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Key Points:

- Modeled barriers with shrubs tend to be narrower, migrate landward more slowly, and be more strongly skewed volumetrically toward the ocean
- Shrubs increase the likelihood of discontinuous barrier retreat and, under some conditions, increase barrier vulnerability to drowning
- Shrubs expand more slowly across barriers experiencing greater dune erosion and overwash disturbance (and vice versa)

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Exploring the Impacts of Shrub-Overwash Feedbacks in Coastal Barrier Systems With an Ecological-Morphological Model

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Abstract Shrubs are common – and presently expanding – across coastal barrier interiors (the land between the foredune system and back-barrier bay), and have the potential to influence barrier morphodynamics by obstructing cross-shore overwash flow. The ecological and geomorphological consequences of ecomorphodynamic couplings of the barrier interior, however, remain largely unexplored. In this contribution, we add an ecological module of shrub expansion and mortality to a spatially-explicit exploratory model of barrier evolution (Barrier3D) to explore the effects of shrub-barrier feedbacks. In our model simulations, we find that the presence of shrubs significantly alters barrier morphology and behavior. Over timescales of decades to centuries, barriers with shrubs (relative to those without) tend to be narrower, migrate landward more slowly, and have a greater proportion of subaerial volume distributed toward the ocean-side of the barrier. Shrubs also tend to increase the likelihood of discontinuous barrier retreat, a behavior in which a barrier oscillates between periods of transgression and relative immobility, because shrubs induce prolonged periods of barrier immobility by obstructing overwash flow. However, shrubs can increase barrier vulnerability to drowning by preventing periods of transgression needed to maintain barrier elevation relative to rising sea levels. Additionally, physical barrier processes influence shrub expansion in our simulations; we find that greater dune erosion and overwash disturbance tends to slow the rate of shrub expansion across the barrier interior. Complementing recent observational studies of barrier islands in Virginia, USA, our results suggest that interior ecology can be a key component of barrier evolution on annual to centurial timescales.

Plain Language Summary Shrubs are common on coastal barriers, typically found sheltered behind dunes. During large storms, sand from the beach is washed into the barrier interior and beyond in a process called overwash. Overwash tends to cause the barrier to gain elevation relative to sea level, and also move the whole barrier landward. Shrubs, however, can obstruct this flow across a barrier. Here we explore how shrubs blocking overwash can impact barrier change, and how barrier change affects the growth of shrubs. We do this by adding new code to represent shrubs to an existing computer model of barrier evolution. Results from the computer model suggest that barriers with shrubs are typically narrower and tend to move landward more slowly compared to barriers without shrubs. Additionally, barriers with shrubs are more likely to move landward in a stop-and-go manner, switching between periods of fast landward motion and no motion. Therefore, barriers with shrubs are less likely to smoothly and continuously move landward. We also find that shrubs expand more slowly across barriers when storms cause significant dune erosion and overwash disturbance. Our work suggests that including shrubs in barrier models helps us better understand the ecological and geomorphological change of barrier systems.

1. Introduction

Ecological and geomorphological processes in coastal barrier systems are tightly coupled (e.g., Durán & Moore, 2013; Godfrey, 1977; Godfrey et al., 1979; Goldstein et al., 2017; Hesp, 2002; Keijsers et al., 2016; Rastetter, 1991; Reeves et al., 2020; Roman & Nordstrom, 1988; Stallins & Parker, 2003; Walters et al., 2014; Zinnert et al., 2017, 2019), owing to the similar spatiotemporal scales over which they operate. Barrier islands and spits comprise 10% of the world's continental coastline (Stutz & Pilkey, 2011), support rich ecosystems, buffer the impacts of storms on coastal regions, and are culturally and economically valuable hosts of human habitation and infrastructure. The future of barrier systems, however, remains uncertain with projected accelerated

relative sea-level rise (RSLR) (Sweet et al., 2017) and changes in storminess, such as increased storm intensity (e.g., Knutson et al., 2020). This uncertainty is further complicated by ecological transformations resulting from global climate change, which have become increasingly apparent in barrier systems in recent decades (Goldstein et al., 2018; Lucas & Carter, 2010; Osland et al., 2016; Zinnert et al., 2016).

Over centurial to millennial timescales, barriers tend to maintain their elevation relative to rising sea level by migrating upward and landward. On shorter timescales, some barriers can also experience intermittent periods of progradation and aggradation (e.g., Ciarletta et al., 2019; van IJzendoorn et al., 2021). Landward barrier migration is facilitated primarily by the process of overwash, whereby sediment eroded from the shoreface and beach is transported landward of the dune crest during high-water events (e.g., Dolan & Godfrey, 1973; Donnelly et al., 2006). As overwash flows landward over the interior of a barrier, flow velocity slows from lateral dispersal, percolation, and frictional drag (e.g., Schwartz, 1982), causing sediment to deposit on and potentially behind the barrier and therefore allowing the barrier to aggrade and translate up slope. Foredune height plays a central role in regulating the volume of overwash flux into the barrier interior (Houser et al., 2018; Rogers et al., 2015; Sallenger, 2000), such that barriers tend to transgress when dunes are low but are relatively stationary when dunes are tall (e.g., Reeves et al., 2021). Over decades to centuries, repeated cycles of dune loss and regrowth can lead to discontinuous barrier retreat (Reeves et al., 2021), a behavior in which barriers oscillate between periods of relative immobility and landward migration. This is in contrast to continuous transgression, the behavior in which barriers consistently retreat over time. Barriers can drown if overwash fluxes are insufficient for maintaining barrier geometry or elevation relative to sea level (e.g., Lorenzo-Trueba & Ashton, 2014; Mellett & Plater, 2018; Moore et al., 2010; Passeri et al., 2020).

An understanding of how overwash processes operate within the interior of a barrier – the land between the foredune and back-barrier marsh or bay – is critical for understanding barrier response to climate change (Zinnert et al., 2016, 2017, 2019). Most observational and modeling studies of barrier evolution typically neglect or average-over interior processes and heterogeneities, despite the fact that the barrier interior often covers a large proportion of total barrier area and can be important in its ecogeomorphic connection to the sandy barrier front (Zinnert et al., 2019). In recent years, studies of interior barrier dynamics in coupled human-natural systems have gained traction (e.g., Lazarus et al., 2021; Magliocca et al., 2011; Rogers et al., 2015), but interior ecology as a control on barrier processes remains understudied. Passeri et al. (2018) add landcover classification to hindcast simulations of barrier response to hurricane events, and find that these additions improve the accuracy of their model in capturing observed morphologic change. However, this approach uses static landcover without dynamic, two-way feedbacks between the ecology and geomorphology, and operates over timescales insufficient for exploring long-term barrier behaviors.

Previous studies on bidirectional ecogeomorphic feedbacks have primarily focused on vegetated dunes (e.g., Biel et al., 2019; Hacker et al., 2019), marshes (e.g., Kirwan & Murray, 2007; Morris et al., 2002), and seagrass communities (e.g., Carr et al., 2018; Reeves et al., 2020), but barriers can also host late successional terrestrial communities such as shrublands and maritime forest that can potentially influence barrier morphodynamics. Shrubs in particular are likely to impact overwash processes because of their tall height, rigidity, and high biomass density near the sediment bed, and are therefore the focus of this work. Earlier studies have qualitatively recognized the ability of woody vegetation to limit overwash penetration during storms (Claudino-Sales et al., 2008; Morton & Sallenger, 2003; Wang & Horwitz, 2007; Williams, 2015; Zinnert et al., 2019). By slowing or preventing overwash flow across a barrier, shrubs may support barrier resistance to storms and perhaps build topographic relief (Zinnert et al., 2017). On the other hand, a reduction in sediment connectivity between the front (shoreface, beach) and back (interior, back-barrier bay) of a barrier in the presence of shrubs could theoretically limit its ability to aggrade and transgress in response to RSLR and future storms (i.e., reduce its resilience). The long-term (decadal to centurial) consequences of these interactions for barrier behavior and evolution have yet to be explored.

Understanding the spatial extent of shrubs on barriers is key to understanding how shrubs impact barrier morphodynamics (Zinnert et al., 2017). Shrub seed dispersal in barrier systems is primarily avian-based (Ehrenfeld, 1990; Shiflett & Young, 2010), and long-distance dispersal (i.e., >100 m from the invasion front) is common (Herrmann et al., 2016; Woods et al., 2019). Given the steep environmental gradients observed in barrier systems (Ehrenfeld, 1990; Enwright et al., 2019; Young et al., 2011) and the particular sensitivity of most shrubs to salinity, freshwater availability, and disturbance events, shrub expansion is strongly influenced by abiotic post-dispersal
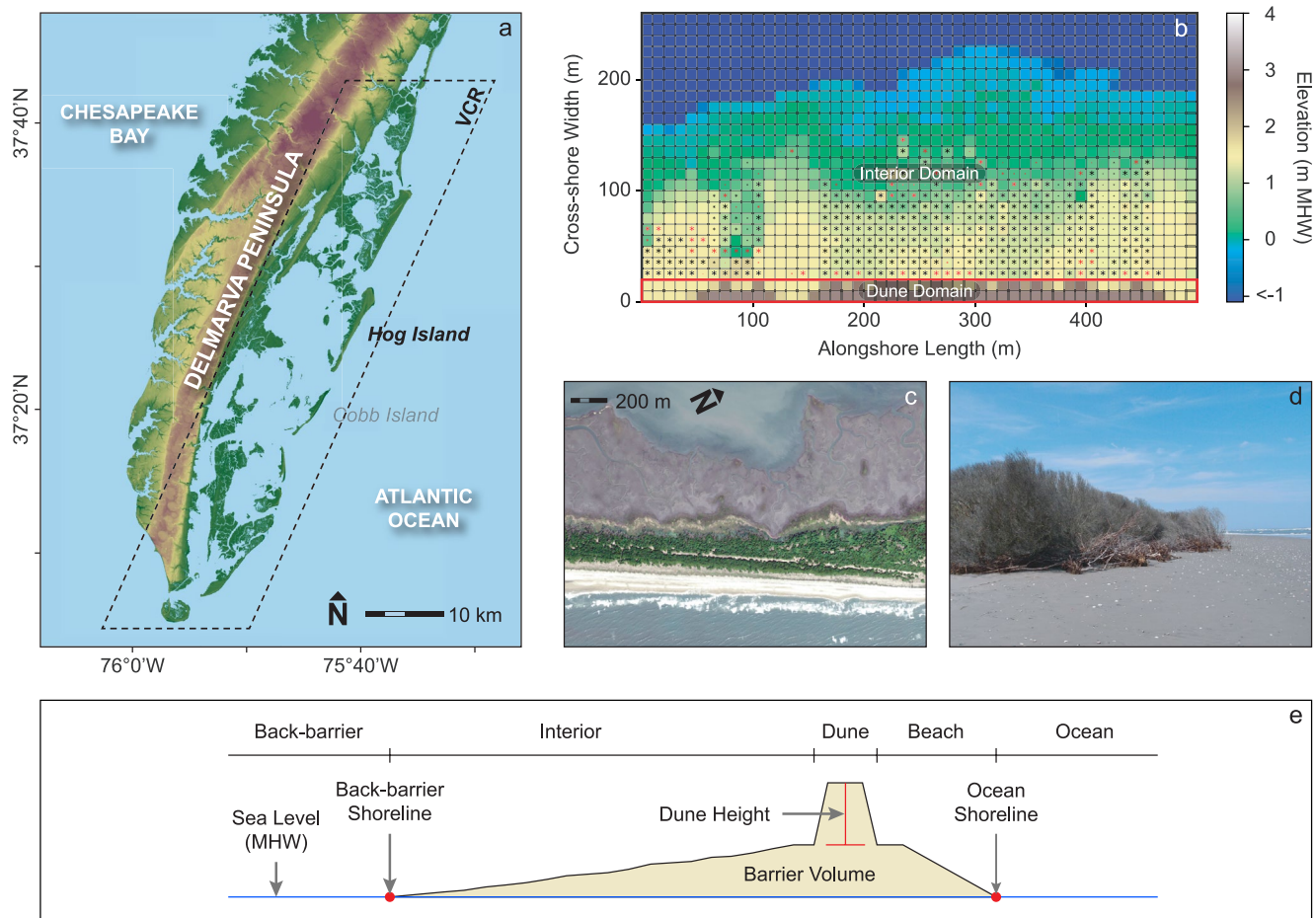
Figure 1. Model domain and parameterization. (a) Map of Hog Island in the Virginia Coast Reserve (VCR), US Mid-Atlantic coast. (b) Example Barrier3D elevation grid, with model domains labeled; each black (red) star represents a single living (dead) shrub plant. MHW is mean high water. (c) Aerial imagery from 2016 of shrub cover on central Hog Island. (d) Dead shrubs on the ocean side of Cobb Island. (e) Schematic barrier cross-section illustrating important variables and metrics discussed in this paper.

