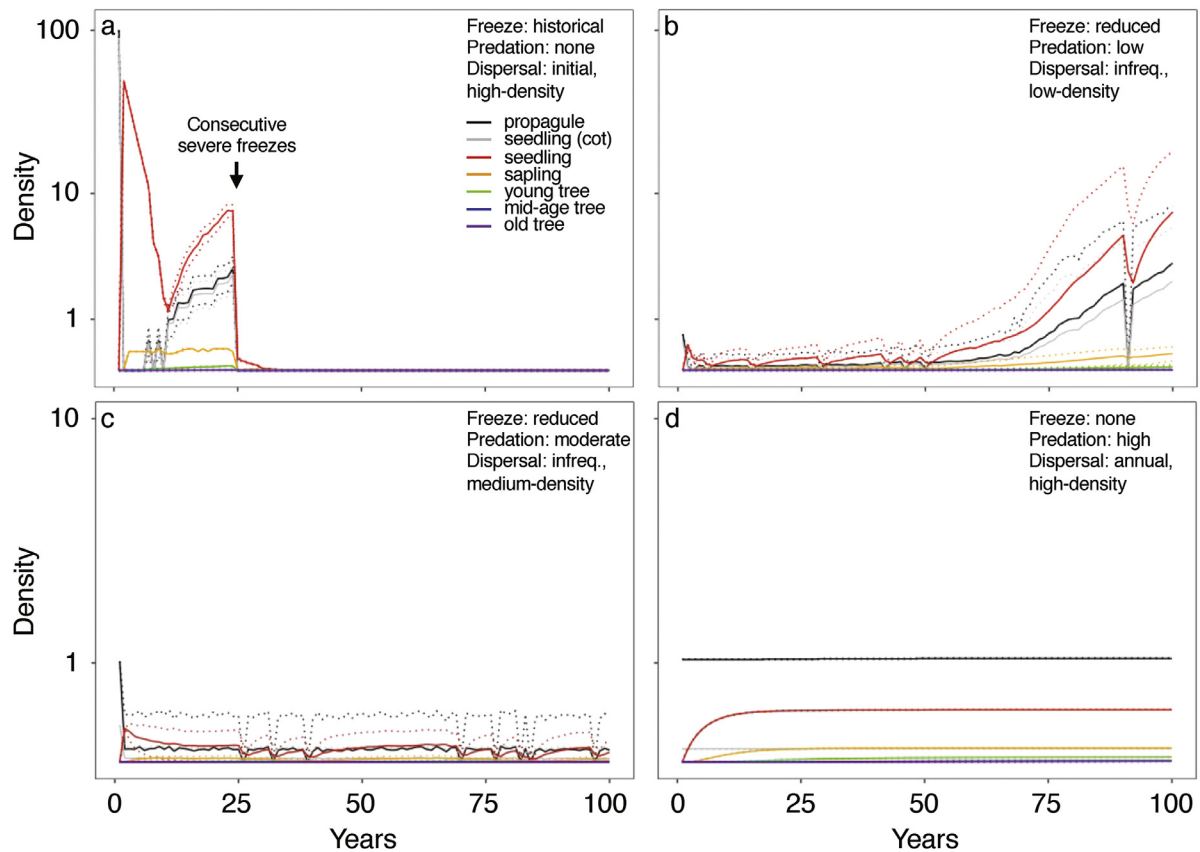


Fig. 5. Life stage densities (m^{-2} ; mean = solid lines; SD = dotted lines) of *Avicennia germinans* in four model scenarios: a) historical freeze regime (arrow marks timing of consecutive severe freezes), no predation, one high-density dispersal event; b) reduced freeze regime, low predation intensity, infrequent low-density dispersal; c) reduced freeze regime, moderate predation intensity, infrequent medium-density dispersal; and d) no freezes, high predation intensity, annual high-density dispersal. In each example, densities were generated from runs ($n = 1000$) across a single freeze time series; timing of dispersal events and rates of propagule production varied between runs. (Note the y-axis on c and d is inflated to better show life stage densities.)

