Received: 29 July 2022 | Revised: 8 February 2023 | Accepted: 10 February 2023

DOI: 10.1002/esp.5565

STATE OF SCIENCE

ESPL WILEY

Examining the commonalities and knowledge gaps in coastal zone vegetation simulation models

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Funding information
US Army Corps of Engineers' Aquatic Nuisance Species Research Program

Abstract

Models can be powerful tools to help scientists, policymakers, and practitioners forecast vegetation dynamics and inform management decisions in a variety of ecosystems. In coastal environments, vegetation moderates physical and hydrodynamic processes that conversely affect vegetation dynamics. Coastal management and the implementation of nature-based solutions in the coastal environment requires models that can predict vegetation dynamics that are driven by ecological processes as well as physical processes (e.g., storms, sea level rise). To determine models that are capable of simulating biomass dynamics and assess their ability to make predictions within the context of climate change and environmental management, we reviewed coastal dynamic vegetation simulation models across the following coastal zone habitats: tidal wetlands (salt marsh, mangroves, and freshwater wetlands), seagrass beds, coastal forests (maritime and floodplain forests), and dune habitats. Fifty-four models met the review criteria and were examined to assess their ability to simulate relevant ecological processes and the spatiotemporal scales at which they are applied. These models included a variety of exogenous and endogenous processes and integrate complex ecogeomorphological feedbacks affecting plant and soil community, hydrodynamic, and sediment transport dynamics. Most models reviewed utilized implicit approaches to predicting vegetation biomass and simulated a limited number of processes based on the principal drivers of habitat of interest. Key gaps identified were the exclusion of below-ground biomass dynamics, limited inclusion of processes such as competition, facilitation, and succession, and the inability to simulate management actions. Future models should seek to move towards process-based approaches where appropriate to enable their application to different systems and facilitate their use under novel environmental conditions.

KEYWORDS
coastal habitats, coastal models, ecological models, ecosystem processes, hydrodynamics, integrated modeling, simulation

1 | INTRODUCTION

Vegetation is often the foundation of ecological systems and the focus of many habitat dynamics models used for forecasting and management (Reichert et al., 2015; Riddick et al., 2017). However, not all vegetation models support forecasting under non-stationary conditions or consideration of the effects of management actions. There is a critical need to evaluate existing vegetation models and synthesize commonalities and gaps amongst them to determine the direction for the development of next generation vegetation models that are capable of high accuracy predictions under changing conditions. Vegetation models vary broadly in intent (i.e., simulative

vs. theoretical), resolution and domain (i.e., cell, organ, organ system, plant, patch, local, regional, global; Figure 1) and inclusion and exclusion of processes and stressors (i.e., acute vs. chronic and exogenous vs. endogenous; Figure 2) (Best et al., 2008; Franklin et al., 2020; Scheiter et al., 2013). The simulated processes often determine model temporal scale – decadal to millennial, for global-scale processes (e.g., carbon storage), seasonal to multi-year for plant-scale processes (e.g., biomass production or fruiting), or minutes to hours for cellular or organ system processes (e.g., stomatal opening or root nutrient uptake) (Moorcroft et al., 2001; Peng, 2000; Riddick et al., 2017; Stallins, 2012; Walker et al., 2017; Zinnert et al., 2017). Similarly, model spatial scale is often a function of model type. Vegetation

FIGURE 1 Coastal zone habitats and spatial scale. Coastal zone habitats are often directly and indirectly linked based on their proximity and similar acute episodic and chronic physical stressors. These habitats occur concomitantly in the broader coastal zone. The spatial scale at which models apply to these habitats can vary from the plant, patch, local, regional, and global level.

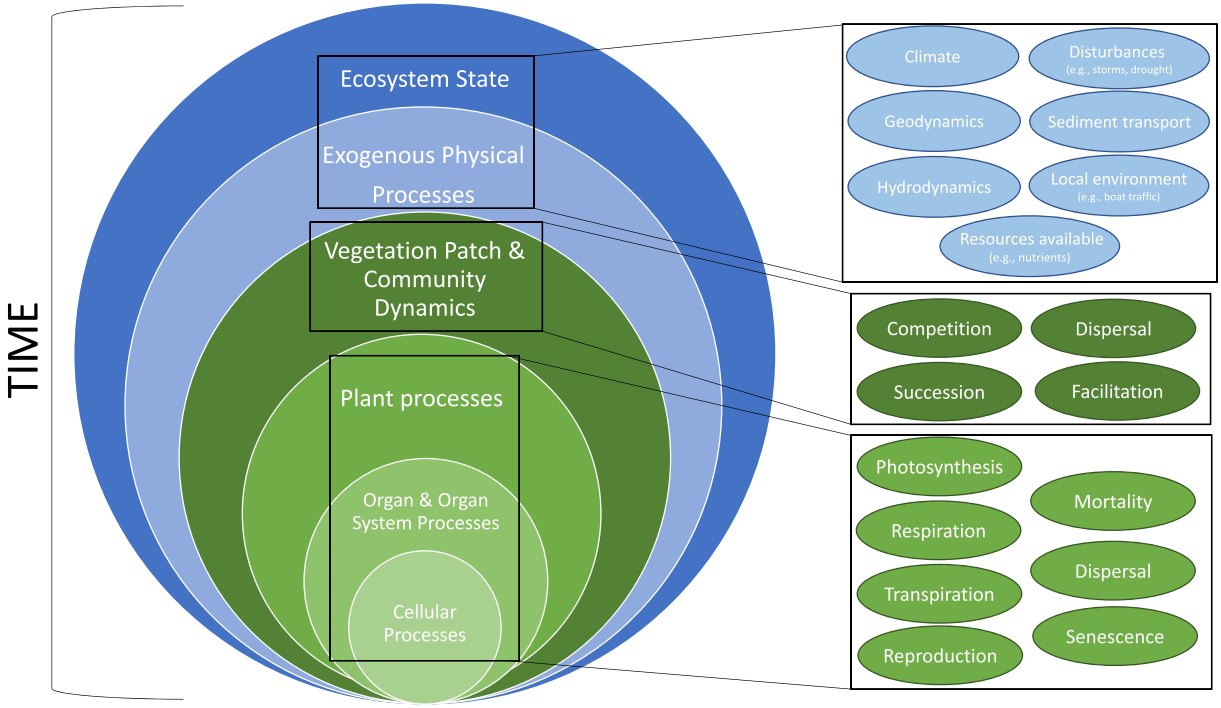

FIGURE 2 Endogenous biotic (green) and exogenous abiotic (blue) processes and stressors associated with ecogeomorphic coastal ecosystems across the spatiotemporal spectrum. Cellular, leaf, canopy, organ system, and plant-scale processes are distilled and lumped together in this diagram. Vegetation patch and community dynamics processes are similarly lumped. Note that exogenous biological processes such as herbivory may also be relevant but are not included in this figure.

dynamics models (i.e., those that simulate changes in vegetation characteristics over time, such as biomass, structure, cover, among others) typically represent smaller scales whereas dynamic global vegetation and terrestrial biosphere models intend to represent global scale processes linked to global water, carbon, or nutrient cycling dynamics, for example (Fisher et al., 2014).

Vegetation dynamics models are often simplified by excluding processes irrelevant to the scale or intent of the questions being asked; in addition, more complex processes might not be included due to computational requirements of executing model runs (Fagherazzi et al., 2020; Wiberg et al., 2020). While these simplifying assumptions are necessary in many cases, models can be constricted to a relatively small domain over which the model equations are applicable. For example, environmental change resulting from climatic shifts or urbanization may lead to changes in exogenous processes where the model no longer applies. Functional predictive vegetation models that can simulate the effects of such changes are necessary to understand how system changes due to climate and other anthropogenic changes may affect vegetation processes and distribution.

Although climate change-driven effects on vegetation occur at global scales, some habitats are predicted to be disproportionately affected (IPCC, 2019). For this reason, models operating at smaller regional and local spatial scales are often necessary to inform practical ecosystem planning and management and have been developed for a broad range of ecological systems from tropical forests to tundra (Franklin et al., 2020; Reichert et al., 2015; Riddick et al., 2017). This review focuses on coastal vegetation models because coastal systems are highly dynamic and are expected to undergo rapid change in the next decades due to climate change, which is predicted to alter the invaluable ecosystem services they provide (Elko et al., 2019; Hanley et al., 2020; IPCC, 2019). In recent decades, there has been a paradigm shift towards more nature-based solutions for coastal flood risk management and to facilitate coastal adaptation to rising sea levels (Bridges et al., 2021; Jackson & Nordstrom, 2019; Powell et al., 2019) requiring predictive vegetation models that can simulate the evolution of these coastal ecological systems under changing conditions (Jackson & Nordstrom, 2019; Roelvink & Renier, 2012; Walker et al., 2017).

The coastal zone is defined as the region of a coast directly influenced by marine hydrodynamic processes, both onshore and offshore (Bridges et al., 2021; USACE, 1995). It encompasses wetlands, seagrass beds, and dune complexes among other habitats, which all maintain a strong and inextricable ecogeomorphological link between biological and geological processes (Corenblit et al., 2015; Viles, 2020; Zinnert et al., 2017). Vegetation impacts physical and hydrodynamic processes and these in turn impact vegetation dynamics and processes. Coastal ecogeomorphic habitats share many of the same natural and anthropogenic threats (Hanley et al., 2020) and disturbance responses can directly and indirectly impact surrounding upland and coastal zone habitats and infrastructure (Zinnert et al., 2017; Figure 1). Plants here act as ecosystem engineers with functional similarities across habitats such that a unifying or universal theoretical, modeling, and managing framework has been suggested across ecosystems (Corenblit et al., 2015). However, similar to other ecogeomorphic systems, many coastal system models focus mainly on exogenous physical processes while simplifying the endogenous vegetation processes at work as opposed to vegetation models developed for agricultural, silvicultural, or natural systems that simulate endogenous vegetation processes using simplified exogenous physical drivers (Figure 2; Larsen et al., 2020).