processes and filtering (Woods et al., 2019). Foredune elevation is a key environmental filter for shrub expansion in barrier systems (Woods et al., 2019), as tall dunes offer protection from salt-spray and overwash (Miller et al., 2008). In the absence of adequate foredune protection, shrubs can also establish if sufficiently far from the ocean shoreline (Miller et al., 2008). Barrier topography is likewise an important control on shrub expansion, as shrubs are typically constrained to a narrow elevation range (Young et al., 2011) that balances the needs of proximity to the freshwater lens with limited exposure to salt-water flooding. While woody encroachment is often related to changes in subaerial barrier area and elevation (relative to sea level; Shao et al., 1998), such as those that occur via shoreline erosion or RSLR, shrubs can temporarily expand even on barriers that are losing subaerial land (Young et al., 2007; Zinnert et al., 2016).

Shrub cover worldwide has expanded across coastal (Battaglia et al., 2007; Huang et al., 2020; Lucas & Carter, 2010), terrestrial grassland (Van Auken, 2000; D'Odorico et al., 2012), desert (Peters et al., 2006), savannah (Stevens et al., 2017), and tundra ecosystems (Shaver et al., 2001; Tape et al., 2006) in recent decades. On the barrier islands of the Virginia Coast Reserve (VCR; Figure 1a), over 40% of land cover changed from grassland to woody shrub thicket between 1984 and 2011 (Zinnert et al., 2016). During this time period, shrub cover on Hog Island, a VCR barrier island, expanded parallel to the ocean shoreline at rates of up to 300 m yr^{-1} (Woods et al., 2019). This ecological transformation is primarily a response to macroclimate warming and is enhanced by positive feedbacks related to shrubs modifying their own microclimate (D'Odorico et al., 2012; Huang et al., 2018; Wood et al., 2020). The accelerated expansion of shrubs in coastal systems in response to global warming suggests that shrubs could play an increasingly dominant role in overwash processes going forward.

The ability of shrubs to obstruct the landward flow of overwash suggests that interior ecology can play an important role in barrier evolution, while the existence of a threshold dune elevation for shrub growth suggests that shrub ecology is strongly dependent on barrier morphodynamics. The effects of these ecological-morphological couplings on barrier and shrub evolution remain unexplored over long (10^1–10^3 yr) timescales. Here we add an ecological module of shrub expansion and mortality to an existing spatially-explicit exploratory model of barrier evolution (Barrier3D; Reeves et al., 2021). Barrier3D tackles the scale separation between event-based and long-term models by explicitly yet efficiently simulating dune evolution, storm overwash, and a dynamically evolving shoreface in response to individual storm events and RSLR. As an important novelty of this work, the ecology and geomorphology in our model framework are bidirectionally coupled, dynamically evolving in response to each other and external forcing conditions. We use this coupled model first to examine how shrubs alter barrier morphology over time and impact the rate and style of barrier migration. Then, we explore the ways in which barrier dynamics influence the rates and patterns of shrub expansion under a range of anticipated future conditions. Rather than numerically predict the evolution of a particular location or setting, the goal of this work is to explore and explain the large-scale, decadal-centurial behaviors that arise from feedbacks between barrier ecology and geomorphology.

2. Model Development

Barrier3D (Reeves, 2021) is an exploratory model (Murray, 2003, 2013) that simulates the morphological evolution of a barrier segment over time scales of years to centuries, resolving spatially explicit cross-shore and alongshore topographic evolution. In the sections below, we provide a brief summary of Barrier3D followed by an introduction to the new shrub expansion and mortality module. Reeves et al. (2021) provide a complete description of the base model formulation.

2.1. Parameterization

By examining across wide ranges of key input values beyond what is observed in any one location, and given the simplistic nature of the model parameterizations, our experiments are designed to investigate coupled dynamics relevant to most barrier systems. To ground the model in reality and provide a common starting point for all simulations, we parameterize Barrier3D and the shrub module using data from Hog Island, located on the Eastern Shore of Virginia, USA (Figure 1a). Hog Island is part of the Virginia Coast Reserve (VCR), a Long-Term Ecological Research site owned by the Nature Conservancy. Since the mid-twentieth century, direct human impact on the barriers, marshes, and bays of the VCR has been minimal (Orth & McGlathery, 2012). Hog Island is a 12 km long, mixed-energy barrier island characterized by high relief relative to other VCR islands, with dune ridges typically 3–4 m above the NAVD 88 datum (Oster & Moore, 2009); consequently, it has been relatively stable and infrequently disturbed in recent decades (Wolner et al., 2013). The dominant shrub species in the VCR is *Morella cerifera* L. (Myricaceae), which can be found in coastal environments along the Gulf of Mexico and the US Atlantic from Florida to New Jersey. *M. cerifera* is an evergreen shrub that can grow to heights of 5–6 m in barrier environments and coalesce into monospecific thickets (Young et al., 1994). The shrub module is therefore parameterized specifically for *M. cerifera*, and we discuss the potential impacts of using different species in Section 5.1 below. The rate of RSLR in the VCR, calculated over the past four decades, is 5.5 mm yr^{-1} (NOAA, 2021). Table 1 lists all variable and input parameter definitions, values, and sources referenced in the main text; for all other input parameter values used in our simulations from the Barrier3D base model, see Table S1 in Supporting Information S1.

2.2. Barrier3D

Barrier3D operates over a 10-by-10 m grid with a 1-year time step. While model parameters are updated once a year, a probabilistically determined number of storm events occur within each year. The barrier segment consists of one or more alongshore rows of dune cells at the front (ocean side) of the grid, backed by an interior domain with a predetermined constant alongshore length and dynamically changing cross-shore width (Figure 1b); dune and interior cells follow different sets of rules as described below. Due to complexities in modeling beach morphodynamics and to focus on dune and interior dynamics, Barrier3D does not explicitly model a beach,

Table 1
Model Parameters and Variables

Parameter/ Variable	Definition	Units	Value	Source
New parameters introduced in shrub model				
ϕ	Shrub percent cover		Dynamic variable	N/A
Λ	Proportion of overwash flow reduction through a shrub cell at full shrub cover		0.15	This work
BurialLimit	Threshold proportion of shrub height that shrubs can be buried, beyond which shrubs are killed		0.75	Keller (2020)
Disp_mu	Mean of lognormal distribution of seed dispersal distance		−0.721891	Woods et al. (2019)
Disp_sigma	Standard deviation of lognormal distribution of seed dispersal distance		1.5	Woods et al. (2019)
D_{shrub}	Threshold elevation of fronting dune needed for shrub establishment	m MHW	2.29	Woods et al. (2019)
Female	Proportion of shrubs that are female		0.5	Hokkanen (2013)
GermRate	Proportion of shrubs that successfully germinate		0.6	Young et al. (1994)
H_s	Shrub height	m	Dynamic variable	N/A
H_{s_max}	Maximum shrub height	m	5.3	Young et al. (1994)
Q_{i_eff}	Effective discharge through cell impacted by shrub	m³ hr⁻¹	Dynamic variable	N/A
SalineLimit	Threshold discharge through a shrub cell beyond which immature (<1 year) shrubs are killed	m³ hr⁻¹	5	Tolliver et al. (1997)
Seedmin	Minimum seeds produced per year per shrub	count	1000	Kwit et al. (2004)
Seedmax	Maximum seeds produced per year per shrub	count	10000	Kwit et al. (2004)
SprayDist	Distance from ocean shoreline that shrubs can establish in absence of sufficient dune	m	170	Miller et al. (2008)
T_{fruit}	Age at which female shrubs start producing seeds	years	5	Zinnert (pers. comm.)
UprootLimit	Threshold depth that shrubs can be buried, beyond which shrubs are eroded	m	−0.2	Conn and Day (1993)
Z_{shrub_min}	Minimum surface elevation for shrubs	m MHW	0.74	This work
Z_{shrub_max}	Maximum surface elevation for shrubs	m MHW	1.84	This work
Parameters from Barrier3D base model formulation referenced in main text				
MHW	Mean high water	m NAVD88	0.46	
Q_i	Overwash discharge received by landward neighbor cell i	m³ hr⁻¹	Dynamic variable	
$\bar{r}$	Characteristic dune growth rate: average of r_{min} and r_{max}	yr⁻¹	0.30–0.90	
R_{high}	Highest elevation of the landward margin of runup (i.e., total water level)	m MHW	Dynamic variable	
R_{low}	Lowest elevation of the landward margin of runup	m MHW	Dynamic variable	
r_{max}	Maximum dune growth rate	yr⁻¹	0.55–1.15	
r_{min}	Minimum dune growth rate	yr⁻¹	0.05–0.65	
RSLR	Relative sea-level rise	mm yr⁻¹	3–15	

instead assuming invariant beach width and slope at the ocean side of the dune cells (see Section 5.1 for a discussion on the limitations of this assumption).