0.059 m^{-2} and trees were present for 1 to 91.9 years (mean = 63.3) out of 100 simulated years (Fig. 6b, c). Stands did not develop under any predation intensity when dispersal was limited to a single low-density (1 m^{-2}) event. When predation intensity was moderate (0.5), at least infrequent dispersal events (0.1 y^{-1}) of medium density (10 m^{-2}) were required for a population to become a regenerating stand. Scenarios with a historical freeze regime and high predation intensity had the least favorable conditions of the 108 scenarios. Specifically, annual high-density (100 m^{-2}) dispersal events were required for a population to become a regenerating stand under this combination of biotic and abiotic constraints.

Under a reduced freeze regime (Fig. 6, middle three rows), regenerating stands developed under the same scenarios as under a historical freeze regime, but the probability of developing into a regenerating stand in scenarios with a single dispersal event or infrequent dispersal events was higher (Fig. 6a). Among regenerating stands, tree densities ranged from 0.01 to 0.076 m^{-2} and were present for 1 to 96 years (mean = 83.7; Fig. 6b, c). In scenarios with no freezes (Fig. 6, top three rows), regenerating stands developed in 24 out of 36 scenarios (Fig. 6a). Regenerating stands always developed when predation intensity was 0. These scenarios provided the most favorable conditions for mangrove population development. Without freezes or predation, tree densities ranged from 0.066 to 0.082 m^{-2} and were present for 84 to 96 years (mean = 93.7; Fig. 6b, c). Under mild predation intensity (0.1), regenerating stands did not develop when dispersal was limited to an initial low-density event. Under moderate predation intensity (0.5), a regenerating population developed from annual dispersal at all propagule densities. Tree density was lowest (0.01 m^{-2}) under moderate predation with annual, low-density dispersal events. In scenarios

of high predation intensity, the population required annual high-density dispersal events to support regenerating trees; it reached a peak density of 0.031 m^{-2} that was present for 84 of 100 simulation years.

Spatial interpretations of stand densities that developed under these modeled scenarios illustrate how canopy layers and areal coverage of life stage densities would appear in the field (Fig. 7). For example, a mangrove stand that developed within a 100-m^2 area under the most favorable conditions (i.e., top left cell in Fig. 6) would become a closed-canopy stand with all life stages occupying canopy layers by year 100 (Fig. 7a). For comparison, visualizations of mangrove stands from the scenarios presented in Fig. 5b-d are included in Fig. 7b-d. Because the model is not spatially explicit and does not include sizes or heights of life stages, the spatial interpretations in Fig. 7 are for illustrative purposes only.

Sensitivity analysis revealed that $\pm 20\%$ differences in parameter values affected model outcomes variably as a function of target model output, population control process, and specific model scenario. Changes in the distribution of scenarios always, sometimes, or never developing regenerating stands for SA parameter sets compared to the original parameter set were relatively small and aligned with expected directions of change (i.e., increased probabilities for parameter sets that decreased mortality and vice versa; Fig. 8a). Shifts in successful regeneration were smallest under reduced density maxima parameters (DM-20%), which showed no change, and largest for changes in predation mortality (PM) parameters, which yielded 7 additional scenarios with 100% probability and 4 additional scenarios with 0% probability for PM-20% and PM+20%, respectively. For the best case parameter set, there were 11 additional scenarios with 100% probability (an