The objective of this study is to review existing vegetation models of coastal zone habitats for the following purposes: to determine their ability to simulate biomass dynamics; to identify commonalities and gaps among the models in terms of scale, processes included, and inputs/outputs; and to assess model applicability to address climate-change related questions. The results represent the state of the science for coastal zone vegetation models, serve as a resource to guide model users, and identify future model development requirements. A literature review was performed to identify coastal vegetation simulation models for common coastal habitats categories. The habitats included in this review must be structured by rooted vegetation and influenced by tidal fluctuations or otherwise coastally influenced (e.g., subjected to inundation from coastal storms, ecological system is structured by salinity gradients). Based on these criteria, the following habitats were included:

- coastal wetlands (e.g., salt marsh, mangroves, freshwater wetlands),
- seagrass beds,
- dune complexes,
- coastal forests (e.g., maritime and floodplain forests), and
- coastal landscape models, including barrier islands, which are often uniquely described in models.

Tidal and freshwater submerged aquatic vegetation aside from seagrass beds, were omitted from this review because they are not typically modeled based on explicit coastal processes (Carr et al., 1997).

2 | METHODOLOGY AND CRITERIA FOR MODEL INCLUSION AND EXCLUSION

A literature review was conducted winter and spring 2021 using a combination of backward and forward snowballing utilizing start sets derived from an initial search using the term "model" plus the habitat name as well as any well-known models of the habitat (Wohlin, 2014). Unique models identified using the snowballing method were screened to determine if they met the following specific criteria:

1. Included relevant exogenous coastal and terrestrial processes that affect vegetation distribution; and
2. Dynamically simulated vegetation biomass (i.e., biomass changed over time within the model) either implicitly or explicitly

These criteria exclude habitat suitability, scaled physical, statistical, species distribution, global, and remote sensing models. Similarly, we do not include global-scale models, plant-scale models where the focus is an individual plant, or where the focus includes simulating organ-level functions. The models discussed were created independently or represent significant modifications to existing models such that they could be considered new. Publications that utilize existing models without significant changes to the model itself were excluded. Integrated or coupled models are mentioned briefly in each habitat section, but are not reviewed in detail unless biomass is dynamically simulated.

3 | RELEVANT MODEL PROCESSES INCLUDED AND EXCLUDED

A standard rubric was developed to compare models across habitat types with respect to model complexity, scale, included endogenous and exogenous processes and resulting vegetation dynamics within the ecological hierarchy (Figure 2), as well as simulated vegetation metrics output (e.g., density, biomass, etc.). The hierarchy presented in Figure 2 is not a representation of model characterization per se but serves to discern between the spatiotemporal scales of the vegetation processes simulated within models. Models may include processes from several spatiotemporal levels explicitly or implicitly.

All ecosystem and exogenous physical processes are described as physical drivers. Physical drivers are a combination of large-scale processes (i.e., climate and geology) and regional and local-scale processes that integrate coastal and terrestrial drivers (e.g., sediment transport, groundwater discharge) as well as possible anthropogenic disturbances. Allocation of biomass among plant organ systems (e.g., roots, stems, leaves) is noted for models whenever possible. Note that plant growth is not considered a separate process in Figure 2, but instead results from endogenous plant processes that produce and consume carbohydrates (e.g., photosynthesis, respiration). For simplicity, growth is documented as a plant-scale process in cases where processes controlling growth such as photosynthesis are not explicitly simulated. Processes that occur at the vegetation patch and community dynamics scales (Figure 2) are also documented for each model and metrics describing these processes such as diversity and plant density are described.

In each habitat section, an overview of the habitat as well as the various models that met the review inclusion criteria are discussed. Models that do not have a specific name are discussed by author name and year. For all models, the processes and stressors included are reviewed in more detail and explicitly denoted within a table that describes model use elements (i.e., spatiotemporal scale and extent, and model-specific details), and the physical and biological drivers and processes included (following Figure 2).

4 | COASTAL ZONE HABITAT VEGETATION SIMULATION MODELS

4.1 | Coastal dune habitats

Coastal dunes line the periphery of beaches in developed and natural settings worldwide as the first line of defense during storms (Martínez & Vázquez, 2006). The role of plants to structure foredunes and other coastal dune habitats was first recognized over a century ago (Cowles, 1899; Warming, 1891). Modeling efforts surrounding this habitat have historically been predominantly geomorphological, lacking the inclusion of vegetation and or biological processes affecting vegetation (Jackson & Nordstrom, 2019; USACE, 1995; Walker et al., 2017). In the past two decades there has been increased inclusion of plants and nature-based solutions as part of beach and dune management (Baas, 2002; Elko et al., 2016; Feagin et al., 2015). There are currently nine dune models that meet the review criteria (Table 1). However, some widely used simulation models did not meet the review criteria, but have been expanded to begin to incorporate vegetation components, namely XBEACH (Roelvink et al., 2009) and CSHORE (Johnson et al., 2012), which can now include how vegetation impacts wave setup and runup, with vegetation treated as a constant static roughness component. Although they do not meet the review criteria because of their lack of hydrodynamic forcings, it should be noted that inland dunefield and arid desert dune models, such as Werner (1995), Nishimori et al. (1998), and Durán and Herrmann (2006), are considered seminal for coastal dune models and can be applied to coastal dunes. The Discrete Ecogeomorphic Aeolian Landscape (DECAL) dunefield model (Nield & Baas, 2008), lacking hydrodynamics, is treated as an exception to this. It is included because it has been applied to coastal systems in multiple instances (e.g., Galiforni-Silva et al., 2020; Zhang & Baas, 2012) and has subsequently served as the theoretical background for other coastal dune models (e.g., Keijsers et al., 2016).

Models have predominantly simulated spatiotemporal changes in dune vegetation as percent cover or height in response to aeolian burial and erosion events where vegetation decreases aeolian sediment transport and causes deposition. Dune habitat models that emphasize landscape evolution through hydrodynamic or aeolian processes have comparatively fewer biological elements. Eight models include vegetation in this manner: de Castro (1995), Baas (2002), DECAL (Nield & Baas, 2008), de Luna et al. (2011), Coastal Dune Model (CDM; Durán & Moore, 2013, 2015), a modified version of the CDM (Moore et al., 2016), Dune, Beach, and Vegetation model (DUBEVEG; Keijsers et al., 2016), and DUNA (Roelvink & Costas, 2019). In comparison, the DOONIES model (Charbonneau et al., 2022) is centered around plant biology as its main emphasis while the geomorphological elements are comparatively simple.

The timestep of all dune habitat models varies from hourly to multi-year largely as a function of the different levels of complexity regarding tidal cycles and aeolian forcings. Model details and the various processes included in the models are in Table 1, respectively, where most grass species are modeled after *Ammophila*.

4.2 | Coastal wetlands

Wetland habitats found along tidal extents of bays, estuaries, and inlets include salt marshes (Section 4.2.1), mangrove forests (Section 4.2.2), and tidal freshwater wetlands (Section 4.2.3). Forested non-tidal coastal wetlands are also discussed (Section 4.4). Coastal landscape models that simulate the vegetation dynamics of all coastal wetland types across coastal ecotones are discussed separately as their spatial scale and scope encompasses multiple habitat types (Section 4.5). Coastal wetlands are highly productive carbon sinks, encompassing a large proportion of the global blue carbon budget (Duarte et al., 2013). They provide storm protection (i.e., wave attenuation and shoreline stabilization), valued at over $23 billion (USD) annually in the United States alone (Costanza et al., 2008), and capture sediment which increases elevation relative to sea level rise (SLR) (Hanley et al., 2020). As a result, models may be applied towards addressing issues related to storm response and coastal squeeze (i.e., coastal habitat loss where natural landward retreat of habitats in response to SLR is blocked by development) under different SLR scenarios. In these habitats, vegetation has predominantly been treated dynamically due to the influence of water levels on biomass.

TABLE 1 Model summary, physical and biological drivers and processes, and vegetation representation included in the nine reviewed dune models.

Model	Model summary and application details	Vegetation	Physical processes	Community-scale processes	Plant-scale processes	Organ system biomass allocation	Vegetation metrics
de Castro, 1995	Beach and dune elevation change on rectilinear grid *Timestep*: Annual *Coupling*: n/a	Single generic dune species	*Geodynamics*: avalanching *Sediment transport*: erosion and accretion (unidirectional aeolian transport), downwind sheltering *Resources available*: water table (phreatic zone) depth	-	*Mortality*: distance to water table and burial	*Implicit*: Above-ground	-Plant density
Baas, 2002	Beach and dune elevation change on rectilinear grid *Timestep*: Seasonal *Coupling*: n/a	Burial tolerant, burial intolerant species	*Geodynamics*: avalanching *Sediment transport*: erosion and accretion (stochastic), downwind sheltering	-	-	*Implicit*: Above-ground	-Percent cover
DECAL (Nield & Baas, 2008)	Dune elevation change on rectilinear grid Successor to Baas[a] *Timestep*: Annual *Coupling*: n/a	Grass, mesquite shrub, shrub	*Geodynamics*: avalanching *Sediment transport*: erosion and accretion (unidirectional aeolian transport), downwind sheltering	-	-	*Implicit*: Above-ground	-"Veg effectiveness" akin to percent cover
De Luna et al., 2011	Beach and dune elevation change on rectilinear grid *Timestep*: Annual *Coupling*: n/a	Single generic dune species	*Geodynamics*: avalanching *Sediment transport*: erosion and accretion (aeolian transport)	-	-	*Implicit*: Above-ground	-Plant height
CDM (Durán & Moore, 2013 & 2015)	Beach and dune elevation change along transect Adapted from Durán and Herrman[b] *Timestep*: sub-daily for physical processes, sub-weekly for vegetation *Coupling*: AEOLIS[c] XBEACH[d] via Windsurf[e] and CreST integrated model[f]	Single generic dune species	*Sediment transport*: onshore aeolian transport, wave transport *Geodynamics*: avalanching *Hydrodynamics*: tidal range; SLR (distance to shoreline, elevation) *Disturbances*: high water events (distance to shoreline, elevation)	-	-	*Implicit*: Above-ground	-Percent cover
Moore et al., 2016	Beach and dune elevation change along transect Modified version of CDM[g] with additional surface and vegetation dynamics	Single generic dune species	*Geodynamics*: avalanching; shoreline progradation *Hydrodynamics*: tide range; SLR *Disturbances*: high water events (distance to shoreline, elevation)		*Mortality*: sand erosion *Dispersal*: lateral (implicit)	*Implicit*: Above-ground	-Percent cover