Dune crest elevation is taken as the sum of the dune toe elevation, which remains fixed over time relative to sea level, and the height of the dune above its toe. Within each model time step, dune cells grow logistically toward a maximum dune height (Houser et al., 2015), with the shape of the logistic curve controlled by r, the intrinsic dune growth rate. Dune growth rates vary randomly alongshore from cell to cell between an r_{min} and r_{max}, with the characteristic dune growth rate ($\bar{r}$) for the barrier segment calculated as the mean of r_{min} and r_{max}. When varying r_{min} and r_{max}, we hold the range between the two values constant at 0.5 yr⁻¹ (Houser et al., 2015). RSLR

is treated using a Lagrangian frame of reference by reducing all elevations relative to a sea level fixed at zero. Because RSLR lowers dune elevations, dune cells effectively at their maximum dune height continue to grow vertically each year and maintain their elevation relative to sea level. Next, a probabilistically determined number of storms occur by random selection from a list of 10,000 synthetic storms, each described by three statistics: (a) Duration; (b) R_{high}, the highest elevation of the landward margin of runup (i.e., the total water level); and (c) R_{low}, the lowest runup elevation. Where water levels overtop the dune crest during storms, dune heights are reduced following an empirical predictor of dune erosion (Goldstein & Moore, 2016; Long et al., 2014) in which higher storm water levels tend to cause greater vertical dune erosion, and overwash flow is routed cell-by-cell over the interior of the barrier, carrying sediment with it (Murray & Paola, 1994, 1997). Finally, shoreline erosion or accretion results from a combination of: (a) RSLR; (b) the cumulative volume of sediment removed from the upper shoreface by overwash and dune growth; and (c) net sediment exchange between the upper and lower shoreface (Lorenzo-Trueba & Ashton, 2014). Shoreface sediment flux depends on the shoreface slope, which tends to dynamically adjust toward an equilibrium in response to perturbations (i.e., overwash and dune growth). When the ocean shoreline erodes landward one cell width, the front row of the dune field is removed and the first row of the barrier interior functionally becomes the back row of the active dune field.

For the experiments presented herein, the initial morphology of the barrier interior comes from a digital elevation model (DEM) of Hog Island (NOAA, 2017) discretized into 10-by-10 m cells. Dune height and dune toe elevations are based on values extracted from the Hog Island DEM, and wave hindcast data offshore Hog Island (USACE Wave Information Studies) and water elevations from the nearest tide gauge in Wachapreague, VA, are run through a copula-based multivariate sea storm model (Wahl et al., 2016) to produce the synthetic storms.

2.3. Shrub Module

In the new shrub module of Barrier 3D, shrub plants occupy cells within the barrier interior, grow in size with age, and disperse seeds, allowing shrubs to expand. Various physical processes and factors influence shrub expansion and can lead to mortality. Conversely, shrubs impact physical processes by reducing overwash flow through cells that are occupied by shrubs. In the following, we describe in detail the parameterizations governing shrub dynamics in the model.

2.3.1. Growth

Established shrubs grow at the beginning of each year, represented by annual increases in percent cover and height – until maximum values are reached. Following observations on Hog Island (Young, unpublished observations) shrub percent cover (ϕ) increases logarithmically, reaching full cover after 9 years of growth. Assuming an allometric relationship between shrub width and height, shrub height (H_s) is taken as a function of percent cover: $H_s = \phi H_{s\_max}$, where H_{s_max} is the maximum shrub height when shrub cover is full. We set H_{s_max} to 5.3 m following the empirical observations of shrub heights on Hog Island from Young et al. (1994).

2.3.2. Seed Dispersal and Establishment

Shrubs expand across the interior domain via seed dispersal at the beginning of each modeled year. Shrubs must be female and greater than or equal to 5 years in age (J. Zinnert, personal communication, 2017) to produce seeds. Of the shrubs that meet these requirements, the fecundity (seeds yr^{-1}) of each plant is determined by random selection from a uniform distribution; we set the bounds for seed fecundity (1,000–10,000) following the empirical measurements of Kwit et al. (2004). Following Hokkanen (2013), each seed has equal probability of being female or male. The number of seeds dispersed is further constrained by a germination rate (60%; Young et al., 1994), which removes seeds that fail to germinate. For each successfully germinating seed, the drop location is determined by the dispersal distance, randomly sampled from a lognormal probability distribution (Woods et al., 2019), and the direction, chosen randomly between 1 and 360°.

Seed establishment is dependent on the local environmental conditions. A seed becomes a new shrub in its determined drop location if the receiving cell is (a) within the interior domain of the barrier; (b) unoccupied by a previously established plant; (c) fronted by a dune cell exceeding an empirical threshold height (approximately 2.75 m on Hog Island; Woods et al., 2019) or, alternatively, is greater than 170 m landward of the shoreline (Miller et al., 2008); and (d) within an empirical elevation range. Because Barrier3D does not model a beach, we divide the static dune toe elevation by the beach slope and round to the nearest decameter to use as a static beach width;

this beach width in our simulations is 40 m, and therefore shrubs can establish in the absence of sufficient dunes if greater than or equal to 130 m from the foredune crest location. To establish the empirical elevation range, we use remotely-sensed land-cover-classification polygons of shrubs on Hog Island from Zinnert et al. (2016) to extract a histogram of land surface elevations from the 2017 DEM, then take the 5th and 95th percentiles as our minimum and maximum elevations for shrubs, respectively.

2.3.3. Mortality

Shrubs in the model are subjected to disturbances and stressors related to a dynamically evolving physical environment, which can lead to mortality. Each cause of mortality in the model is described below. Once dead, a shrub remains temporarily in place and can continue to influence overwash flow routing (as explained in Section 2.3.4), but can no longer grow or disperse seeds. Shrub mortality via natural senescence is not explicitly included in the model, under the assumption that gaps in shrub cover that arise from natural senescence are rapidly recolonized (Crawford & Yaoung, 1998). Shrub mortality therefore relies solely on physical conditions and stressors described below.

2.3.3.1. Elevation Change

Shrub mortality occurs if the surface elevation, relative to mean high water (MHW), of a cell containing a living shrub falls outside the established elevation range (e.g., via RSLR). Additionally, if a dead shrub plant falls below MHW, the plant is removed entirely from the model domain.

2.3.3.2. Burial

To represent the effects of burial (e.g., via overwash deposition), a shrub is killed if deposition in the cell since the time of initial shrub establishment exceeds 75% of the plant's height (Keller, 2020); a shrub plant, dead or alive, is removed from the interior domain completely if buried past 100% of its height.

2.3.3.3. Uprooting

To represent the effects of uprooting (e.g., via overwash scouring), a shrub is removed from the barrier interior if erosion in the cell since the time of initial establishment exceeds a threshold depth. We set this threshold to 0.2 m, as a majority of *M. cerifera* root biomass on Hog Island is found in the top 0.2 m of soil (Conn & Day, 1993).

2.3.3.4. Saline Flooding

To account for the effects of short-duration saline flooding (i.e., overwash events) on immature shrubs (Tolliver et al., 1997), the model kills all one-year-old plants through which discharge greater than 5 m^3 hr^{-1} is routed.

2.3.3.5. Shoreline Erosion

During barrier migration, when the front row of the interior domain becomes the back row of the dune field, all shrub plants dead and alive are removed from the interior domain to represent the impacts of shoreline erosion.

2.3.4. Interaction With Overwash

Shrubs in the model obstruct the flow of overwash across the barrier. The discharge of water leaving a cell with a living shrub plant is reduced according to the maximum flow reduction coefficient (Λ) and the plant's percent cover:

$$Q_{i\_eff} = Q_i(1 - \Lambda)\phi$$

where Q_{i_eff} is the effective discharge leaving the cell in question for the neighboring cell i, and Q_i is the calculated discharge leaving for neighboring cell i in the absence of a shrub plant. In this way, the flow of water through a cell with a shrub plant is reduced (relative to if no shrub is present), with larger shrubs reducing more flow than smaller shrubs. In turn, a reduction in discharge leaving a cell tends to cause greater net deposition of sediment within the cell, as a greater proportion of sediment is transported into the cell than carried out. In the absence of empirical measurements for the maximum flow reduction coefficient, we test the sensitivity of this parameter by varying Λ from 0.05 to 0.35 (Figure S1 in Supporting Information S1), as discussed below in Section 3.

Table 2
Parameter Values for Model Experiments

Experiment		RSLR (mm yr^{-1})	$\bar{r}$ (yr^{-1})	Duration (yrs)	Barrier segment length (m)	Initial dune heights (m)	Λ	Seed placement
Impacts of shrubs on barrier morphology and migration	Varying RSLR (Figures 2 and 3)	3, 6, 9, 12, 15	0.6	1,000	500	0.1–1.4	0.15	Entire barrier
	Varying $\bar{r}$ (Figures 4 and 5)	9	0.3, 0.45, 0.6, 0.75, 0.9	1,000	500	0.1–1.4	0.15	Entire barrier
Geomorphological controls on shrub expansion	Varying RSLR (Figure 6)	3, 6, 9, 12, 15	0.6	150	5,000	1.0–1.4	0.15	First 100 m alongshore
	Varying $\bar{r}$ (Figure 7)	9	0.3, 0.45, 0.6, 0.75, 0.9	150	5,000	1.0–1.4	0.15	First 100 m alongshore

In the model, dead shrub plants are only two-thirds as effective at blocking overwash flow as living shrubs. We derived this ratio by comparing "summer" versus "winter" Manning's n values from floodplains of "medium to dense brush" (Chow, 1959) as proxies for living and dead shrubs, respectively. Therefore, when water is routed through a cell with a dead shrub, Λ is multiplied by 0.66 and ϕ refers to the shrub's percent cover at time of death.