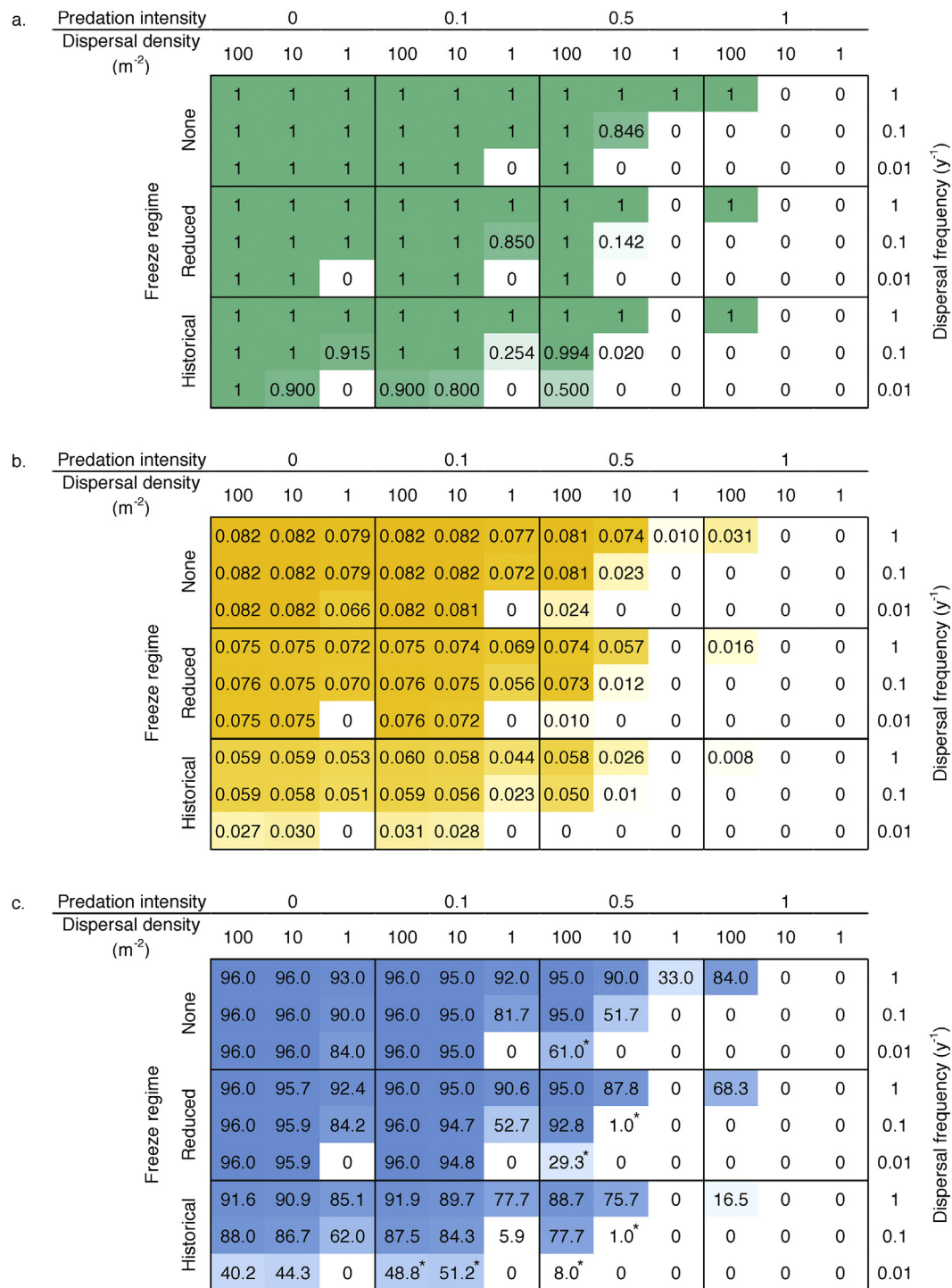


Fig. 6. Summary of model results for all 108 scenarios: a) mean probability of a regenerating stand developing; b) mean peak tree density (m⁻²); and c) mean number of simulation years with a regenerating stand (i.e., tree density > 0; * indicates stand was no longer regenerating in year 100). Color-coding corresponds with highest (darkest shade) to lowest (white) values across 108 scenarios.

increase of 19%), and the worst case parameter set had 9 additional scenarios with 0% probability (an increase of 22%).