(Continues)

TABLE 1 (Continued)

Model	Model summary and application details	Vegetation	Physical processes	Community-scale processes	Plant-scale processes	Organ system biomass allocation	Vegetation metrics
	Timestep: sub-daily for physical processes, sub-weekly for vegetation *Coupling*: n/a		*Sediment transport*: aeolian transport; wave transport				
DUBEVEG (Keijsers et al., 2016)	Integrated (wind, tide, vegetation modules) beach and foredune elevation change on a rectilinear grid Modified from DECAL[h] *Timestep*: weekly wind, biweekly tides, and annual vegetation change *Coupling*: n/a	Burial tolerant, burial intolerant	*Geodynamics*: avalanching *Hydrodynamics*: tidal fluctuations; wave runup and dissipation; SLR *Sediment transport*: unidirectional aeolian transport; downwind sheltering *Resources available*: groundwater level	*Dispersal*: Seed	*Dispersal*: lateral expansion	*Implicit*: Above-ground	-Percent cover
DUNA (Roelvink & Costas, 2019)	Beach and dune elevation change along transect *Timestep*: hourly *Coupling*: XBEACH[d]	Erect and spreading herbaceous, small rounded stemless plants	*Geodynamics*: avalanching *Hydrodynamics*: wave runup (XBEACH[d] coupling) *Sediment transport*: multidirectional aeolian transport; downwind sheltering *Resources available*: soil moisture	-	-	*Implicit*: Above-ground	-Height -Percent cover
Dune ecOgeOmorphic vegetatioN communIty photosynthEsis-driven Spatial model DOONIES (Charbonneau et al., 2022)	Modular beach and dune elevation and vegetation change on a rectilinear grid *Timestep*: daily *Coupling*: CSHORE[i]	Dune builders, burial tolerant stabilizers, burial intolerant stabilizers (can be parameterized for more)	*Climate*: temperature *Hydrodynamics*: water level *Disturbances*: simulated storm event *Sediment transport*: multidirectional stochastic aeolian transport	*Dispersal*: seed/wrack	*Dispersal* *Mortality*: elevation, distance to ocean, erosion, burial *Photosynthesis* *Respiration* *Senescence* (seasonal)	*Explicit*: Above- and below-ground -Dead biomass (root, stem, and leaf) -Green biomass (root, stem, and leaf)	-Community density -Plant -Density -Stem diameter -Root length -Height -Stem density

Note: n/a, not applicable.
[a]Baas (2002),
[b]Durán and Herrmann (2006),
[c]Hoonhout and de Vries (2016),
[d]Roelvink et al. (2009),
[e]Cohn et al. (2019),
[f]Ruggiero et al., 2019,
[g]Durán and Moore (2013, 2015),
[h]Nield and Baas (2008),
[i]Johnson et al. (2012).

TABLE 2 Model summary, physical and biological drivers and processes, and vegetation representation included in the 17 reviewed salt marsh models.

Model	Model summary and application details	Vegetation	Physical processes	Community-scale processes	Plant-scale processes	Organ system biomass allocation	Vegetation metrics
MEM/CWEM (Morris et al., 2002)	Marsh elevation change (point-based) *Timestep*: Annual *Coupling*: *n/a*	Single species, (parameterized as *Spartina alterniflora*)	*Hydrodynamics*: tide range; SLR *Sediment transport*: deposition	-	*Production*: Inundation	*Implicit*: Above-ground	-Biomass productivity
Mudd et al., 2004	Marsh surface evolution along transect (perpendicular to tidal creek) *Timestep*: Month *Coupling*: n/a	Single species (parameterized as *Spartina alterniflora*)	*Hydrodynamics*: tide range; SLR *Sediment transport*: (as function of plant structure) deposition	-	*Production*: Seasonality, Inundation	*Implicit*: Above-ground	-Biomass productivity
D'Alpaos et al., 2007	Long-term marsh platform and channel network evolution on a rectilinear grid *Timestep*: Annual *Coupling*: n/a	Single species (parameterized as *Spartina alterniflora*)	*Hydrodynamics*: tide range; SLR *Sediment transport*: (as function of plant structure) deposition; erosion	-	*Production*: Inundation	*Implicit*: Above-ground	-Biomass productivity
Kirwan & Murray, 2007	Marsh platform and channel network evolution on a rectilinear grid *Timestep*: Monthly *Coupling*: n/a	Single species (parameterized as *Spartina alterniflora*)	*Hydrodynamics*: tide range; SLR *Sediment transport*: (as function of plant presence) deposition; erosion	-	*Production*: Inundation	*Implicit*: Above-ground	-Biomass productivity
Temmerman et al., 2007	Marsh platform and channel network evolution via, and vegetation model *Timestep*: Hydrodynamics aggregated over tidal cycle, morphodynamics and vegetation dynamics annual *Coupling*: integrated Delft3D[a] hydrodynamic, morphodynamic	Single species (parameterized as *Spartina anglica*)	*Hydrodynamics*: tide range *Sediment transport*: (as function of plant structure) deposition; erosion	*Dispersal*	*Establishment Growth Mortality*: inundation, flow	*Explicit*: Above-ground	-Stem density
Mariotti & Fagherazzi, 2010	Marsh surface and tidal flat evolution (perpendicular to tidal creek) along transect *Timestep*: Sub-hourly *Coupling*: n/a	Single species (generic)	*Hydrodynamics*: tide range; SLR; wind-induced waves *Sediment transport*: (as function of plant structure) deposition; erosion	-	*Production*: inundation	*Implicit*: Above-ground	-Biomass productivity
Marani et al., 2013	-Marsh surface and tidal flat evolution along transect	Three species (generic)	*Hydrodynamics*: tide range; SLR		*Production*: inundation	*Implicit*: Above-ground	-Biomass productivity

(Continues)

TABLE 2 (Continued)

Model	Model summary and application details	Vegetation	Physical processes	Community-scale processes	Plant-scale processes	Organ system biomass allocation	Vegetation metrics
	(perpendicular to tidal creek) *Timestep*: Annual *Coupling*: n/a		*Sediment transport*: deposition	*Dispersal*: fittest-take-all or random colonization *Competition*: stochastic			
WARMER (Swanson et al., 2014)	Marsh elevation change (point-based) *Timestep*: Monthly *Coupling*: n/a	Three species (parameterized as *Spartina alterniflora*, *Spartina foliosa*, *Spartina pacifica*	*Hydrodynamics*: tide range; SLR *Sediment transport*: deposition	-	*Production*: inundation	*Implicit*: Above-ground	-Biomass productivity
Belliard et al., 2015	Marsh platform and channel network evolution via integrated hydrodynamic, morphodynamic, and vegetation model on an unstructured grid *Timestep*: Hydrodynamics aggregated over tidal cycle, morphodynamic and vegetation adjusted by variable morphological factors (M*tidal period) *Coupling*: n/a	Single species (parameterized as *Spartina alterniflora*) or multiple species	*Hydrodynamics*: tide range; SLR *Sediment transport*: (as function of plant structure) deposition; erosion	-	*Production*: inundation	*Implicit*: Above-ground	-Biomass productivity
Hydro-MEM (Alizad et al., 2016)	Marsh platform and channel network evolution via integrated hydrodynamic and marsh (MEM) models on a rectilinear grid *Timestep*: Annual *Coupling*: ADCIRC[b]	Single species (parameterized as *Spartina anglica*)	*Hydrodynamics*: tide range; SLR *Sediment transport*: deposition	-	*Production*: inundation	*Implicit*: Above-ground	-Biomass productivity
Kirwan et al., 2016	Marsh surface and tidal flat evolution and migration along transect (perpendicular to marsh edge) *Timestep*: Annual *Coupling*: n/a	Single species (parameterized as *Spartina alterniflora*)	*Hydrodynamics*: tide range; SLR *Sediment transport*: (as function of plant type and presence) deposition; erosion	-	*Production*: inundation	*Implicit*: Above-ground	-Biomass productivity
Bio-geomorphological model (Best et al., 2018)	Marsh platform and channel network evolution/ vegetation model *Timestep*: Seasonal	Single species (parameterized as *Spartina anglica*)	*Hydrodynamics*: tide range; SLR; wave action *Sediment transport*: deposition; erosion	*Dispersal*: random colonization	*Growth*: seasonality *Senescence* *Dispersal*: diffusion	*Explicit*: Above-ground	-Stem density

(Continues)

TABLE 2 (Continued)