## 3. Impacts of Shrubs on Barrier Morphology and Migration

To assess the ways in which shrubs alter barrier morphology and the rate and style of barrier retreat, we run simulations with and without shrubs across broad ranges of two key input parameters: RSLR and characteristic dune growth rate ($\bar{r}$). Dune growth rate is an important factor in controlling shrub expansion and mortality and in determining the vulnerability of a barrier to storm impacts (Durán Vinent & Moore, 2015; Goldstein & Moore, 2016; Reeves et al., 2021). Varying dune growth rates is also akin to varying storm frequency – that is, faster growth rates reduce the time needed for a dune to ecover before the next storm, and vice versa. RSLR is fundamental to barrier evolution, and varies spatially while also depending on future carbon emissions (e.g., Sweet et al., 2017).

Each simulation runs for 1,000 years or until the barrier drowns, with the alongshore length of the barrier segment set to 500 m. A duration of 1,000 years is able to capture trends in barrier migration (Reeves et al., 2021) and equilibrium morphologies, and is also designed to control for the effects of stochastic processes happening on shorter time scales (not necessarily to quantitatively predict a millennium of morphological or ecological evolution). The initial dune height is set randomly for each simulation between 0.1 and 1.4 m (with 0 and 1.5 m as the minimum and maximum dune heights, respectively), with random white noise perturbations alongshore of ±0.1 m. To allow shrubs to repopulate a barrier bereft of any fruiting plants, a single shrub seed is dropped randomly across the barrier interior each year. We use a relatively conservative value of 0.15 as the maximum flow reduction coefficient (Λ), which produces qualitatively realistic morphology. Varying Λ from 0.05 to 0.35 results in little difference in our results and does not qualitatively change our conclusions (Figure S1 in Supporting Information S1). See Table 2 for the values of parameters used in our experiments. We consider a barrier to have drowned when the maximum subaerial width of the interior domain thins to less than 10 m (one cell width), at which point the simulation ends. To determine the style of barrier retreat (i.e., continuous or discontinuous), we use an algorithm from Reeves et al. (2021): Discontinuous retreat occurs if the simulation includes two or more alternating periods of both transgression and relative immobility; otherwise, the behavior is considered continuous. Periods of immobility (transgression) are defined as 30 years or more of shoreline change rates under (over) 0.5 m yr^{-1}.

3.1. RSLR

In the first set of experiments we vary RSLR from 3 to 15 mm yr^{-1} in increments of 3, while holding $\bar{r}$ at 0.6 yr^{-1}. At this intermediate value of $\bar{r}$, dune heights tend to be bistable; that is, dunes tend to fluctuate between a high-and low-elevation state (e.g., Durán Vinent & Moore, 2015) instead of remaining within one elevation state for the duration of the simulation. To account for storm stochasticity within each unique simulation, we run simulations at each RSLR rate 100 times and present the mean ($n = 100$) time series of different morphological metrics for each RSLR value (Figure 2).
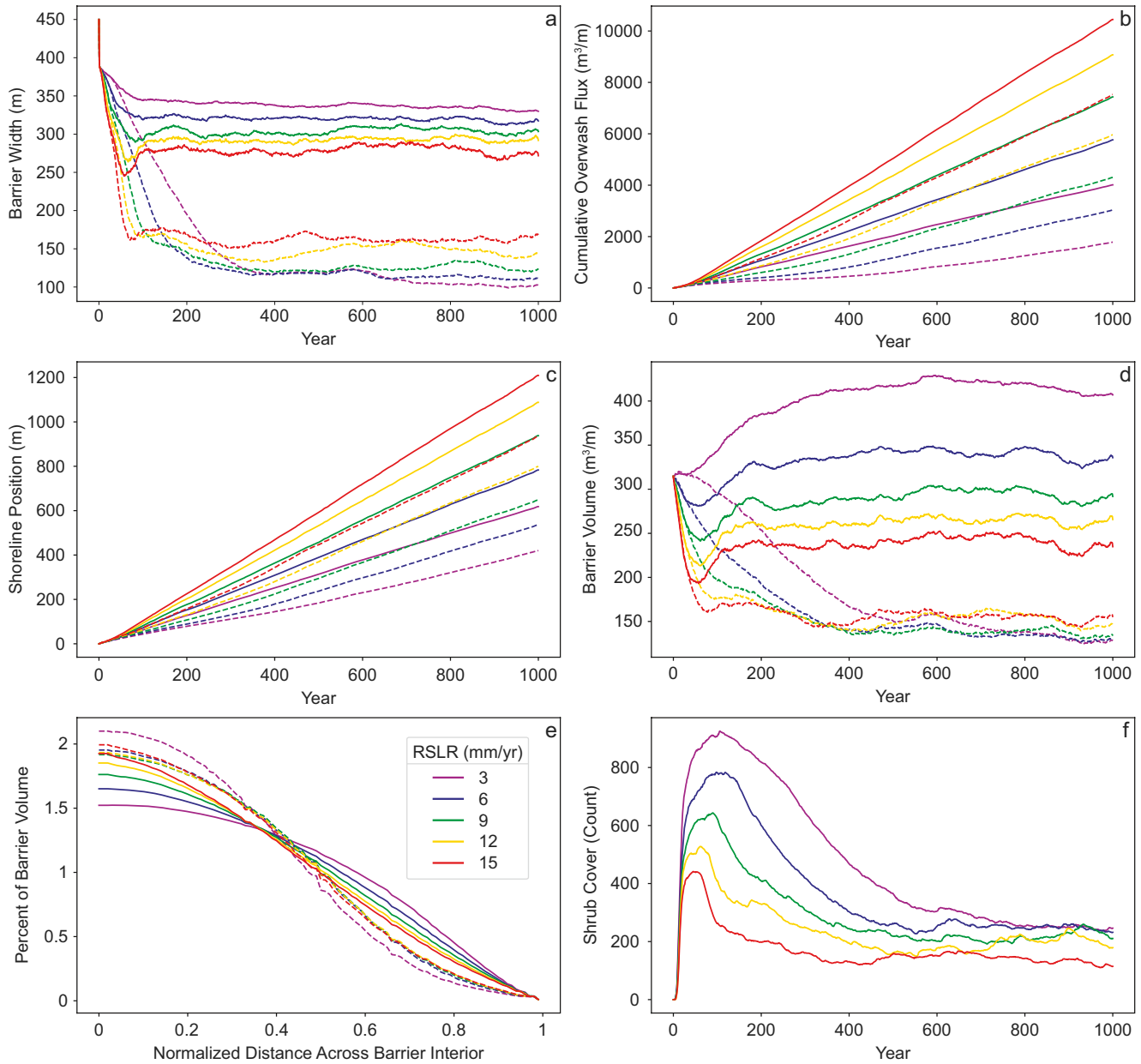
Figure 2. Varying relative sea-level rise (RSLR). Averaged ($n = 100$ simulations) time series of key variables for barriers with shrubs (dashed lines) and without shrubs (solid lines), with lines colored by RSLR rate used in the simulations.

For each RSLR rate we explore, each of the average time series flatten toward a steady equilibrium value after approximately 200–500 years of adjustment (Figures 2a–2d and 2f). The trajectories of individual simulations do not reach any sort of equilibrium state, as a barrier in any one simulation is constantly changing in morphology and shrub cover as the simulation progresses through time. Instead, trajectories of individual simulations tend to oscillate around the equilibrium values of the averaged time series that they collectively produce (Figure S2 in Supporting Information S1). These steady states are not conditioned by the initial barrier morphology, for the average time series approach the same steady state values even if the simulations begin with much narrower initial barrier morphology (Figure S3 in Supporting Information S1). Across all RSLR rates, barrier widths, volumes, and elevations approach steady attracting values maintained consistently above zero both with and without shrubs, indicating that drowning is not a steady state under these particular forcing conditions. Only 1.0% of all
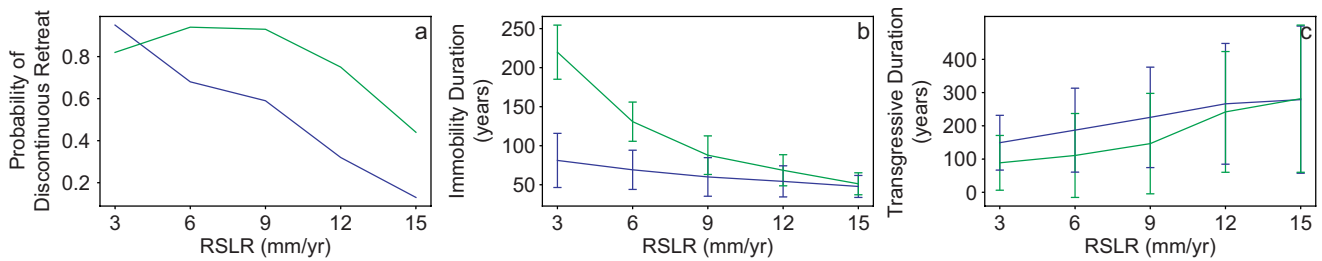
Figure 3. Discontinuous behavior with shrubs (green) and without shrubs (blue) across a range of relative sea-level rise rates. (a) Probability of discontinuous retreat, (b) average duration of immobile periods, and (c) average duration of transgressive periods. Error bars are one standard deviation.

simulations with shrubs, and 0.4% of simulations without shrubs, drowned over the course of 1,000 years. However, there are significant morphological and behavioral differences between barriers with and without shrubs.

Overall, barriers with shrubs tend to be narrower, have less overwash flux, and migrate landward more slowly relative to barriers without shrubs (Figures 2a–2c). Additionally, barrier volume above MHW tends to be smaller with shrubs (Figure 2d), and distributed more toward the front (ocean-side) of the barrier (Figure 2e). With the effects of increased frictional drag, overwash through shrub thickets is deposited over shorter distances, resulting in volumetric distributions skewed more strongly toward the barrier front (Figure 2e). By building topography toward the front of the barrier, shrubs inhibit additional sediment transport into the barrier interior and therefore reduce volumetric overwash flux (Figure 2b). With reduced overwash fluxes deposited over shorter distances, barriers with shrubs tend to be narrower than barriers without (Figure 2a), and smaller average barrier volumes (Figure 2d) follow as a consequence of narrower widths. Lastly, because less sediment is removed from the shoreface/beach environment and deposited as washover in the interior, shrubs slow the landward translation of the ocean shoreline (Figure 2c). These findings are consistent across all RSLR rates.