Across all scenarios, mean peak tree density was most sensitive to density maxima parameters (increasing and decreasing by 18% under DM-20% and DM + 20%, respectively) and least sensitive to propagule production (PP) parameters (< 1% change; Fig. 8b). Best and worst case parameter sets caused a 53% increase and 34% decrease in peak tree density, respectively. The number of years a regenerating stand was present was most sensitive to predation mortality (PM) parameters

(increasing by 10% and decreasing by 8% under PM-20% and PM + 20%, respectively) but insensitive to both propagule production (PP) and density maxima (DM) parameters (< 1% change; Fig. 8c). Best and worst case parameter sets yielded a 25% increase and 16% decrease, respectively, in mean number of years with a regenerating stand. Variation in SA outcomes (illustrated by the error bars in Fig. 8b-c) was driven by scenario-specific responses to changes in parameters summarized in the Appendix. The greatest sensitivity was for scenarios that converted among always, sometimes, and never supporting

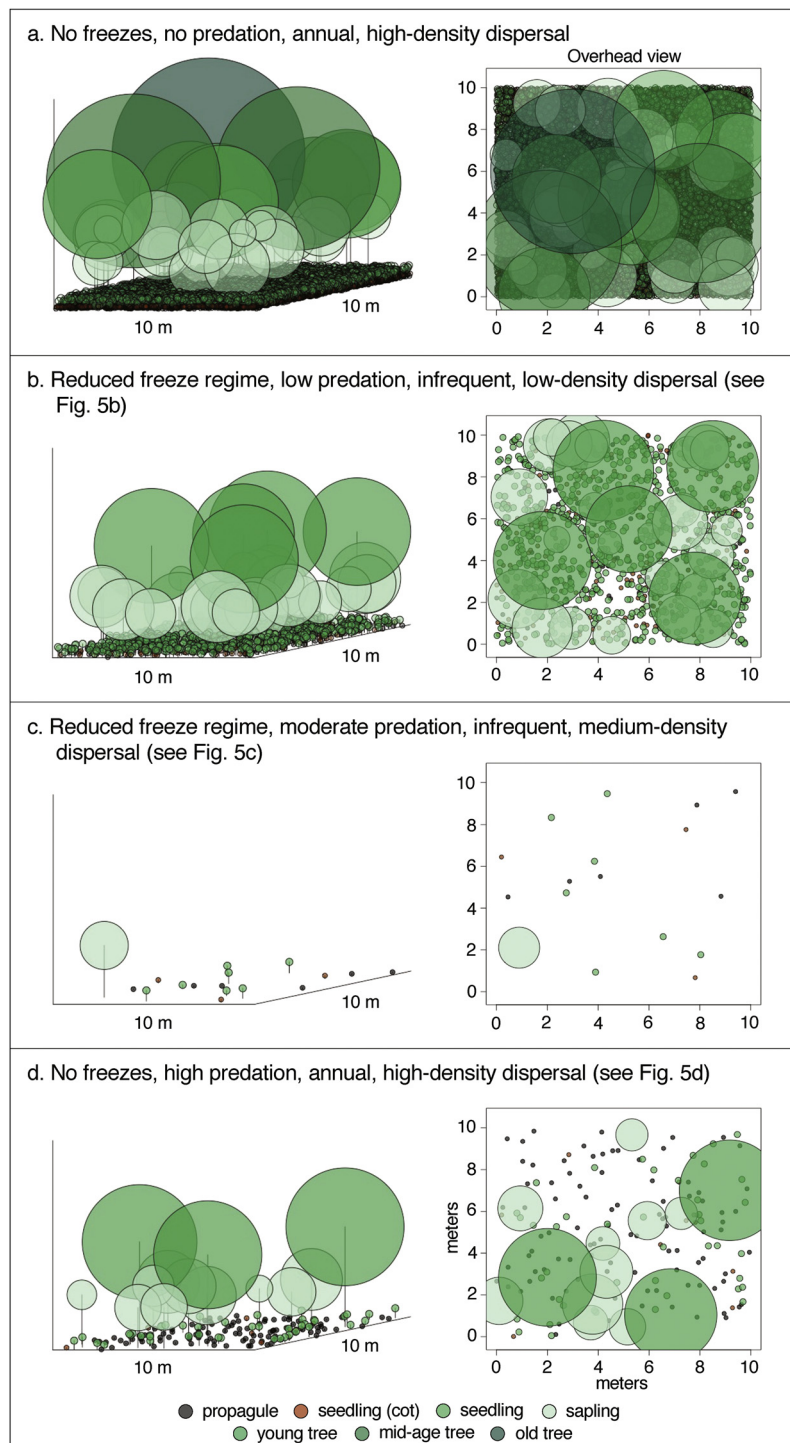


Fig. 7. Spatial interpretations of stand densities in year 100 under a) the most favorable scenario, and b-d) under scenarios presented in Fig. 5b-d. Spatial interpretations are based on life stage densities (m^{-2}) that were converted to individuals occupying a model domain representative of $100 m^2$. Individuals in each life stage are represented by points that reflect their relative size. Positions of individuals were randomized along x and y axes. In 3D panels on the left, positions along the z axis were assigned to approximate heights of life stage canopy layers.

regenerating populations, with subsequently large effects on peak tree density and years with a regenerating stand (Appendix).

4. Discussion