Model	Model summary and application details	Vegetation	Physical processes	Community-scale processes	Plant-scale processes	Organ system biomass allocation	Vegetation metrics
	Coupling: integrated Delft3D[a] hydrodynamic and morphodynamic submodel				*Mortality*: erosion, deposition, inundation, flow (uprooting)		
Brückner et al., 2019	Marsh platform and channel network evolution via integrated hydromorphodynamic and vegetation model on a rectilinear grid *Timestep*: Hydrodynamics and vegetation aggregated over tidal cycle (~12 h), morphodynamics scaled to spring/neap cycle (~12 days) *Coupling*: n/a	Single generic species (based on *Spatina anglica* and *Salicornia* spp.)	*Hydrodynamics*: water level; uprooting *Sediment transport*: deposition; erosion	*Dispersal*: colonization	*Establishment* *Growth* *Mortality*	*Explicit*: Above- and below-ground	-Stem density -Stem diameter -Stem height -Percent cover -Root length
Sedveg (Brown et al., 2019)	Wetland sediment model (integrated into SEDLIB) that includes vegetation productivity *Timestep*: seconds *Coupling*: Adaptive Hydraulics (AdH)[c]	Single generic species	*Hydrodynamics*: water level (tides + river level); SLR *Sediment transport*: deposition; erosion	-	*Production*: inundation	*Implicit*: Above-ground	-Biomass productivity
Langston et al., 2020	Marsh elevation change on a rectilinear grid *Timestep*: Annual *Coupling*: n/a	Two species (parameterized as *Spartina alterniflora* and *Spartina patens*)	*Hydrodynamics*: SLR; elevation as proxy for water levels *Sediment transport*: deposition	-	*Production*: elevation	*Implicit*: Above-ground	-Biomass productivity
Marsh Morpho2D (Mariotti, 2020)	Marsh surface, flat, channel, pond, and edge evolution on rectilinear grid *Timestep*: Annual *Coupling*: n/a	Single generic species	*Hydrodynamics*: tide range; ponding; SLR; wave action *Sediment transport*: deposition; erosion	-	*Production*: inundation, erosion, ponding	*Implicit*: Above-ground	-Biomass productivity
Rietl et al., 2021	Marsh elevation and carbon content evolution in soil column (point-based) *Timestep*: Annual *Coupling*: n/a	Two species (parameterized as *Spartina patens* and *Schoenopletus americanus*)	*Climate*: changing CO_2 concentrations *Hydrodynamics*: SLR; water level *Local environment*: salinity	-	*Growth*: inundation, response to elevated CO_2	*Implicit*: Above- and below-ground	-Total biomass productivity

Note: n/a, not applicable.
[a]Deltares (2014),
[b]Luettich et al. (1992),
[c]Savant et al. (2020).

4.2.1 | Salt marsh

The term coastal salt marsh includes brackish and intermediate marshes with average salinity levels greater than 5 ppt using the limits described in Mitsch and Gosselink (2015). Like dune models, numerical modeling applications in salt marshes initially focused on geomorphic evolution (i.e., vertical accretion) under varying SLR and sediment supply scenarios (e.g., Allen, 1990; French & Spencer, 1993; Krone, 1985; Temmerman et al., 2003). However, marsh ecology and geomorphology are tightly coupled such that the presence of vegetation further enhances vertical accretion by trapping mineral sediment and directly adding organic material (Fagherazzi et al., 2012; Morris et al., 2002). There are currently 17 salt marsh models that meet the review criteria (Table 2).

The basis of most salt marsh models is a sediment cohort modeling approach simulating autochthonous organic sediment production (Allen, 1990; Callaway et al., 1996; Morris & Bowden, 1986), but vegetation productivity and model parameters related to vegetation in these models is assigned rather than explicitly simulated. For an overview of salt marsh morphodynamic processes, modeling approaches, and challenges, see Fagherazzi et al. (2020). The Marsh Equilibrium Model (MEM), renamed the Coastal Wetland Equilibrium Model (CWEM) (Morris et al., 2019), a zero-dimensional (i.e., patch-scale) model that predicts marsh elevation change, is the first model implicitly incorporating biomass productivity using the sediment cohort modeling approach; it simulates biomass productivity in single-species zones as a function of hydroperiod (Morris et al., 2002). This model is further discussed in Section 4.2.2.

The biomass productivity-inundation relationship utilized in MEM/CWEM has been adapted and/or reformulated for more spatially complex models (i.e., transect and two-dimensional [2D] local and regional models) demonstrating feedbacks between hydrodynamics, vegetation, and sedimentation (Alizad et al., 2016; D'Alpaos et al., 2007; Kirwan et al., 2007; Kirwan et al., 2016; Langston et al., 2020; Marani et al., 2013; Mudd et al., 2004), additional species (Swanson et al., 2014), and/or additional physical processes (Mariotti, 2020; Mariotti & Fagherazzi, 2010). In these models, biomass increases sediment deposition and elevation, altering inundation frequency and duration, leading to further biomass adjustments. Temmerman et al. (2007), Best et al. (2018), and Brückner et al. (2019) modeled marsh evolution at a local scale through a coupled hydrodynamic, morphodynamic, plant growth model using Delft3D software with varying levels of ecological complexity. Belliard et al. (2015) similarly determined the impact of vegetation parameterization on channel morphology using a different set of coupled hydrodynamic and morphodynamic models. Plant structure directly impacts hydrodynamics (i.e., turbulence and drag), which affect plant establishment, growth, dispersal, and mortality explicitly calculated through the plant growth module. More recent models have explicitly incorporated additional physical process feedbacks to simulate the effects climate change on salt marsh systems (i.e., Rietl et al., 2021) or have been employed to assess the effects of marsh management techniques such as freshwater diversions using the similar inundation-biomass relationships as other patch-scale marsh models such as MEM (e.g., Brown et al., 2019). For simplicity, most of these models assume a single vegetation class (commonly *Spartina alterniflora*) that represents a marsh vegetation zone as opposed to a broader suite of taxa and communities impacting landscape level dynamics (Section 4.6).

Salinity gradients control the distribution of salt marsh species, with biodiversity inversely correlated with salinity. Since many models were developed for classical salt marsh communities with salinity levels close to those of seawater, salinity is not explicitly considered in all models, limiting their value in brackish and transitional marsh systems where salinity gradients control productivity and distribution (Mitsch & Gosselink, 2015).

4.2.2 | Mangroves

Mangrove forests are highly productive, salt-tolerant habitats found in tropical and subtropical coastal regions. Because individual mangrove trees evolve over relatively long temporal scales, relative to other coastal vegetation (i.e., salt marshes), making it more difficult to collect observational and experimental data, models are useful tools to simulate these longer-term forest dynamics.

Canopy dynamics and the effect of resource availability, mainly light availability, drive growth, survival, and seedling success in mangrove and other woody vegetation forest models (Busing & Mailly, 2004). Most mangrove models are individual-based gap models focusing on stand and canopy-level changes induced by localized change in individual trees or tree patches. Forest gap models are discussed in more detail in Section 4.4. Most mangrove models quantify above-ground biomass, but very few calculate below-ground biomass due to limited allometric relationships between above- and below-ground biomass (Komiyama et al., 2005, 2008).

There are currently five models that meet the review criteria for mangroves (Table 3). FORMAN was the first application of an individual-based gap model in mangrove habitats, and simulated establishment, growth, and mortality as a function of soil characteristics and light availability (Chen & Twilley, 1998). Both KIWI (Berger & Hildenbrandt, 2000) and mesoFON (Grueters et al., 2014) build upon FORMAN and include a field of neighborhood (FON) approach, which considers density-dependent interactions in both above- and below-ground resources. BETTINA (Peters et al., 2014), also applies the FON, but explicitly includes below-ground biomass and allocation adjustments between above- and below-ground biomass based on resource limitations. While the former models mostly focused on general competition between trees, Teh et al. (2008) explores competition between mangroves and hardwood hummocks following a disturbance. Additional notable mangrove models are MANGO (Doyle, Girod, & Books, 2003) and MANHAM (Sternberg et al., 2007), but are not included in the table given that the necessary details to recreate the model and determine how it functions are absent from the literature (Doyle et al., 2003) and because it does not simulate growth or the plant-scale processes that determine growth, respectively. Additionally, there are two integrated models of note not included in Table 3, MANTRA (Teh et al., 2013) which is the integration of Teh et al. (2008) and MANHAM for modeling vegetation and vadose zone hydrology combined with the USGS model SUTRA (Voss & Provost, 2002) for groundwater hydrology and salinity, and MANGA (Bathmann et al., 2020) which is the coupling of BETTINA for

TABLE 3 Model summary, physical and biological drivers and processes, and vegetation representation included in the five reviewed mangrove models.