Among barriers without shrubs, increasing the rate of RSLR tends to decrease the equilibrium barrier width (Figure 2a). This occurs because higher rates of RSLR increase landward translation of the ocean shoreline (e.g., Bruun, 1962) and seaward translation of the back-barrier shoreline, especially during periods of barrier immobility, and thereby narrow the barrier from both the front and back. The opposite outcome is observed for barriers with shrubs, which tend to be wider with increasing RSLR rates because overall shrub cover is lesser (Figure 2f). Higher RSLR rates reduce the available habitat for shrubs and lead to mortality via passive inundation and shoreline erosion. Thus, for the case of barriers with shrubs, the geomorphological effect of higher RSLR rates decreasing equilibrium barrier width is exceeded by the ecological effects of higher RSLR rates on shrub expansion and mortality (which tend to increase barrier width).

The presence of shrubs also increases the likelihood of discontinuous retreat and the average duration of immobile periods (Figure 3). Periods of immobility tend to be longer with shrubs (Figure 3b) because shrubs delay the onset of overwash flux after dunes transition to a low-elevation state. When dunes are tall, overwash is typically limited and the barrier tends to be immobile, which favors shrub expansion across the barrier interior. If dune heights are consequently reduced via vertical (storm) or lateral (shoreline change) erosion, shrubs limit overwash flux across the barrier that would otherwise lead to rapid barrier transgression. Since overwash flux is limited, the barrier tends to remain relatively immobile until shrub cover has been effectively removed by mortality and shoreline erosion; alternatively, shrubs may prevent immobile periods altogether if the dunes can recover to a high-elevation state before shrub cover is lost. This lag in the onset of transgression is longer at lower RSLR rates because shrub cover is greater; at higher RSLR rates, there are fewer shrubs to be removed before substantial overwash – and therefore transgression – can commence. Additionally, shrubs tend to reduce the average duration of transgressive periods (Figure 3c). This occurs because shrubs can establish in the absence of sufficient dune heights if the barrier is wide enough, eventually work their way to the front of the barrier via shoreline erosion (i.e., as the shoreline recedes toward them), and impede overwash, thereby potentially leading to immobility sooner. This process is less impactful at higher RSLR rates because barriers tend to be narrower, making it more difficult for shrubs to establish in the absence of dunes. Shrubs increase the probability of discontinuous retreat (Figure 3a) by providing the prolonged cessation of transgression needed to produce discontinuous behavior. This impact is greatest at higher RSLR rates which produce conditions that, in the absence of shrubs, rarely result in

barrier immobility (Reeves et al., 2021). The large variance in immobility and transgressive durations (Figures 3b and 3c) is a product of the stochastic nature of storms and their interactions with dune dynamics, emphasizing the importance of dune-storm interactions in controlling the evolution of barriers over decadal-centurial timescales (Reeves et al., 2021).
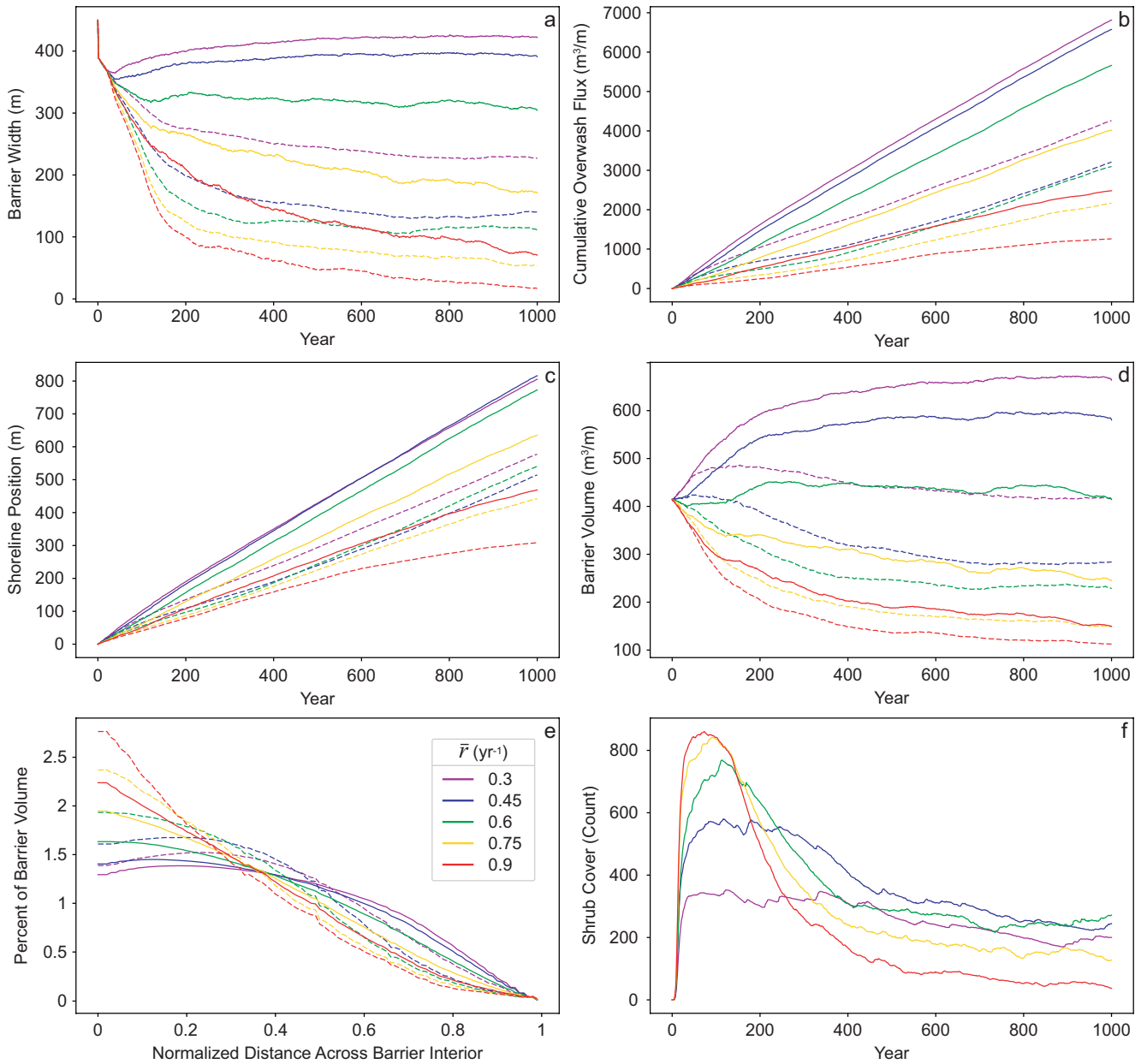
3.2. Characteristic Dune Growth Rates

Next, we vary $\bar{r}$ (the characteristic dune growth rate) from 0.3 to 0.9 yr^{-1} in increments of 0.15, while holding RSLR at 6 mm yr^{-1}, the present RSLR rate in the VCR and a conservative estimate of the near future global mean sea-level rise rate (Sweet et al., 2017). As before, we run 100 simulations at each $\bar{r}$ and present the mean of these 100 simulations as our results.

At high dune growth rates ($\bar{r}$ = 0.75 and 0.9 yr^{-1}), average barrier trajectories trend toward steady states of drowning (Figures 4a and 4c). For the highest rates of dune growth ($\bar{r}$ = 0.9 yr^{-1}), 74% of simulations with shrubs drowned after an average of 562 years ($\pm$200), while 38% of simulations without shrubs drowned after an average of 568 years ($\pm$224). At low to intermediate RSLR rates ($\bar{r}$ = 0.3–0.6 yr^{-1}), only 0.7% of barriers in all simulations drowned. Drowning in the model is more likely at higher dune growth rates because tall dunes limit washover deposition in the barrier interior and back-barrier bay, allowing for passive inundation of the barrier interior that outpaces the rate that overwash events (which occur infrequently when dunes are tall) are able to build elevation. Shrubs increase the vulnerability of barriers to drowning by further starving the barrier interior of washover deposition needed for the barrier to maintain its elevation relative to sea level.

Consistent with the RSLR simulations of Section 3.1, barriers with shrubs tend to be narrower, have less overwash flux, and migrate landward more slowly across all characteristic dune growth rates (Figures 4a–4c). Likewise, barrier volume with shrubs tends to be lesser and skewed more strongly toward the front (ocean-side) of the barrier (Figures 4d and 4e). Dune growth rate is a strong regulator of barrier width, with slower-growing dunes allowing greater cumulative overwash fluxes (Figure 4b) and therefore wider barriers (Figure 4a); smaller cumulative overwash fluxes at higher dune growth rates maintain narrower barriers. The difference in barrier width between barriers with shrubs and without tends to be greatest at intermediate dune growth rates, where shrub-overwash interaction is large enough to cause significant width differences, yet disturbances are small enough to allow significant shrub expansion across the barrier. These experiments also provide insight into the effects on barrier evolution on shrub ecology. For example, even though foredunes of a threshold height are necessary for the establishment of shrubs, the fastest dune growth rates lead to the least shrub cover (Figure 4f). This occurs because consistently tall foredunes result in barriers that are both narrower and lower in elevation, thereby limiting suitable shrub habitat. The greatest shrub cover over time is observed on barriers with intermediate dune growth rates, where the effects of overwash creating or maintaining habitat are balanced with the tendency of overwash to physically disturb the ecology.

At low to intermediate dune growth rates ($\bar{r}$ = 0.3–0.6 yr^{-1}), the presence of shrubs increases the likelihood of discontinuous retreat (Figure 5a). Periods of transgression are typically prevalent at low dune growth rates because dunes are slow to recover following disturbance; however, the presence of shrubs induces prolonged cessations of transgression needed to produce discontinuous behavior, thereby increasing the likelihood of discontinuous retreat. At high dune growth rates ($\bar{r}$ = 0.75–0.9 yr^{-1}), periods of immobility are common; therefore, the shrub lag in overwash flux either has little to no effect on the probability of discontinuous behavior, or can in fact reduce the probability of discontinuous behavior in favor of continuous immobility by preventing periods of transgression altogether.