4.1. Biotic interactions – quantifying propagule predation

The relationship between predation and propagule density suggests

that extant densities of *S. reticulatum* in the Big Bend region can consume only a limited number of propagules from when they settle onto substrate to when they establish as seedlings (Fig. 4a). Typically, propagules either succumb to mortality or establish within 7 to 21 days once they are stranded on substrate (McKee, 1995; Osborne and Smith, 1990; Patterson et al., 1997). At a low propagule density ($1 m^{-2}$), *S. reticulatum* were able to consume all available propagules during the experiment (within 23 days), consistent with a previous

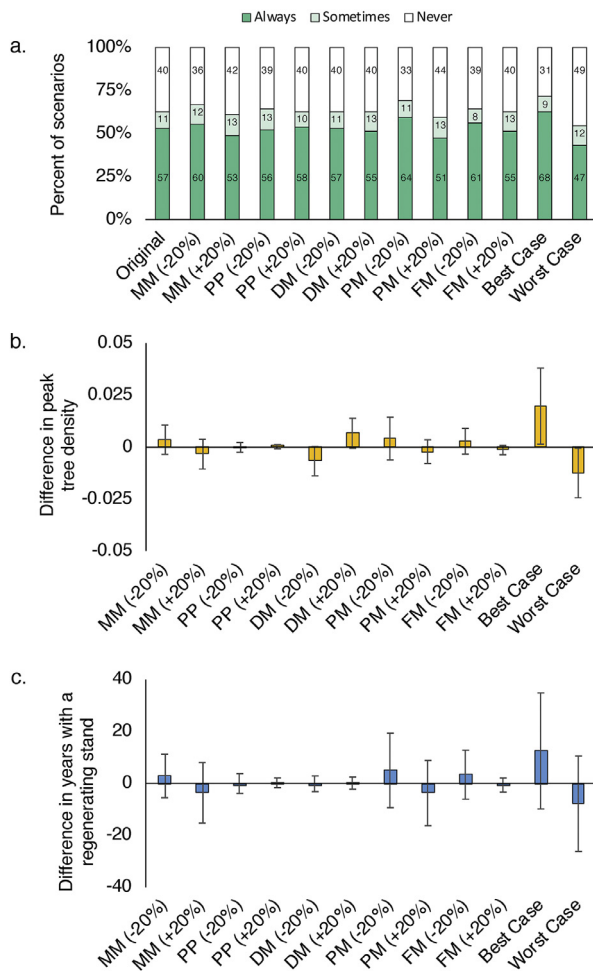


Fig. 8. Sensitivity analysis (SA) results, summarizing a) the probability of a regenerating stand occurring (as percent of scenarios), b) differences in mean peak tree density between SA parameter sets and the original model, and c) differences in mean number of years a regenerating stand was present between SA parameter sets and the original model. Error bars in (b) and (c) represent standard deviation of mean difference values averaged across all 108 model scenarios.

study in which *S. reticulatum* depredated 99% of propagules at a low density (10 m^{-2}) in 12 days in Big Bend salt marsh (Langston et al., 2017a). Assuming long-distance dispersal generally delivers *A. germinans* propagules in low densities (Clarke, 1993; Nathan et al., 2008; Nathan and Casagrandi, 2004), most propagules dispersing into salt marsh are likely to be depredated in most years where *S. reticulatum* or other predators exhibiting type II or type III responses are present. At higher propagule densities, *S. reticulatum* may either be satiated before all propagules are consumed, or not have enough time to consume all propagules before they establish (Fig. 4b; Holling 1959a, b).