Model	Model summary and application details	Vegetation	Physical processes	Community-scale processes	Plant-scale processes	Organ system biomass allocation	Vegetation metrics
FORMAN (Chen & Twilley, 1998)	Gap dynamic model to simulate demographic processes of mangroves on a rectilinear grid Based on JABOWA and FORET models *Timestep*: Annual *Coupling*: n/a	Three species (parameterized as *Laguncularia racemose, Rhizophora mangle, Avicennia germinans)*	*Climate*: temperature *Hydrodynamics*: flooding *Disturbances*: storms *Resources available*: light; soil phosphorus	*Competition*: light *Dispersal*: Seed/sapling	*Mortality*	*Explicit*: Above-ground	-Diameter at breast height (DBH) -Basal area -Leaf area index (LAI)
KIWI (Berger & Hildenbrandt, 2000)	Mangrove demographic processes using a field of neighborhood approach *Timestep*: Annual *Coupling*: n/a	Two species (parameterized as *A. germinans, R. mangle*	*Local environment*: soil salinity Any abiotic factor varying spatially can be included with bitmap representation	*Competition*: generic *Dispersal*: Seed/sapling	*Mortality*	*Explicit*: Above-ground	-Biomass (t ha^{-1}) -DBH -Height
Teh et al., 2008	Competition between mangroves and hardwood hammocks on a rectilinear grid *Timestep*: Daily *Coupling*: n/a	Woody freshwater hammock and mangrove	*Climate*: precipitation; evaporation *Hydrodynamics*: tidal range *Disturbances*: storms (flooding) *Local environment*: soil salinity; soil infiltration *Resources available*: light	*Competition*: light *Dispersal*: seed	*Resource availability*: water *Respiration* *Transpiration*	*Explicit*: Above-ground	-Active leaf tissue -Biomass (carbon) -Dead leaf tissue -LAI
MesoFON (Grueters et al., 2014)	Individual-based mangrove forest dynamics model using field of neighborhood approach *Timestep*: Annual Coupling: n/a	Multispecies (parameterized as *R. mangle* of two functional types, but can take up to 10 species)	*Local environment*: soil salinity; hydraulic conductivity *Disturbances*: storms *Resources available*: light; soil phosphorus	*Competition*: above- and below-ground *Dispersal*: function of tree size	*Mortality* *Morphology*: crown displacement *Growth*: function of salinity, nutrients, and competition	*Explicit*: Above-ground	-DBH -Height -LAI -Quadratic mean DBH -Stand basal area -Stand stem volume
BETTINA (Peters et al., 2014)	Individual-based model to assess mangrove biomass and distribution *Timestep*: variable *Coupling*: n/a	Single generic species	*Hydrodynamics* *Local environment*: soil salinity; hydraulic conductivity *Resources available*: light	-	*Growth*: implicit empirical relationships representing photosynthesis and respiration *Morphology*: biomass allocation *Mortality* *Translocation*	*Explicit*: Above- and below-ground	-Basal area -Height -Volume -Root types -Root radius

Note: n/a, not applicable.

mangrove dynamics and OpenGeoSys (Kolditz et al., 2012) to model porewater salinity hydrodynamics.

As noted previously in Section 4.2.1, the MEM was recently re-parameterized for mangroves as a CWEM case study simulation in an ongoing effort to expand the model (Chapman et al., 2021; Morris et al., 2019). Valuable resources on the state of mangrove modeling are Twilley and Rivera-Monroy (2005) with an in-depth review of mangrove models and Peters et al. (2020) with an updated synopsis on the state-of-the-art in mangrove stand modeling. Both provided commentary on existing model shortcomings and suggested processes and measurements relevant for conservation and management that an "ideal" mangrove model should include.

4.2.3 | Tidal freshwater wetlands

Tidal freshwater wetlands extend inland past the extent of saline waters (salinity < 5 ppt) to the head of tide. This zone varies in extent by topography and tide range with the widest tidal freshwater wetland bands occurring along river deltas and coastlines (moderate to high tide ranges) of low relief. These wetlands can be split into two sub-habitats by the dominant vegetation community: herbaceous marshes and tidal swamp or floodplain forests. Herbaceous marshes include two distinct sub-types: floating marshes regionally referred to as flotant and newly formed marshes within large river deltas (Mitsch & Gosselink, 2015). With the continued influence of tidal exchange absent salinity stresses, tidal freshwater wetlands tend to be high in diversity and productivity. Tidal floodplain forests resemble bottomland hardwood forests in structure and function although their morphology is characterized by ridges and swales.

Few models have been specifically designed for tidal freshwater wetlands given that they are geographically constrained and encompass many species (Morris & Bowden, 1986; Temmerman et al., 2003). Only three tidal forest models were included in this review (Carr et al., 2020; Hoeppner & Rose, 2011; Rybczyk et al., 1998) and are described in Section 4.4. The salt marsh models (Section 4.2.1), WARMER (Swanson et al., 2014; Thorne et al., 2018) and MEM (Schile et al., 2014), and forest model FORFLO (Section 4.4; Conner & Brody, 1989) have been adapted and applied to herbaceous tidal freshwater marsh and tidal swamp forests, respectively.

4.3 | Seagrass beds

Seagrasses are submerged, flowering plants found in shallow temperate and tropical marine environments. They provide a wealth of ecosystem services including critical fish and endangered species habitat, nutrient cycling and sequestration, and sediment stabilization (Hanley et al., 2020; Unsworth et al., 2019). However, seagrass populations are globally in decline, largely due to poor water quality, increased coastal development, and climate change (Duarte et al., 2013; Orth et al., 2006). Numerical model development has aided in efforts to restore, expand, and protect these sensitive habitats by improving distribution predictions to better understand habitat dynamics and inform management actions.

Of the 15 models meeting the review criteria (Table 4), some were developed aiming to improve mathematical simulations of seagrass growth (i.e., Short et al., 1980) or community distribution (Baird et al., 2016; Fong & Harwell, 1994), while others have direct management applications (i.e., Carr et al., 2012; Cerco & Moore, 2001; Yoshikai et al., 2021). All models simulate seagrass dynamics, usually at a patch scale, but Cerco and Moore (2001), Plus et al. (2003), Baird et al. (2016), and Yoshikai et al. (2021) are spatially explicit, calculating seagrass distribution at local and regional scales.

All models incorporate light and water temperature as physical climactic drivers and photosynthesis and respiration as plant-scale drivers. Although respiration is considered a loss term in all models, mortality is explicitly defined, as senescence or physical stress, except in Bocci et al. (1997), Cerco and Moore (2001), and Elkalay et al. (2003). Nutrient concentration is omitted as a physical driver in Short et al. (1980), Verhagen and Nienhuis (1983), Zharova et al. (2001), and Carr et al. (2010, 2012) and translocation is not explicitly included as a plant-scale process in Short et al. (1980), Verhagen and Nienhuis (1983), Fong and Harwell (1994), Zharova et al. (2001), and Carr et al. (2010).

Light availability and water temperature constrain seagrass growth in all included models. Light attenuation through the water column due to water color and turbidity is accounted for in all models. Some models also include epiphytic attenuation (e.g., Cerco & Moore, 2001; Madden & Kemp, 1996; Wetzel & Neckles, 1986) and self-shading in canopy dynamics affected by density and/or leaf area (Baird et al., 2016; Wetzel & Neckles, 1986). Photosynthesis and respiration rates are both temperature-dependent and seasonally variable in all models. However, the relative importance of temperature likely varies latitudinally with less import in tropical regions (Yoshikai et al., 2020). Additional growth limiting factors in some models include water column and sediment nutrients affecting shoot and belowground growth, respectively (i.e., Bocci et al., 1997; Cerco & Moore, 2001, etc.) and space (i.e., Bocci et al., 1997; Elkalay et al., 2003; Verhagen & Nienhuis, 1983; Wetzel & Neckles, 1986; Zharova et al., 2001).

4.4 | Coastal forests

Coastal forests (i.e., maritime and floodplain forests) are important woody-dominated, semi-terrestrial, peripheral habitats, but are coastally influenced to a lesser extent than the previously discussed habitats because they are typically more inland and typically non-tidal. Unlike dunes, tidal wetlands, and seagrass beds, coastal forests are unlikely to keep pace with SLR via vertical growth or landward migration given the intolerance to saltwater inundation combined with the relatively longer timespan of successional processes as well as proximity to surrounding development (Grieger et al., 2020).

Inland along many sandy coasts, including barrier islands, maritime forests are the apex or final successional stage of dune ecosystems. They provide critical habitat and stopover sites for resident vertebrates and migratory birds worldwide, respectively (Chamberlain, 1982). They potentially sequester more carbon than associated non-coastal inland forests (Smart et al., 2020), but their role in carbon budgets has not been incorporated (Howard et al., 2014). Despite their importance, maritime forests are generally research-poor and no habitat-specific modeling efforts were found.

TABLE 4 Model summary, physical and biological drivers and processes, and vegetation representation included in the 15 reviewed seagrass models.

Model	Model summary and details	Vegetation	Physical processes	Community-scale processes	Plant-scale processes	Organ system biomass allocation	Vegetation metrics
Short, 1980	Seagrass dynamics (point-based) *Timestep*: Daily *Coupling*: n/a	Single species (parameterized as *Zostera marina*)	*Climate*: water temperature *Hydrodynamics*: current speed *Resources available*: light	-	*Mortality* *Photosynthesis* *Respiration* *Translocation*	*Explicit*: Above- and below-ground	-Biomass (leaves, roots, and rhizomes) -Blade length -Leaf area index -Rhizome length
Verhagen & Nienhuis, 1983	Seagrass dynamics (point-based) *Timestep*: sub-daily *Coupling*: n/a	Single species (parameterized as *Zostera marina*)	*Climate*: water temperature *Hydrodynamics*: wind-generated waves *Resources available*: light	*Competition*: Space (density-dependent above-ground limiting factor)	*Mortality* *Photosynthesis* *Respiration*	*Explicit*: Above- and below-ground	-Biomass (shoot, roots, and rhizomes) -Shoot density
Wetzel & Neckles, 1986	Seagrass dynamics (point-based) *Timestep*: Hourly *Coupling*: n/a	Single species (parameterized as *Zostera marina*)	*Climate*: water temperature *Resources available*: light (includes epiphyte growth and self-shading); CO_2 concentrations	*Competition*: Space (density-dependent above-ground limiting factor)	*Mortality* (includes grazing) *Photosynthesis* *Respiration* *Translocation*	*Explicit*: Above-ground	-Biomass (leaves and epiphytes)
Bach, 1993	Seagrass dynamics (point-based) *Timestep*: Daily *Coupling*: n/a	Single species (parameterized as *Zostera marina*)	*Climate*: water temperature *Hydrodynamics*: waves *Resources available*: light; nutrient concentrations (sediment and water column)		*Mortality* *Photosynthesis* *Respiration* *Translocation*	*Explicit*: Above- and below-ground	-Biomass (shoots and roots) -Shoot density
Fong & Harwell, 1994	Seagrass community dynamics *Timestep*: Daily *Coupling*: n/a	Three species (*Thalassia testudinum, Halodule wrightii, Syringodium filiforme)*	*Climate*: water temperature *Local environment*: salinity *Resources available*: light (includes epiphyte growth); nutrient concentrations (sediment and water column)		*Mortality* *Photosynthesis* *Respiration*	*Explicit*: Above-ground	-Biomass (shoots and epiphytes)
Madden & Kemp, 1996	Ecological model to investigate eutrophication on seagrass (point-based) *Timestep*: Sub-daily *Coupling*: n/a	Single species (parameterized as *Potamogeton perfoliatus*)	*Climate*: water temperature *Resources available*: light (includes epiphyte growth); nutrient concentrations (sediment and water column)		*Photosynthesis* *Respiration* *Translocation*	*Explicit*: Above- and below-ground	-Biomass (shoots, roots and rhizomes, epiphytes)
Bocci et al., 1997	Biomass and nutrient dynamics in seagrass bed (point-based) *Timestep*: Daily *Coupling*: n/a	Single species (parameterized as *Zostera marina*)	*Climate*: water temperature *Resources available*: light; nutrient concentrations (sediment and water column)	*Competition*: Space (biomass-dependent above-ground limiting factor)	*Photosynthesis* *Respiration* *Translocation*	*Explicit*: Above- and below-ground	-Biomass (shoots, roots, and rhizomes)