At low to intermediate dune growth rates, shrubs also increase the average duration of immobile periods (Figure 5b) and reduce the average duration of transgressive periods (Figure 5c). Without shrubs, the average duration of immobile periods tends to increase with higher dune growth rates (Figure 5b, blue line) because taller dunes reduce overwash fluxes necessary for transgression. Interestingly, the opposite is observed with shrubs: The average duration of immobile periods tends to decrease with higher dune growth rates (Figure 5b, green line). This is because higher dune growth rates lead to narrow barrier interior widths and limited suitable shrub habitat, resulting in less shrub cover and less impact on immobile durations. Similarly, shrubs have a negligible effect on the average duration of transgressive periods at high dune growth rates (Figure 5c) because suitable habitat is

Figure 4. Varying characteristic dune growth rates ($\bar{r}$). Averaged ($n = 100$ simulations) time series of key variables for barriers with shrubs (dashed lines) and without shrubs (solid lines), with lines colored by $\bar{r}$ used in the simulations.
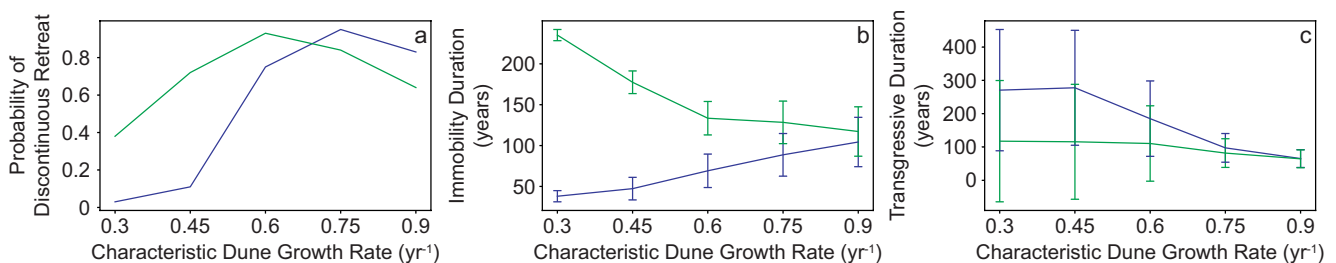
Figure 5. Discontinuous behavior with shrubs (green) and without shrubs (blue) across a range of characteristic dune growth rates. (a) Probability of discontinuous retreat, (b) average duration of immobile periods, and (c) average duration of transgressive periods. Error bars are one standard deviation.
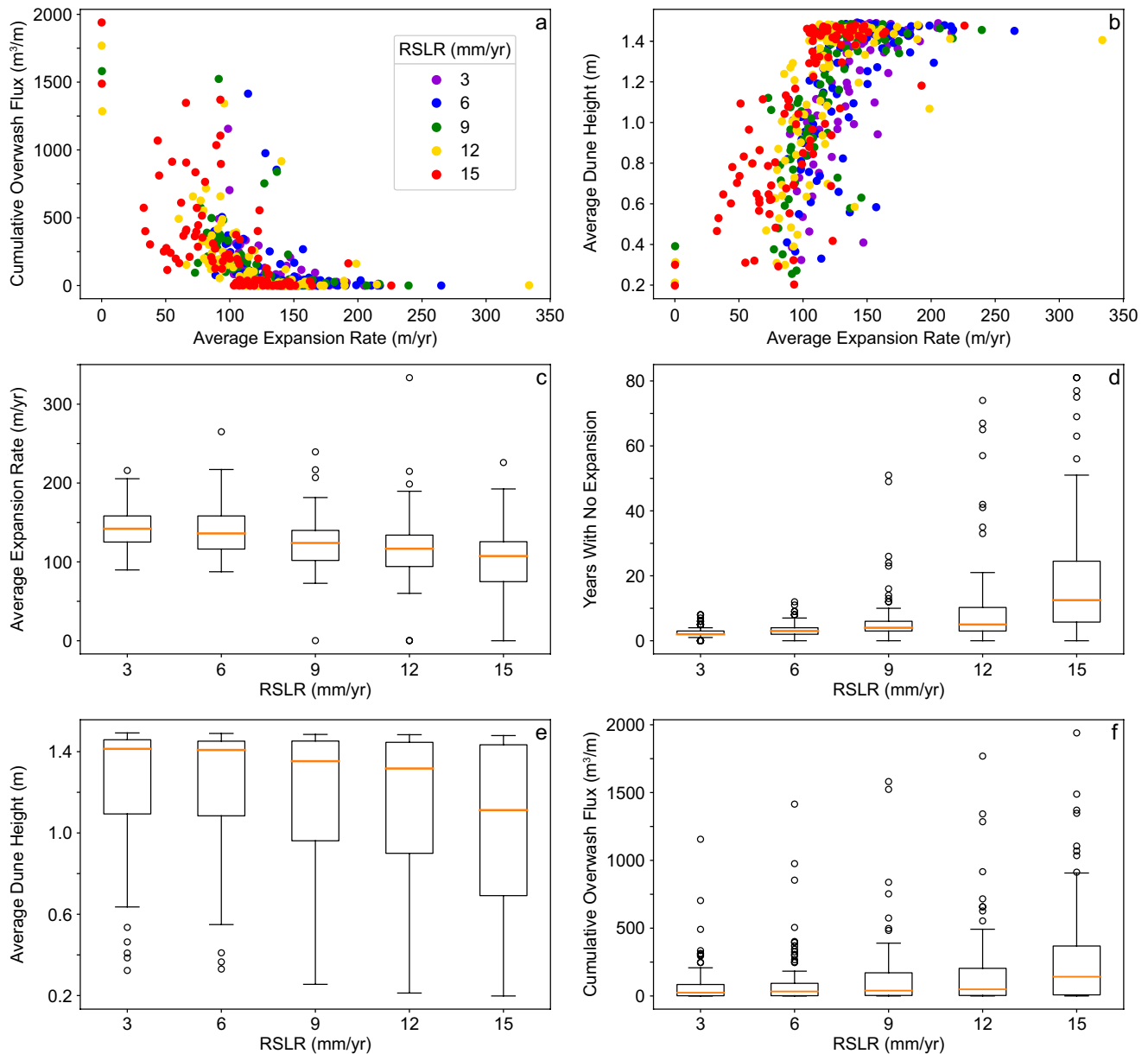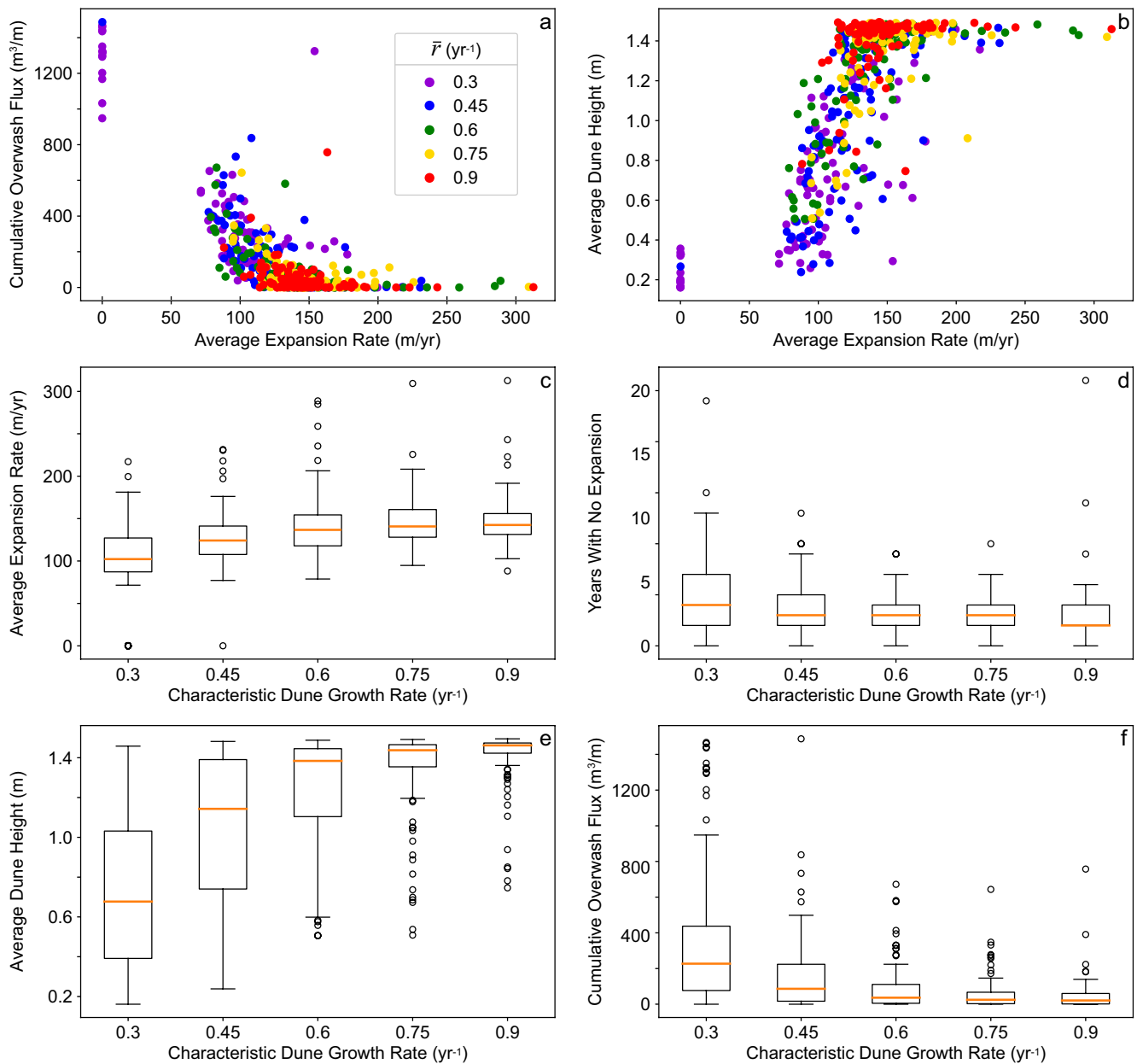
Figure 6. Rate and pattern of shrub expansion across a range of relative sea-level rise (RSLR) rates. (a and b): Average shrub front expansion rate as a function of (a) cumulative overwash flux and (b) average dune height, with points colored by the RSLR rate used in the simulation. (c–f): Box plots separated by RSLR rate of (c) average shrub front expansion rate, (d) number of years with no expansion of the shrub front, (e) average dune height, and (f) cumulative overwash flux.

limited. Regardless of these trends, immobile periods tend to be longer, and transgressive periods shorter, in the presence of shrubs.