Propagule survival and subsequent forest stand establishment thus likely depend on occasional high-density dispersal events by storms, or by tides and currents repeatedly delivering propagules to the same area of marsh within a season (Peterson and Bell, 2012; Van der Stocken et al., 2019). In this way, the ability of mangroves to produce high densities of propagules adapted for long-distance dispersal may offer similar evolutionary benefits as mast seeding. When high density dispersal events “synchronize” delivery of propagules from many individuals to an area populated by a predator, some propagules can escape predation, potentially initiating a new forest stand. Critically, in settings where even a single propagule survives to reproductive maturity (which can occur in as few as 5 years; Clarke 1995), subsequent propagule production supports both local stand expansion and the

potential for additional distal colonization.

4.2. Biotic-abiotic interactions – connecting freezes, predation, and dispersal

Our model results demonstrated that freezes, predation, and dispersal were important population controls, individually and collectively, on *A. germinans* stand development. Freezes (particularly single and consecutive severe freezes) were “pulse” disturbances that caused sporadic drops in overall population density (Fig. 5). Predation was a constant stressor on propagules and young seedlings in the model population, reducing their probability of recruiting to later life stages. When both freezes and predation acted on the model population, they exacerbated the individual stress of each control on stand development, including the probability of regeneration, tree density, and stand duration (Fig. 6). Dispersal events moderated freeze and predation intensities by delivering pulses of propagules that aided recovery from freezes and increased the density of propagules available for recruitment.

Historically, severe freeze events have caused intermittent mortality of *A. germinans* and suppressed propagule production along the Big Bend (Montague and Odum, 1997; Pickens and Hester, 2011; Stevens et al., 2006). The series of consecutive severe freezes in the 1980s caused 98% mortality to mangrove stands in Cedar Key, FL, and a recent single severe freeze in 2018 caused mangrove mortality across the southeastern US ranging from 4–75%, depending on local minimum freeze temperature (Montague and Odum, 1997; Osland et al., 2019). Our model results demonstrated that single and consecutive severe freezes that occurred under the historical freeze regime drastically reduced population density. The frequency of repeated severe freezes limited life stage development and recovering stand density. Without a large propagule supply or dispersal events following severe freezes, a stand could not establish, even without the added stress of predation (Fig. 6). Under a reduced freeze regime, the population was more likely to survive scenarios with more limited propagule supply and reach greater stand densities that were present for more years. Longer time periods between freeze events allows a population to develop stand complexity (i.e., support different life stages with varying degrees of resistance to freezes; Figs. 5, 7), increase stand density, and reach a regenerating stage, potentially boosting its resilience to future severe freezes (Osland et al., 2015).

Though a reduced freeze regime creates a favorable environment for *A. germinans* expansion on a regional scale, successful establishment of individual populations also depends on local conditions, including biotic interactions (Cavanaugh et al., 2018; He and Silliman, 2016). Predation was a strong biotic control on the model population; increased predation intensity greatly reduced the probabilities of stand regeneration across freeze regimes (Fig. 6). By reducing propagule and seedling supply, predation exacerbated the effects of freezes on the model population. Low-intensity predation slowed population recovery from severe freezes (indicated by decreased tree density and stand duration; Figs. 5, 6, 7), whereas high-intensity predation generally prevented population recovery from severe freezes. We expect predation intensity across Big Bend salt marshes to vary depending on local densities of propagule predators relative to propagule supply, which would in turn influence patterns and rates of mangrove expansion within the region. Salt marsh invertebrates such as *S. reticulatum* tend to have spatially and seasonally patchy distributions dictated by temperature, tidal cycle, soil, and local flora and fauna composition (Evin and Talley, 2002; Rader, 1984). The few reported propagule predation rates in the region range from low to high (Langston et al., 2017a; Patterson et al., 1997; Peterson and Bell, 2018). Hence, our parameters for predation by *S. reticulatum* were representative of predation by a generic predator or suite of predators exhibiting type II or type III responses across a density gradient; this approach can easily be modified for other specific salt marsh fauna via additional field studies.