(Continues)

TABLE 4 (Continued)

Model	Model summary and details	Vegetation	Physical processes	Community-scale processes	Plant-scale processes	Organ system biomass allocation	Vegetation metrics
Cerco & Moore, 2001	Seagrass biomass dynamics on a rectilinear grid *Timestep*: Daily *Coupling*: Part of Chesapeake Bay Environmental Modeling Package	Two species (parameterized as *Zostera marina* and *Ruppia maritima*)	*Climate*: water temperature *Resources available*: light (includes epiphyte growth); nutrient concentrations (sediment and water column)		*Photosynthesis* *Respiration* *Translocation*	*Explicit*: Above- and below-ground	-Biomass (shoots, roots, and epiphytes)
Zharova et al., 2001	Seagrass dynamics (point-based) *Timestep*: Daily *Coupling*: n/a	Single species (parameterized as *Zostera marina*)	*Climate*: water temperature *Hydrodynamics*: waves *Resources available*: light	*Recruitment* *Competition*: Space (density-dependent above-ground limiting factor)	*Mortality* *Photosynthesis* *Respiration*	*Explicit*: Above- and below-ground	-Biomass (shoots and roots) -Shoot density
Elkalay et al., 2003	Seagrass biomass and production dynamics (point-based) *Timestep*: Daily *Coupling*: n/a	Single species (parameterized as *Posidonia oceanica*)	*Climate*: water temperature *Resources available*: light (includes epiphyte growth); nitrogen concentrations (sediment and water column)	*Competition*: Space (limiting factor based on above- and below-ground biomass and epiphyte presence)	*Photosynthesis* *Respiration* *Translocation*	*Explicit*: Above- and below-ground	-Biomass (leaves, roots, rhizomes, and epiphytes) -Nitrogen concentration in seagrass
MEZO-1D (Plus et al., 2003)	Integrated ecosystem model on a rectilinear grid *Timestep*: Sub-hourly *Coupling*: seagrass biomass, plankton, and nitrogen dynamics	Single species (parameterized as *Zostera noltii*)	*Climate*: water temperature *Hydrodynamics*: waves *Resources available*: light (includes epiphyte growth); nitrogen concentrations (sediment and water column)	*Recruitment*	*Mortality* *Photosynthesis* *Respiration* *Translocation*	*Explicit*: Above- and below-ground	-Biomass (shoots, roots, rhizomes, and ephiphytes) -Nitrogen concentration (above- and below-ground) -Shoot density
Carr et al., 2010	Point-based *Timestep*: Hourly *Coupling*: Integrated hydrodynamic model of vegetation, sediment, and water flow interactions	Single species (parameterized as *Zostera marina*)	*Climate*: water temperature *Resources available*: light		*Photosynthesis* *Respiration*	*Explicit*: Above-ground	-Shoot density
Carr et al., 2012	Point-based *Timestep*: Hourly hydrodynamics, daily vegetation growth *Coupling*: Integrated hydrodynamic and vegetation growth	Single species (parameterized as *Zostera marina*)	*Climate*: water temperature *Resources available*: light	*Recruitment*	*Mortality* *Photosynthesis* *Respiration* *Translocation* *Morphology*: leaf elongation	*Explicit*: Above- and below-ground	-Biomass (shoots, roots, and rhizomes) -Shoot density

(Continues)

TABLE 4 (Continued)

Model	Model summary and details	Vegetation	Physical processes	Community-scale processes	Plant-scale processes	Organ system biomass allocation	Vegetation metrics
Baird et al., 2016	Seagrass processes module on a curvilinear grid *Timestep*: Daily *Coupling*: Integrated biogeochemical model	Two genera (parameterized as *Zostera* and *Halophila*)	*Climate*: water temperature *Resources available*: light (includes self-shading); nutrient concentrations (sediment and water column)		*Mortality* *Photosynthesis* *Respiration* *Translocation*	*Explicit*: Above- and below-ground	-Biomass (leaves and roots)
Yoshikai et al., 2021	Seagrass bed dynamics model on non-orthogonal grid *Timestep*: Hourly *Coupling*: Integrated hydrodynamic-biogeochemical (Delft3D-FLOW[a]) model	Two species (parameterized as *Thalassia hemprichii* and *Enhalus acoroides*)	*Resources available*: light (includes epiphyte growth); nitrogen concentrations (near-bottom water)	*Competition* (light)	*Mortality* *Photosynthesis* *Respiration* *Translocation*	*Explicit*: Above- and below-ground	-Biomass (shoots, roots, and epiphytes)

Note: n/a, not applicable.
[a]Deltares (2014).

Similarly, to our knowledge, no existing models, such as forest gap models, have been adapted or applied to this habitat.

Like maritime forests, coastal floodplain forests provide invaluable habitat, but are more globally abundant and diverse both in community composition and spatial extent (Wang et al., 2010). Coastal floodplain forests are seasonally or irregularly flooded by both coastally influenced stream or river levels and storms, but otherwise function like bottomland forests, allowing models developed for those systems to be applied directly or with minimal modification.

Few models have been explicitly designed for coastal forests; rather, models of these systems are often based on underlying principles of the seminal gap models JABOWA (Botkin et al., 1972), FORET (Shugart, 1984; Shugart & West, 1977), SORTIE (Pacala et al., 1993), and LANDIS II (de Jager et al., 2019; Scheller et al., 2007; Scheller & Mladenoff, 2004), which largely vary in how growth, competition, and seedling establishment are treated. Although some of these models would be applicable to the coastal forest system with some limited modifications, we only include models developed specifically for these systems in Table 5.

Both Rybczyk et al. (1998) and Hoeppner and Rose (2011) were specifically developed as coastal forest models. Carr et al. (2020) evolved from an earlier iteration of a coastal salt marsh model (Kirwan et al., 2016), incorporating coastal forest dynamics to better capture the migration of salt marsh into formally forested areas. Many hydrodynamic fluvial models were excluded from this review because vegetation is treated as a non-dynamic roughness component affecting shear stress, and reviewed in Corenblit et al. (2007).

4.5 | Coastal landscape models

Landscape vegetation models use observed or predicted changes in the spatial configuration of the landscape and associated autogenic physical drivers to predict associated changes in vegetation communities. Coastal change models that predict landcover categorically and lack productivity or biomass elements, such as SLAMM (Park et al., 1989; Warren-Pinnacle Consulting, 2016), MAIM (Cadol et al., 2016), and SLOPE (Doyle et al., 2010) are not included.

Six landscape models meet the review criteria, four of which were developed for simulating long-term changes in coastal Louisiana starting in the 1980s and the other two were developed for barrier islands (Table 6). Modeling efforts specific to coastal Louisiana began with the Coastal Ecological Landscape Spatial Simulation (CELSS; Costanza et al., 1988, 1990) which was developed from a more general landscape model (Sklar et al., 1985) and estimates primary productivity by wetland classes incorporating many abiotic forcings. The Barataria Terrebonne Ecological Spatial Simulation (BTELSS; Reyes et al., 2000) utilizes an expanded study area, and more advanced hydrodynamics and biomass simulation algorithms. Like CELSS, BTELSS classifies vegetation into broad habitat classes, but those classes are defined and parameterized for specific dominant species. The Louisiana Vegetation Model (LaVegMod; Visser et al., 2013; Visser & Duke-Sylvester, 2017) was designed to integrate with more advanced hydrodynamic models to better predict eco-geomorphic processes affecting topography. Its second version, LaVegMod v2 (Visser & Duke-Sylvester, 2017) includes 36 plant species simulated as mixed assemblages and includes more biological drivers

TABLE 5 Model summary, physical and biological drivers and processes, and vegetation representation included in the three reviewed coastal floodplain models.