4. Geomorphological Controls on Shrub Expansion

To explore the ways in which barrier morphologic evolution influences the rate and pattern of shrub expansion, we conduct two sets of experiments across the same ranges of RLSR (Figure 6) and characteristic dune growth rates (Figure 7) as in Section 3. Unlike the preceding simulations, however, the simulations in these experiments use a 5,000 m-long segment of Hog Island as the initial morphology and run for 150 years (Table 2), a duration that is long enough to capture a full cycle of shrub expansion and significantly reduces model run time given the ten-fold increase in barrier length relative to the preceding simulations. In addition, each simulation begins with

Figure 7. Rate and pattern of shrub expansion across a range of characteristic dune growth rates ($\bar{r}$). (a and b): Average shrub front expansion rate as a function of (a) cumulative overwash flux and (b) average dune height, with points colored by the value of $\bar{r}$ used in the simulation. (c–f): Box plots separated by $\bar{r}$ of (c) average shrub front expansion rate, (d) number of years with no expansion of the shrub front, (e) average dune height, and (f) cumulative overwash flux.

a foredune that is in a high-elevation state. The initial foredune height is chosen randomly between 1.0 and 1.4 m, and a single seed is dropped randomly each year on one end of the barrier within the first 100 m (2%) alongshore. Controlling for the location of the initial cluster of shrub establishment ensures that all simulations are able to expand the same maximum distance (here, 5 km). To account for storm and seed dispersal stochasticity, we run 100 simulations at each RSLR and $\bar{r}$ value.

We calculate the alongshore location of the shrub front as the 95th quantile of the alongshore distribution of all cells with living shrubs, which helps capture the front of the main thicket while disregarding small outlying patches or singular plants. Additionally, we calculate an average shrub expansion rate ($\bar{e}$) as 90% of the barrier length (L_{end}; i.e., the distance at which the change in shrub front location fully saturates) divided by the time it takes for the shrub front to reach L_{end} (t_{Lend}): $\bar{e} = L_{end}/t_{Lend}$. Because shrub expansion does not always begin
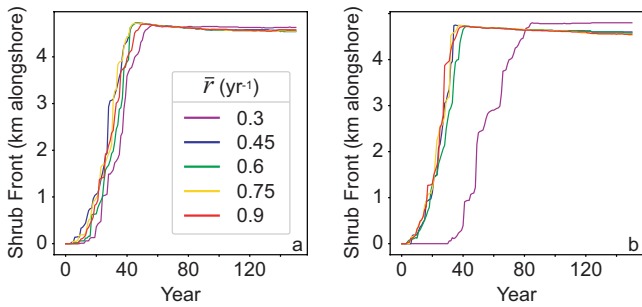
Figure 8. Examples of (a) rapid continuous and (b) slower interrupted expansion (at $\bar{r} = 0.3$ yr^{-1}) of the shrub front across a range of characteristic dune growth rates ($\bar{r}$). All simulations were run with the same initial and forcing conditions; differences in the behavior of shrub expansion arise from the stochasticity in seed dispersal and storm disturbance dynamics.

immediately at the start of each simulation, t_{Lend} begins when the shrub front location exceeds the first 100 m of the barrier.

Slower shrub front expansion rates are correlated with dune erosion and overwash disturbance (Figures 6a, 6b, 7a and 7b). These disturbances slow the rate of shrub encroachment by both promoting environmental conditions within the barrier interior that restrict successful post-dispersal establishment (e.g., salinity intrusion), and by killing or eroding away shrubs (which also has the effect of reducing the number of seeds dispersed). If undisturbed, the expansion of the shrub front over time can be described as logarithmic, with slow initial expansion, followed by rapid acceleration, then deceleration as the shrub front approaches the end of the barrier segment (e.g., Figure 8a). Disturbance events can cause arrested expansion of the shrub front (e.g., Figure 8b), leading to prolonged periods with no net change, or sometimes negative change, in the alongshore location of the shrub front.

Overall, there is significant variance in shrub expansion rates across all parameter combinations. Despite such variance, shrub expansion tends to be faster at lower RSLR rates (Figure 6c), and the number of years in which no positive shrub expansion is observed (i.e., no movement or negative movement of the shrub front location occurs) tends to be fewer (Figure 6d). This is because dunes are typically higher (Figure 6e) and overwash fluxes lower (Figure 6f) under these conditions. Higher rates of RSLR also lower a greater number of interior cells below the elevation threshold for shrub establishment, and therefore reduce expansion rates by limiting suitable habitat. At higher dune growth rates, shrub expansion tends to be faster (Figure 7c) and the number of years without positive expansion tends to be lower (Figure 7d). Higher dune growth rates reduce dune and overwash disturbances (Figures 7e and 7f) because dunes are more likely to recover before the next storm event.

5. Discussion

5.1. Model Limitations

The goal of this work is to investigate barrier and shrub dynamics and the ecological-geomorphological feedbacks that give rise to them, rather than to numerically predict or reproduce barrier/shrub evolution of a particular setting or under specific conditions. The parameterizations encoded in our shrub module are considerable simplifications of real-world processes, which may limit quantitative precision of model results. Yet, the assumptions and simplifications we have made are constrained by or derived from empirical data such that the compound effects of many processes operating at smaller spatiotemporal scales are represented. Basing the model on emergent variables (e.g., shrub elevation range) and interactions rather than the finer scale processes that collectively produce them is the most appropriate modeling approach for exploring and explaining complex behaviors of large-scale systems (Murray, 2007). As discussed in Reeves et al. (2021), the Barrier3D base model formulation assumes invariant beach width and slope. In reality, beach characteristics can vary over timescales of hours to decades (e.g., O'Dea et al., 2019) and length scales of 10^2–10^3 m (Vos et al., 2020) in ways that can affect dune growth (Durán & Moore, 2013), dune erosion (Beuzen et al., 2019), and overwash (Donnelly et al., 2006). The base model also does not account for tidal inlet processes, which can constitute a significant proportion of overall transgressive flux in barrier systems (e.g., Leatherman, 1979; Nienhuis & Lorenzo-Trueba, 2019), or other sediment pathways that can lead to deflation of the barrier (Passeri et al., 2020), such as gradients in alongshore transport, breaching, or storm-driven seaward transport. Below, we focus on the most consequential limitations related specifically to the new dynamics introduced by barrier-shrub feedbacks.

First, the model does not simulate a freshwater lens, which changes in size in response to barrier morphologic evolution. Freshwater availability is especially limited in narrow barriers (e.g., Bolyard et al., 1979; Rastetter, 1991; Shao et al., 1995). Thus, our parameterization of a shrub elevation range from Hog Island (0.74–1.84 m MHW) may be less suitable for barriers of different morphologies. Incorporation of groundwater dynamics would increase shrub expansion when barriers are wider (and vice versa). Modeled shrubs cannot occur on the beach (because Barrier3D does not model a beach) or, for model simplicity, on the foredune as a result of landward translation of the ocean shoreline. When the shoreline erodes landward one cell width, any shrubs occupying

the front (ocean-side) row of the interior domain are removed from the system entirely. In reality, shrubs can be found on beaches of rapidly transgressing barriers (Figure 1d), and persist until the ocean shoreline recedes far enough landward such that shrubs are impacted by swash zone dynamics. Because this would effectively extend the duration of shrub presence within the barrier system, shrub impacts are likely underestimated in the model in this regard. Shrubs also have the potential to influence aeolian reworking of the barrier interior by causing sand to deposit in and around shrub thickets. Aeolian dynamics of the barrier interior, however, are not included in Barrier3D. In reality, interactions between shrubs and wind-driven sediment transport during interstorm periods may increase surface roughness of the barrier interior, and potentially influence overwash routing.

In the absence of empirical measurements for the effects of shrubs on overwash flow across a barrier, we parameterize Λ, the maximum flow reduction coefficient, with a conservative value that produces qualitatively realistic morphology. In situ measurements of shrub-overwash flow hydrodynamics are needed to increase confidence in the quantitative accuracy of the model results, though sensitivity tests across a broad range of Λ values suggest that the parameter ultimately has limited impact on barrier morphology (Figure S1 in Supporting Information S1). In addition, mechanical damage to shrubs from waves or overwash bores is absent from the model formulation, as is the decay of dead shrubs over time, both of which are difficult processes to parameterize within our exploratory framework. In the absence of these dynamics, shrub longevity and their ability to limit overwash are likely to be marginally overestimated within the model.

We do not include biotic interactions between different plant species, such as facilitation or competition. Similarly, we do not explicitly simulate other finer scale environmental filters of shrub establishment, such as the distance to groundwater, soil salinity, or nutrients, but the collective effects of many of these factors are represented by our larger-scale parameterizations of a threshold dune height for shrub growth and a shrub elevation range. We also do not incorporate positive feedbacks related to shrubs modifying their own microclimate. Shrub thickets modify their microclimate by increasing overnight temperatures as well as soil nutrients and moisture (D'Odorico et al., 2012; Huang et al., 2018; Wood et al., 2020), thereby enhancing shrub growth and facilitating further localized shrub establishment. Incorporating these positive feedbacks within the model would likely increase shrub expansion rates. While our simulations are calibrated for *M. cerifera*, a common shrub along the Atlantic and Gulf coasts of North America and the dominant species in the VCR, parameterizing the model to represent other shrub species would result in differences to our results but would unlikely change the fundamental conclusions we draw from them. Although our model does not include the possibility for eventual succession of shrubland to maritime forest (the typical climax community on Atlantic barriers), frequent reworking of the barrier and rapid expansion of full monospecific shrub thickets can delay or prevent this successional development (Bissett et al., 2016). Therefore, given projected climate-related increases in atmospheric temperatures, RSLR rates, and storminess, development of new maritime forest is likely to be rare.

5.2. Ecological Impacts on Barrier Morphology

Our results suggest major morphological and behavioral differences between barriers with and without shrubs, as proposed by Zinnert et al. (2017). In our simulations, the time-averaged morphology of barriers with shrubs is narrower and less voluminous than the time-averaged morphology of barriers without shrubs. Across the broad ranges of RSLR and characteristic dune growth rates we simulate, we find that the presence of shrubs reduces barrier widths and volumes by as much as 40%–65%, and that volumes tend to be more distributed toward the front of the barrier. These morphological differences are the result of shrubs limiting overwash flow into and across the barrier in the model: Sediment carried into the barrier interior is deposited over shorter distances from the effects of frictional drag of the shrub thicket on the overwashing flow, which in turn builds topographic relief that limits continued transgressive flux into the barrier interior. The distance over which overwash sediment is deposited is a function of both storm intensity and the density/extent of woody cover.