Avicennia germinans relies on passive propagule dispersal to expand into new locations within its ecological niche (Higgins and Richardson, 1999; Nathan et al., 2008; Sousa et al., 2007; Van der Stocken et al., 2019; Van der Stocken and Menemenlis, 2017). Our model demonstrated that propagule dispersal was also critical in moderating climate and predation controls on a population establishing in a new location (Fig. 6). In other words, the model population's resilience to freezes and predation depended on propagule dispersal density and frequency. Our results show that populations of *A. germinans* supported by frequent, high-density dispersal events have the best chance of establishing in salt marsh under all freeze and predation scenarios, suggesting that mangrove expansion most often occurs via dispersal from neighboring regenerating stands. Single or infrequent, low-density dispersal events into Big Bend salt marshes (i.e., long-distance dispersal via tides and ocean currents) are less likely to initiate a regenerating stand, especially when subject to the combined effects of freezes and predation. However, even if low-density dispersal rarely creates new mangrove stands, it is still a viable means of population expansion. In fact, long-distance propagule dispersal has played a critical role in establishing global mangrove distributions (Lo et al., 2014; Nettel and Dodd, 2007). We found single or infrequent high-density propagule dispersal (i.e., dispersal via storm surge) would likely be sufficient to establish a new stand, depending on local predation pressure (Fig. 6). Storm surge has been recognized as a dispersal mechanism shaping spatial patterns of mangroves in south Florida (Jiang et al., 2014, 2012). Given that increased frequency and intensity of coastal storms is expected due to climate change, storm surge may become an increasingly important mechanism for *A. germinans* expansion, not only in terms of propagule delivery to new locations, but also in providing large densities of propagules that can withstand high rates of predation and develop into stands resilient to severe freeze events.

4.3. Model assumptions and sensitivity

The goal of this work was to create a relatively simple population model to better understand the individual and interactive effects of freezes, predation, and dispersal on *A. germinans* expansion in Big Bend salt marshes. To maintain model simplicity and focus on the interactive effects of freezes, predation, and dispersal, we assumed a salt marsh setting that otherwise met environmental, ecological, and physiological requirements for *A. germinans* survival. We excluded other stochastic climatic events like storms and droughts as causes of mortality; we referenced storms only as mechanisms for delivering high densities of propagules to the model domain. Since tropical storms are known to damage or destroy stands of mangroves in Florida and the Caribbean (Cahoon et al., 2003; Smith, et al., 1994; Smith et al., 2009) and are expected to increase in intensity and frequency due to climate change, excluding them as a source of mortality potentially overestimates modeled probabilities of *A. germinans* establishment. Droughts, as drivers of hypersaline conditions, are less likely to be a major source of mortality along the Big Bend, which is less vulnerable to changing rainfall regimes than freeze regimes resulting from climate change (Osland et al., 2016). We also did not explicitly model biotic interactions between mangroves and salt marsh plants. Instead, positive effects (e.g., propagule trapping) were implied in the probability of propagule recruitment, and negative effects (e.g., competition) were implied in miscellaneous mortality rates for propagules and seedlings (Guo et al., 2013; McKee et al., 2007; Peterson and Bell, 2012).