Model	Model summary and application details	Vegetation	Physical processes	Community-scale processes	Plant-scale processes	Organ-system biomass allocation	Vegetation metrics
Rybczyk et al., 1998	Wetland elevation model application in subsided forested wetland (point-based) *Timestep*: Weekly *Coupling*: n/a	Aggregated forested wetland species	*Climate*: temperature *Hydrodynamics*: inundation	-	*Biomass turnover*: Decomposition, leaf litter production *Primary productivity*	*Implicit*: Above- and below-ground	-Leaf biomass -Leaf litter production -Root biomass -Total floating aquatic vegetation biomass -Wood biomass
Hoeppner & Rose, 2011	Individual-based swamp forest succession model on a rectilinear grid *Timestep*: Weekly *Coupling*: n/a	Two species (parameterized as *Taxodium distichum* and *Nyssa aquatica*)	*Climate*: season *Hydrodynamics*: inundation *Local environment*: salinity *Resources available*: light	*Competition* (light) *Dispersal* *Recruitment* *Space*	*Mortality*	*Explicit*: Above-ground	-Basal area -Seedling density -Wood production
Carr et al., 2020	Marsh to upland forest transgression along a transect *Timestep*: Annual *Coupling*: n/a	Two general taxa (Herbaceous/saltmarsh, tree)	*Climate*: wind *Hydrodynamics*: inundation (tidal) (elevation); SLR *Local environment*: salinity *Resources available*: light	*Competition*: space *Dispersal*	*Mortality* *Morphology*: root depth	*Implicit*: Above-ground	-

Note: n/a, not applicable.

compared to its predecessors. The LaVegMod habitat selection and allocation algorithms were incorporated into the Delft3D environment for the Integrated Biophysical Model to better represent vegetation dynamics by modeling species distribution and biomass allocation (Baustian et al., 2018). Biomass was simulated using the VEGMOD process within the Delft Water Quality library of Delft3D (Deltares, 2021). More information on VEGMOD is included in Section 4.6.

There were only two barrier island models that included vegetation, the ISLAND model and Barrier3D. The ISLAND model is a temporally-explicit blend of biological, geomorphological, and groundwater barrier island processes simulating four different generic vegetation taxa densities (Rastetter, 1991). Barrier3D it is a spatially-explicit exploratory model of barrier evolution where a recent shrub vegetation expansion and mortality module was created to simulate how changing vegetation dynamics impact barrier island topography over decades to centuries (Reeves, 2021; Reeves et al., 2022).

4.6 | Other relevant models

Throughout the course of the literature review, several models did not strictly fit the categories prescribed, but warrant mention given their advanced treatment of vegetation and potential applicability to coastal systems. This is not intended to be an exhaustive list of potentially applicable models as many water quality and hydrodynamic models include a wide variety of methods to account for the role of vegetation.

VEGMOD (Deltares, 2021) is a module within the Delft3D water quality suite and was designed to simulate terrestrial and macrophyte biomass as a nutrient cycling element for waterbodies such as manmade reservoirs. Carbon, nitrogen, phosphorus, and sulfur stored in vegetation stems, leaves, branches, roots, and fine roots are released to the detritus pools in the water and sediment matrix following inundation-induced vegetation mortality. Habitat niche spaces are defined so the model can be applied to a wide variety of systems (e.g., Baustian et al., 2018, see details on its application in Table 6).

The Soil Water Assessment Tool (SWAT; https://swat.tamu.edu) is a spatially semi-distributed, non-point source watershed to basin scale model that has been used to simulate groundwater dynamics, land-use change, environmental impacts, and climate change (Wang et al., 2019). SWAT is unique in that is has been used extensively (e.g., over 3400 papers published from 2008 to 2019; Wang et al., 2019). It contains a process-based native vegetation growth module that treats vegetation as a generalized entity where biomass production (in kg ha^{-1}) of a single plant community is a function of temperature, intercepted photosynthetic radiation (PAR), and leaf area index (LAI) (Neitsch et al., 2011). Parameterizations can vary for the species being modeled; SWAT contains a suite of species-specific parameters in its database. Similar to VEGMOD, vegetation is included as part of SWAT to quantify its effects on flow and nutrient dynamics. Vegetation outputs are coarse in comparison to the other vegetation dynamics models described previously. Recently, several modules have been developed to improve upon SWAT's vegetation growth functionality, from multispecies-based approaches (Lai et al., 2020) to refinements of processes included to better represent non-temperate species (Alemayehu et al., 2017; Ma et al., 2019;

TABLE 6 Model summary, physical and biological drivers and processes, and vegetation representation included in the six reviewed coastal landscape models.

Model	Model summary and application details	Vegetation	Physical and ecosystem processes	Community-scale processes	Plant-scale processes	Organ system biomass allocation	Vegetation metrics
CELSS (Costanza et al., 1988; Sklar et al., 1985; Costanza et al., 1990)	Habitat model on a rectilinear grid *Timestep*: Weekly *Coupling*: Integrated hydrodynamic, productivity, and soil building modules	Three habitat types (freshwater, brackish, saline marshes)	*Climate*: temperature *Hydrodynamics*: water level *Local environment*: salinity; turbidity *Resources available*: nitrogen	-	-	-	-Gross primary productivity (grams C)
BTELSS (Reyes et al., 2000)	Habitat model on a rectilinear grid *Timestep*: Daily *Coupling*: Integrated hydrodynamic, biological productivity, and soil-building modules	Four habitat types (Freshwater– *Panicum hemitomon*; Swamp – *Taxodium distihium*; Brackish– *Spartina patens*; Saline – *Spartina alterniflora*)	*Climate*: temperature *Hydrodynamics*: tidal inundation; SLR *Sediment transport*: deposition *Local environment*: salinity	-	*Production* *Respiration* *Mortality*	*Explicit*: Above- and below-ground biomass	-Net productivity
LaVegMod (Visser et al., 2013, 2017)	Wetland vegetation change integrated with on a rectilinear grid *Timestep*: Annual *Coupling*: Hydrology dynamics and morphodynamics models	14 species (six habitats in version 1; 36 habitats in version 2)	*Geodynamics*: land loss/gain *Hydrodynamics*: water level *Local environment*: salinity	*Dispersal*	*Establishment* *Growth* *Mortality* *Senescence*	*Explicit*: Above-ground	-Percent cover
Integrated Biophysical Model (Baustian et al., 2018)	Integrated vegetation dynamics model Utilizes and modifies components of LaVegMod[b] and VEGMOD[c] *Timestep*: 1 year for taxa distribution, 10 min for VEGMOD processes *Coupling*: Delft3D-FLOW[a] hydrodynamics, morphodynamics, nutrient dynamics	Seven species (parameterized as *Typha* spp., *Phragmites* spp., *Spartina alterniflora*, *Spartina patens*, *Sagittaria lancifolia*, *Sagittaria latifolia*, *Zizaniopsis miliacea*)	*Climate*: temperature (water and air) *Hydrodynamics*: tides, winds, and riverine *Sediment transport*: erosion *Local environment*: salinity; water quality; sediment quality *Resources available*: light; nutrient availability	*Dispersal*	*Photosynthesis* *Mortality* *Growth* *Establishment* *Senescence* *Herbivory*	*Explicit*: Above- and below-ground	-Biomass (above- and below-ground) -Percent cover
ISLAND (Rastetter, 1991)	Barrier island evolution model with individual-based vegetation submodel *Timestep*: annual *Coupling*: Geomorphology, and groundwater submodels	Four-species community of two grass species, one annual, and one perennial shrub	*Climate*: wind exposure *Local environment*: groundwater level; salinity	*Competition*	*Establishment* *Mortality*	*Explicit*: -Above-ground abundance	-Stem count

(Continues)

TABLE 6 (Continued)

Model	Model summary and application details	Vegetation	Physical and ecosystem processes	Community-scale processes	Plant-scale processes	Organ system biomass allocation	Vegetation metrics
Barrier3D (Reeves, 2021; Reeves et al., 2022)	Exploratory model of barrier evolution with ecological module of shrub expansion and mortality on a rectilinear grid *Timestep*: Annual *Coupling*: n/a	Single species (parameterized as *Morella cerifera*)	*Hydrodynamics and Disturbances*: water level (including storm events) *Sediment transport*: erosion; deposition	*Dispersal*	*Establishment* *Growth* *Mortality*	*Explicit*: -Above-ground	-Percent cover -Height

Note: n/a, not applicable.
[a]Deltares (2014).
[b]Visser et al. (2013, 2017).
[c]Deltares (2021).

Strauch & Volk, 2013; Valencia et al., 2022). For a more comprehensive review of SWAT, see Krysanova and Arnold (2008) and Wang et al. (2019).

The Riparian Vegetation Simulation model (RVSM; Zhang et al., 2019) is a model designed to simulate the evolution of floodplain forest and the associated alteration in floodplain current velocities, water levels, scour, and deposition. While it could be included in the collection of forest models (Section 4.4) given its potential for application to model ecogeomorphic floodplain forests interactions, it does not explicitly output biomass metrics, although some related metrics such as tree diameter are calculated. Like other forest models, RVSM includes many abiotic and biotic drivers such as drought stress, flooding duration, scour, deposition/burial, water table depth, competition, seed dispersal, establishment, growth, mortality, senescence, and shading. However, this model has not been applied to coastal settings and would require alterations to produce similar outputs to models listed in Section 4.5.

5 | MODEL COMMONALITIES AND GAPS

5.1 | General observations

No models surrounding any habitat explicitly simulated all the plant or patch and community processes listed in Figure 2. Most models focused on the effect of exogenous processes, largely hydrodynamically-influenced, on vegetation and typically simulate only two or three endogenous vegetation processes (most commonly growth and mortality). Though, at the intended spatial and temporal application of most models, fully simulating all endogenous processes is not necessary to produce usable results. Timesteps varied depending on the processes included in models and questions being asked. In general, models that were only focused on exogenous factors, especially those intended to couple with geomorphological models, had larger timesteps (e.g., annual) compared to models that included endogenous factors had shorter timesteps (e.g., days) (Stallins, 2012; Viles, 2020). Some models explicitly incorporated different timesteps for hydrodynamic processes, which exhibit obvious changes over hourly to daily timescales, and morphodynamic and vegetation growth processes, which occur more gradually (e.g., Belliard et al., 2015; Carr et al., 2012).