We also find that barriers with shrubs tend to migrate landward more slowly and are more likely to experience discontinuous retreat. Migration rates in our simulations tend to be approximately 20%–40% slower with shrubs because overwash fluxes are lesser (i.e., less sediment is removed from the shoreface and beach to be deposited as washover). Meanwhile, discontinuous retreat is more likely because shrubs extend the duration of immobile periods by delaying the onset of overwash flux after dunes are lost, providing prolonged periods of immobility needed to produce discontinuous behavior. This lag lasts until shrub cover has sufficiently decreased, and can extend periods of immobility in our simulations by as much as 340%. However, under conditions that tend to result in

relatively immobile barriers (i.e., fast dune growth rates, low RSLR rates), this lag effect can potentially prevent any transgressive periods from occurring at all, which tends to reduce the likelihood of discontinuous behavior in favor of continuous immobility and increase the likelihood of barrier drowning. At high dune growth rates in our simulations, barriers with shrubs are twice as vulnerable to drowning within 1,000 years as barriers without.

Our results suggest that interior ecology is a critical component of barrier evolution on timescales of a single storm to many centuries, complementing recent studies by Zinnert et al. (2016, 2017, 2019). In our simulations, dune growth rates and the presence or absence of shrubs are the primary drivers of barrier width and vulnerability to drowning, not RSLR. This emphasizes the prominent role of internal dynamics – as opposed to external forcing – in controlling barrier evolution (Ciarletta et al., 2019; Lorenzo-Trueba & Ashton, 2014; Reeves et al., 2021). In this way, the impacts of shrubs are similar to those of dunes (Reeves et al., 2021) and human infrastructure (Lazarus et al., 2021; Rogers et al., 2015), two additional suites of processes internal to barrier systems that can restrict sediment delivery into and across the barrier interior.

The significant morphologic and behavioral differences we observe in our simulations between barriers with shrubs and without suggest major disparities in barrier functionality and services, with potentially broad impacts on the ecological, physical, and human components of the coastal barrier system. For example, barriers with shrubs may be unable to support fringing back-barrier marshes that rely on overwash sediment deposition to keep pace with RSLR (Walters et al., 2014; Walters & Kirwan, 2016); barriers that are narrow in the presence of shrubs may have limited freshwater lenses (Bolyard et al., 1979), and might support less rich ecosystems and human activities; and, the tendency for nonlinear behavior and drowning of barriers with shrubs could lead to cascading state changes across the entire coastal system (e.g., Deaton et al., 2017; FitzGerald et al., 2018). With shrub expansion worldwide linked to global warming, these internal shrub dynamics may become increasingly important in the future across barrier systems with climatologies that had precluded shrub establishment in the past. However, as sea level rises and rates of dune growth (relative to the frequency of intense storms) decrease, our results suggest that the impacts of shrubs on barrier morphology and behavior (relative to barriers without shrubs) may become less influential because of a consequent decline in shrub cover.

Our results also highlight complex, sometimes counterintuitive feedbacks and relationships between shrub ecology and barrier geomorphology. For instance, the tendency for higher rates of RSLR to reduce barrier widths is reversed when shrubs are included in the simulations. In addition, despite the fact that sufficiently tall dunes are required for shrub growth, faster dune growth rates typically lead to less shrub cover over long time scales because tall dunes limit overwash deposition needed to offset habitat loss from passive drowning of the back-barrier shoreline via RSLR. Further, the average duration of immobile periods tends to decrease with higher dune growth rates in the presence of shrubs. These complexities emphasize the importance of explicitly modeling barrier ecology and its interactions with the physical environment when exploring long-term barrier evolution, as opposed to using static representations of land-cover that would be unable to capture these dynamics.

5.3. Geomorphological Impacts on Shrub Expansion

The substantial variance in shrub expansion rates in our simulations can be attributed to the stochasticity of not only shrub seed dispersal but also dune-overwash dynamics. Our results suggest that dune and overwash dynamics are important for understanding or predicting the rate and pattern of shrub expansion. Over annual to decadal timescales, we find that storm-related disturbances of dune erosion and overwash are associated with slower expansion rates and more years without any positive translation alongshore of the shrub front. Higher rates of RSLR and slower dune growth typically induce more frequent disturbance events. In this way, storms act as a destructive force that both kills and/or erodes away established shrubs, which has the additional effect of reducing the number of seeds dispersed, and prevents the establishment of shrub seedlings by enabling unsuitable environmental conditions. Rapid, uninterrupted shrub expansion is therefore most likely to occur across barriers that are disturbance resistant, such as Hog Island (Wolner et al., 2013) where shrubs have expanded at surprisingly rapid rates of up to 300 m yr^{-1} (Woods et al., 2019).

However, over longer, decadal to centurial time scales, the physical impacts of storms are both destructive and constructive in the context of shrub ecology. Washover deposition can both maintain existing shrub habitat by raising interior elevations relative to sea level, and build new shrub habitat by extending the back-barrier shoreline landward. These constructive tendencies in the model tend to contribute (over long timescales) toward habitat

exchange, a component of habitat change in which the loss of a habitat type is offset by gain of that habitat else-where; Enwright et al. (2021) find a potential relationship between barrier migration and barrier habitat exchange from change component analysis of Dauphin Island, Alabama, USA. Our simulations suggest that, over multiple cycles of shrub expansion and mortality, shrub cover (and, by extension, shrub impacts) is often greatest when the constructive and destructive tendencies of overwash processes are balanced. Although warming macroclimate temperatures are likely to stimulate shrub expansion in the future, our results suggest this tendency may be tempered in part by increases in disturbances related to higher RSLR rates and slower dune growth rates (i.e., relative to increases in the frequency of more intense storm events) – or the greater vulnerability of barriers with shrubs to drowning. While we examined shrub expansion across a range of RSLR and characteristic dune growth rates, future work should include the effects of climate warming on ecological aspects of shrub expansion (e.g., seed production, germination rate) in addition to these physical drivers.

5.4. Comparisons to Observations

Comparing our model results to observations is important for understanding the explanatory power of the model. Making such comparisons, however, is challenging because the durations of our simulations and the characteristic timescales of dynamics we observe within them are often much greater than the durations of most observational time series. Nevertheless, although quantitative comparisons are inappropriate given the exploratory nature of our model, key aspects of our results are qualitatively consistent with documented real-world behavior.

Comparisons between shrub expansion in our model and on Hog Island in the VCR suggest that our new shrub module is capable of producing realistic shrub behavior. Shrub expansion rates observed on Hog Island from 1984 to 2010 average 164 m yr^{-1} and reach a maximum of 300 m yr^{-1} (Woods et al., 2019), well within the range of average expansion rates from our simulations of 0–334 m yr^{-1} described in Section 4 above. Additionally, Woods et al. (2019) observe a logarithmic trend in shrub front expansion over time on Hog Island, a dynamic that is captured in our model simulations as well (Figure 8). Our model results also identify conditions in which barrier processes construct new shrub habitat; this is supported by the empirical observations of Young et al. (2007), who find a positive relationship between change in subaerial barrier area and change in shrub cover for the larger barriers of the VCR, and shrub expansion onto newly-created washover deposits has been observed on Fire Island, NY (Leatherman, 1985), Nauset Spit, MA (Zaremba & Leatherman, 1986), and Smith Island, VA (Young et al., 2007).

In our model simulations, barriers with shrubs tend to be narrower, less voluminous, and be more strongly skewed volumetrically toward the ocean. Woody vegetation has been observed to block overwash flow and build topographic relief both in natural barrier settings (Claudino-Sales et al., 2008; Wang & Horwitz, 2007) and within physical models (Kobayashi et al., 2013). In an analysis of remotely-sensed observations from VCR barrier islands, Zinnert et al. (2019) find an important relationship between woody cover and back-barrier shoreline extension, suggesting that shrub cover reduces the landward translation of back-barrier shorelines by decreasing overwash sediment delivery across the barrier, thereby leading to barrier narrowing.

Our model results also suggest that barriers with shrubs are more likely to experience discontinuous retreat and longer periods of immobility because shrubs delay the onset of transgression after dunes transition to a low-elevation state. This lag effect is supported by observational evidence from Cobb Island in the VCR of a temporal correlation between the onset of rapid landward translation of the back-barrier shoreline and the loss of woody cover from erosion (Zinnert et al., 2019). From 1984 to 1998, shrubs expanded rapidly across Cobb Island during a prolonged period of stability. From 1998 to 2011, extensive shoreline erosion occurred (likely because of a change in sediment supply or dune elevation state) but the back-barrier shoreline experienced little change, leading to the barrier losing 63% of its subaerial area (which can be taken as a proxy for barrier width and volume). Back-barrier shoreline extension increased rapidly between 2011 and 2016 once shrub cover was reduced to nearly zero by erosion and exposure to the open ocean.

The connections we have highlighted in this section between model findings and empirical observations suggest our model qualitatively captures real-world barrier-shrub behavior. Observational analyses beyond the scope of this study are needed to continue testing the ideas presented herein. More broadly, our results suggest the need for more observational research that integrates interior barrier dynamics with geomorphological change over time.

6. Conclusions

We introduce shrub expansion and mortality processes within an exploratory model of barrier morphodynamics, and point to the essential role of interior ecology in barrier evolution. Our model simulations suggest that barriers with shrubs, relative to those without, tend to be narrower and migrate landward more slowly, with subaerial volume distributed more toward the front (ocean-side) of the barrier. In addition, in our model simulations, shrubs generally increase the likelihood of discontinuous retreat by providing prolonged cessations in overwash flux needed to produce periods of immobility. However, under conditions where periods of immobility are common, shrubs can altogether inhibit periods of transgression that are needed for barriers to maintain elevation relative to sea level, leading to increased vulnerability to drowning in the presence of shrubs. Additionally, our model experiments suggest that shrub expansion is highly dependent on geomorphological barrier processes. Slower shrub front expansion rates are correlated with greater dune erosion and overwash disturbance, which occur more often, on average, at higher rates of RSLR and slower rates of dune growth. In our model, shrub-barrier couplings lead to complex and sometimes counterintuitive outcomes that emphasize the need to explicitly account for ecological processes and their interactions with the physical environment when exploring decadal to centurial barrier evolution.

Data Availability Statement

Barrier3D (Reeves, 2021) is available for download from the online Community Surface Dynamics Modeling System model repository at https://csdms.colorado.edu/wiki/Model:Barrier3D. Data for experimental results are in repository at https://doi.org/10.6073/pasta/5b59143f40b0b73f01337281f1ae1b51.

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