While relatively simple, our model still had 25 parameters (Table 1), with values derived from the literature and the field study presented here. Understanding model sensitivity to these parameters is important both for interpreting results and guiding future research into parameters associated with the greatest sensitivity (Cariboni et al., 2007). We found that different model outputs were more or less sensitive to parameter sets associated with different ecological processes. For example, the likelihood of developing a regenerating forest was most

sensitive to variation in parameters describing propagule predation (i.e., the two “predation coefficients” in Table 1), followed by parameters associated with miscellaneous mortality (seven parameters controlling mortality unrelated to crowding, freezing, or predation at each life stage; Fig. 8a). These results highlight the role of predation pressure as a primary filter for forest establishment (Langston et al., 2017a; Osborne and Smith, 1990; Smith et al., 1989) and are reflective of our empirically derived relationship between crab density and proportion of propagules consumed, which transitions very rapidly from 0 to 100% (Fig. 4c). Small changes in this parameter can drive large changes in proportional propagule consumption for a given crab density, suggesting that site-specific studies should be used to parameterize propagule predation. Sensitivity to miscellaneous mortality rates (even though they were relatively low) also motivates further study of how to incorporate this “lumped” parameter into models that consider mortality from multiple specific causes.

Peak tree densities were also sensitive to miscellaneous mortality but even more so to density maxima (six parameters controlling maximum density for each life stage, excluding propagules; Fig. 8b), and this outcome follows directly from the model structure, which limited densities at a fixed “ceiling”. While these density maxima parameters were selected from the literature, they were derived from a number of *Avicennia* species as well as *A. germinans* growing in different regions; better characterizing *A. germinans* forest structure in the southeastern US remains an important knowledge gap. For years that a regenerating forest was present, results were most sensitive to predation and miscellaneous mortalities, a combination of the likelihood that forests establish at all (i.e., predation mortality) and direct mortality across all life stages (miscellaneous mortality). In general, all model outputs were only moderately sensitive to variation in parameters describing freeze mortality, likely because freezes, while potentially catastrophic, are relatively rare compared to the potential for yearly mortality from all other causes. For all outputs, the model was insensitive to variation in parameters that controlled maximum propagule production, likely because stochastic variation from sampling a uniform distribution (bounded by 0 and a maximum propagule production value) “swamped” variation driven by relatively small increases or decreases in those maxima.

Finally, the parameter sensitivities reported here are likely conservatively large estimates since unique freeze, dispersal, and propagule production time series were randomly generated for all model runs (both original and SA parameter sets), which could inflate differences between the two sets of results. It is also important to note that Figure 8 summarizes SA results across all 108 scenarios, representing average differences between base and SA parameter sets for each individual scenario. For many scenarios that either always or never developed regenerating stands, model outputs were largely insensitive to input parameter variation, regardless of which ecological process they represented. This is evidenced in the many zero values in the Appendix. In contrast, for scenarios that *sometimes* developed a regenerating stand, as well as those that transitioned between always, sometimes, and never supporting reproduction, differences between original and SA parameter sets could be quite large (e.g., dark red and green entries in the Appendix). It is in these transitional scenarios, where freezes, predation, and dispersal patterns yield varying ecological outcomes that reducing parameter uncertainty is most critical.

4.4. Looking ahead

A reduced freeze regime appears to be underway along the Big Bend coast. The lack of consecutive severe freezes in the past 30 years and infrequent individual severe freezes are facilitating the poleward expansion of *A. germinans* in the region. Meanwhile, local conditions are dictating the establishment of new stands, as rates and patterns of *A. germinans* expansion into salt marsh depend on predation and propagule dispersal. Our findings highlight the importance of incorporating

the individual and collective effects of climate, biotic interactions, and dispersal into research on poleward mangrove expansion. We present this model as an easily parameterized tool that can be combined with future field studies and remote sensing efforts to predict spatially-explicit patterns of expansion along the Big Bend.

CRedit authorship contribution statement

Amy K. Langston: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Data curation, Writing - original draft. **David A. Kaplan:** Conceptualization, Methodology, Writing - review & editing, Supervision, Funding acquisition.

Declaration of Competing Interest

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

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.ecolmodel.2020.109245](https://doi.org/10.1016/j.ecolmodel.2020.109245).

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