5.2 | Plant-scale processes

Across all habitats, few models explicitly include processes or produce outputs at the organ or organ system level, especially with respect to root systems. Plant organ and organ system processes are modeled implicitly in plant-scale allocation of carbohydrate and biomass, which results in many models only simulating above-ground biomass metrics. Seagrass models were more likely to include below-ground biomass than the other models. This may be because submerged aquatic vegetation root and rhizome biomass are considered reliable proxies for the effects of longer-term environmental stressors (Vonk et al., 2015). The exclusion of below-ground biomass maybe from limited above- and below-ground allometric relationships in many habitats (Adame et al., 2017; Komiyama et al., 2005, 2008) or the model intended use

(e.g., forest production). Neglecting below-ground biomass may inadvertently exclude key elements of resource scarcity (e.g., space, nutrients, water, oxygen; Biondini, 2001) or competition. More robust handling of root organ systems may require the inclusion of additional biotic and abiotic drivers, such as soil and microbial properties, which are not currently included in most of the models (Laniak et al., 2013). Integration with existing soils dynamics models can facilitate future development of vegetation dynamics models that better represent below-ground biomass dynamics.

Most models, with the exception of seagrass, rely on implicit, empirically-derived relationships linking biomass and/or growth and mortality to abiotic drivers such as water depth or temperature. In addition to seagrass models, four models simulated photosynthesis and/or respiration explicitly (DOONIES, Charbonneau et al., 2022; Integrated Biophysical Model, Baustian et al., 2018; SWAT, Neitsch et al., 2011; and VEGMOD, Visser et al., 2013 & 2017).

5.3 | Community-scale processes

Dispersal is one of the more common patch/community scale processes simulated. When considered, dispersal is largely handled in a rudimentary way based on the presence of suitable local environmental conditions. Dispersal can be further refined by explicitly simulating dispersal mechanisms (i.e., clonal, allochory seed or autochory seed) to duplicate vegetation distribution patterns more realistically (Brückner et al., 2019). However, simulating realistic patterns of plant distribution may require the inclusion of other related processes such as inter- and intra-specific competition and facilitation, as well as the simulation of more advanced below-ground metrics and abiotic conditions.

Dispersal dynamics, including establishment and the resulting plant distribution, ultimately underpin succession; however, succession is only explicitly simulated in forest models, like LANDIS II (de Jager et al., 2019; Scheller et al., 2007; Scheller & Mladenoff, 2004) where forest gaps are colonized by shrub species. Habitat switching due to land-use or environmental changes is mostly confined to the set of landscape models. While some models (e.g., Kirwan & Murray, 2007) support limited vegetation change as a result of geomorphological change brought on by hydrodynamic forcings, the habitat-specific focus of many models limits their use.

Competition is only explicitly included in mangrove and coastal floodplain forests, where it is often simulated implicitly using space as a proxy or explicitly as above-ground competition for resources; one salt marsh model is an exception to this (Marani et al., 2013), but competition is treated as probabilistic based on habitat suitability, not process-based. Models that utilize dispersal rules that prevent plants from colonizing or dispersing into cells occupied by other plants include a de facto form of competition but competition as a process was not explicitly conceptualized in most of models that utilize such rules.

The models reviewed, excluding landscape models, typically simulated between one and three species, consistent with the low diversity of prominent species in most coastal habitats. Some dune and marsh habitat models use functional communities or broader taxa to represent a group of species, often modeling one generic grass species representing a habitat-building species (Table 1) (Rastetter, 1991), while others simulate the dominant species. Within habitats this may not limit model applicability given similarities among plant functional types across latitudinal gradients. However, across habitats, species-specificity may hinder applicability to other systems. For example, species common to brackish, intermediate, and tidal freshwater wetlands are not as well studied as those found in saltwater environments (Rivera-Monroy et al., 2019). Similar limitations have been cited for inland freshwater wetlands, limiting the development and application of process-based models to relatively few well-studied systems (Williams et al., 2020).

5.4 | Applicability to ecosystem management questions

While the models discussed are advanced in many ways and often represent years of dedicated work, their use in coastal vegetation and habitat management is limited. Most models do not explicitly simulate anthropogenic influences such as potential management actions or the influence of invasive species, which limits their use for coastal management planning and adaptive management (Reichert et al., 2015). Newer versions of the MEM/CWEM (Morris et al., 2019) do include the effects of thin layer sediment placement at pre-defined intervals, SedVeg (Brown et al., 2019) was explicitly designed to analyze the effects of freshwater diversions, a new interface with CDM is designed to simulate common beach and dune management actions such as planting, beach nourishment, or grading (Ruggiero et al., 2019), a few seagrass models explore growth dynamics under nutrient and sediment reduction scenarios (Cerco & Moore, 2001; Carr et al., 2012; Yoshikai et al., 2020), and some forest models such as LANDIS II (de Jager et al., 2019; Scheller et al., 2007; Scheller & Mladenoff, 2004) to simulate the effects of harvest and prescribed burning. This set of models is not unique in that sense as even terrestrial biosphere models grapple with how to simulate the effects of human interventions (Fisher et al., 2014). However, to advance the use of such models in coastal management, the effects of management actions or other human activities such as restoration, invasive species removal or beach nourishment should also be simulated. As climate change and human development exacerbates the rate of coastal change, new model functionality will be required. Modelers should pursue opportunities to partner with managers via workshops or mediated modeling approaches to identify and realistically represent relevant management actions within existing models and model applications.

5.5 | Applicability to climate change questions

Even in relatively undisturbed coastal settings, the rate of observed and predicted coastal change necessitates examination and inclusion of additional exogenous and endogenous plant, patch, and community-scale processes to account for complex interactions between biotic or abiotic drivers, such as the effect of increased air and soil temperatures, changes in water availability, or introduction of new invasive or non-invasive plant and/or faunal species. Patch and community scale processes such as dispersal, competition, facilitation, and succession are required to understand how species ranges may

change or shift. Further unification of habitat-specific and landscape approaches (such as in Baustian et al., 2018) will facilitate additional predictive power of coastal vegetation models across a mosaic of changing coastal habitats. Shifting towards prognostic models of plant-scale processes (e.g., directly simulating photosynthesis and respiration as opposed to relying on implicit relationships between biomass and known stressors) required to extend the applicability of models for Anthropocene-related issues (e.g., climate change, development) where past empirical relationships may break down. There are promising approaches for bridging this gap, such as implementing functional-structural plant modeling into an agent-based framework. This approach would provide a three-dimensional (3D) structure of plants (e.g., leaf curvature, plant height, shape, etc.) with the bottom-up scalability of spatially-explicit agent-based modeling. Approaches used in terrestrial biosphere models may need to be scaled down to understand how changes to global-scale processes (e.g., changes in atmospheric carbon dioxide concentrations) will manifest at a local or project scale where they may facilitate species shifts (Rietl et al., 2021).

6 | CONCLUSIONS

Fifty-four coastal zone habitat simulation models met the review criteria and were examined to determine the biotic and abiotic exogenous and endogenous processes included and the scale and scope of applications. While the level of detail varied and was driven by the questions being asked, there were some general commonalities across the models. Biomass accumulation was often quantified correlatively and treated as a deterministic rather than dynamic (e.g., using constants for biomass allocation to plant parts and root–shoot ratios), and most models neglected below-ground biomass which is an important stabilization component in coastal ecogeomorphic systems. By not capturing the inherent processes and dynamism of biological growth, the models are limited in their applications for predicting growth outside of the system for which they were developed. For example, changes in abiotic drivers such as those caused by climate change could invalidate some empirical growth relationships, especially those that are developed from limited datasets.

Similarly, apart from dispersal and instances of competition being included, community and patch scale processes were largely neglected. Future models should move towards explicit incorporation of these and other broader scale biological processes to more accurately predict how biomass and species composition respond to changes in coastal landscapes. Coastal systems are influenced by numerous exogenous drivers over large spatial and temporal scales, such as hydrodynamic forcings, climate change, sea level rise, management, among others but most models were applied at a patch to local scale (excluding landscape models), where these drivers were either absent or modeled at a local level. In most models, these drivers were limited to local hydrodynamically-related factors.

Potential opportunities to improve coastal vegetation models largely mirror similar discussions with respect to terrestrial biosphere, global vegetation dynamics, and other ecological models (Franklin et al., 2020; Fulton et al., 2019). A move towards prognostic vegetation dynamics models that include community-scale processes such as succession and facilitation is necessary to understand potential coastal vegetation community shifts in response to climate change and human development. Shifting model development to a landscape-based approach will be critical to capture these large-scale processes. This shift will likely include multidisciplinary model integration and coupling (e.g., integrating engineering, physics, and ecological models into a useable framework). The integration of landscape and habitat-specific models will be necessary to understand and inform management of coastal ecosystems as climate change shifts habitat boundaries, and this understanding is paramount to plan and develop sustainable coastal futures.

AUTHOR CONTRIBUTIONS

Candice D. Piercy: conceptualization, funding acquisition, methodology, investigation, supervision, writing – initial draft, reviewing, and editing. **Bianca R. Charbonneau:** conceptualization, methodology, investigation, writing – initial draft, reviewing, and editing. **Emily R. Russ:** investigation, writing – initial draft, reviewing, and editing. **Todd M. Swannack:** funding acquisition, investigation, supervision, writing – initial draft, reviewing, and editing.

ACKNOWLEDGMENTS

The use of products or trade names does not represent an endorsement of these products by the authors or the Department of the Army. Any opinions expressed here are those of the authors and not necessarily those of the agencies they represent. This work was funded by the US Army Corps of Engineers' Aquatic Nuisance Species Research Program's focus on next generation ecological modeling.

CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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How to cite this article: Piercy, C.D., Charbonneau, B.R., Russ, E.R. & Swannack, T.M. (2023) Examining the commonalities and knowledge gaps in coastal zone vegetation simulation models. *Earth Surface Processes and Landforms*, 1–25. Available from: https://doi.org/10.1002/esp.5565