Chapter 3
Variability of Mangroves Along the Brazilian Coast: Revisiting

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3.1   Introduction

Considering the high dynamism of coastal systems, the advances in the concepts of complex systems theory to illuminate contemporaneous coastal management issues related to multiple spatial and temporal scales, and the recent knowledge produced on Brazilian mangroves and saltmarshes in this chapter, we revisit and expand the contribution presented by Schaeffer-Novelli et al. (1990) (hereafter referred to as the *1990 paper*) to understand mangrove and salt marsh patterns and processes along the Brazilian coast and to discuss the originally proposed macroecological concepts.

The 1990 paper was written at a time when interest in mangroves on a global scale was beginning to blossom triggered mainly by a series of outstanding publications, that is, Chapman's (1975) book on mangrove biogeography, Walsh's (1974) seminal work on mangrove zonation, and the concept of "outwelling" by Odum (1971) and Odum and Heald (1975). Seminal papers such as The Ecology of Mangroves by Lugo and Snedaker (1974) were shifting attention from vegetation to ecological processes. Other major contributions were the UNESCO's release of the world's most thorough mangrove bibliographic survey since 1614 (Rollet 1981), and the Handbook for Mangrove Area Management (Hamilton and Snedaker 1984). The Association of Marine Science Researchers (ALICMAR) was created in 1974 and provided the first social-technical platform for sharing ecological knowledge in the Americas. At about the same time, the Organization of American States (OEA) and UNESCO's Regional Office for Latin America subsidized the participation of researchers in various meetings in Hawaii, United States (1974), and Cali, Colombia (1978). Simultaneously, several academic institutions initiated local activities supported by national research organizations, which also sponsored academic exchanges, planting the seed of mangrove ecology on increasingly fertile ground.

Thus, the 1990 paper was an outgrowth of the convergence of attention from multiple Brazilian organizations being directed at coastal systems and the emerging recognition that ecological knowledge would contribute significantly to administer systems that were being recognized for their ecologic importance for coastal fisheries, whereas just a decade earlier, they had been misjudged as useless wastelands suitable for reclamation – a mindset that had prevailed since colonial times and was firmly entrenched in society. What was emerging since the 1960s and early 1970s (Odum 1969; Odum 1970) was the realization that perhaps these lands were not wastelands after all, and that they merited to be managed more rationally, in terms of what today is termed an ecosystem services-based approach (Gregory and Goudie

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2011). Changing deeply seated mindsets requires considerable efforts, such as increasing research levels for understanding the behavior of these systems and building a cadre of human resources that could increase societal awareness to promote their conservation rather than their reclamation and transformation.

The 1990 paper adopted a mesoscale (landscape) perspective for convenience. Landscapes are the most tangible ecological criteria and remain an appropriate level of observation for broad-scale management as well as for focusing on smaller scales. In this respect, we propose a refinement of the mesoscale classification scheme used in the 1990 paper and argue that the application of the coastal environmental setting (CES) framework (Thom 1982; Woodroffe 1992; Twilley et al. 2018;) improves our capacity to appropriately understand and scale mangroves' macroecological attributes and responses to natural and anthropogenic stressors at larger spatial and temporal scales.

In addition, later in this chapter, we discuss an approach we call *dynamic framing* as complementary for adopting a landscape perspective coherent with nature's investment and endurance strategy. However, of critical importance is that the mesoscale landscape approach merges human social systems and geomorphic systems into a unitary system, and recognizes multiple interactive and intercausal scales, geomorphological, social, and ecological processes (Huggett 1995) that are interdependent and vital for sustainability.

3.2   Scales and Variability in Mangrove Macroecology

The Brazilian coast is characterized by mangrove forests along most of its 10,959.52 km length (IBGE 2016), between the latitudes 04°20′12″N and 33°45′07″S. The measured length of any coast is a function of the scale and resolution of the measurement (Mandelbrot 1983), so it is not surprising that various length estimates exist in the literature (see Chap. 1 for more details). On a global scale, Brazil's coastline length ranks 12th (IBGE 2016), but shelters the second-largest mangrove area cover in the world (FAO 2007; Giri et al. 2011; Hamilton and Casey 2016). This suggests that from a broad perspective, this coast contains landscape features that are particularly favorable for mangrove development. Because a broad view subdues detail, processes, and structures, it is not surprising that a closer look often reveals unexpected variability at different levels.

Reality is complex and stratified into characteristic scales, dynamics, and patterns. These tend to be bundled into discrete scales of interaction (Rowe 1961; Simon 1962). Variability is the result of complexity; the diversity of components compounded by the spatiotemporal diversity of factors influences landscape responses and development at various scales, leaving distinct signatures that reveal dominant influences. The interaction between factor regimes and scales results in relatively distinct landforms. Thus, the original paper intended to examine zonality, that is, Brazilian coastal patterns, in terms of features and regional environments. The outcome was a proposed division of the coast into segments within which

similar broad climatic, geomorphologic, and oceanographic features and comparable management needs are found. Mangroves were accounted as mostly azonal perhaps because of the dominance of local (site) factors in influencing development. Complexity defies any attempt of classifying any coast where the diversity of landscape elements is high and where these elements and forcing functions act in combination and interact in complex ways.

In the context of revisiting the 1990 paper, we find it desirable to review some aspects of the notion of variability, considering that coasts are the most dynamic places on the planet. It is misleading to consider coastal features as static or perceive variability as problematic. Variability is a manifestation of complexity and although it presents obstacles to generalizing and identifying clear-cut patterns in nature, it is part of it and is present at all scales driven by external and internal factors such as self-organization. Variability paradoxically entails the iterative power of order, of system-level responses that eventually can lead to adaptive change and the capture of environmental energies to gradually perform increasingly more complex geoecologic work that makes more complete use of all available energies.

Furthermore, categorizations are based on generalizations and variability tends to obscure categories. In fact, all categorization schemes are simplifications and ignore variability at some scale. In nature, absolute categories do not exist, because categories exist only as (human) ideas, whereas reality is a *continuum*; change, variability, and transformation are pervasive but until very recently we have perceived reality in terms of static components and neglected processes and change. A shift taking place in ecology is the increasing adoption of a process-based perspective. The relationships between ecological processes and spatiotemporal patterns on a variety of scales are one of the most relevant research topics for most unresolved questions in ecology. Even climate was accounted as constant until very recently. What is pertinent in this appreciation is that temporal variability is an important area of concern, because the temporal scope of human observation is often very limited when considering the extended endurance of many geomorphic features. Focusing on the narrow spatiotemporal window of human experience inevitably provides a "keyhole" or partial view of coastal systems that ignoring its limitations can undermine management efforts no matter how well-intended they might be. In general, ecological events have a characteristic frequency and a corresponding spatial scale, and an ecological study of the landscape must conform to these scales (Turner 1998; Blackburn and Gaston 2002).

The Brazilian coast has been divided into different segments by several authors for different purposes, highlighting certain features and processes. The complexity of responses from a complex system approach is obviously overwhelming. In our 1990 paper, the purpose was to highlight geographic variability in the context of settings for mangrove establishment and development. That paper did not intend to describe causal factors or system dynamics but was limited to describing patterns of mangrove structure along the coast in very broad terms. To do that we conveniently divided the coast into eight broad segments oriented to mangrove abiotic drivers (Fig. 3.1) such as climatological (temperature, precipitation, and potential evapotranspiration), hydrographic (river order rank), and oceanographic (tidal amplitude),
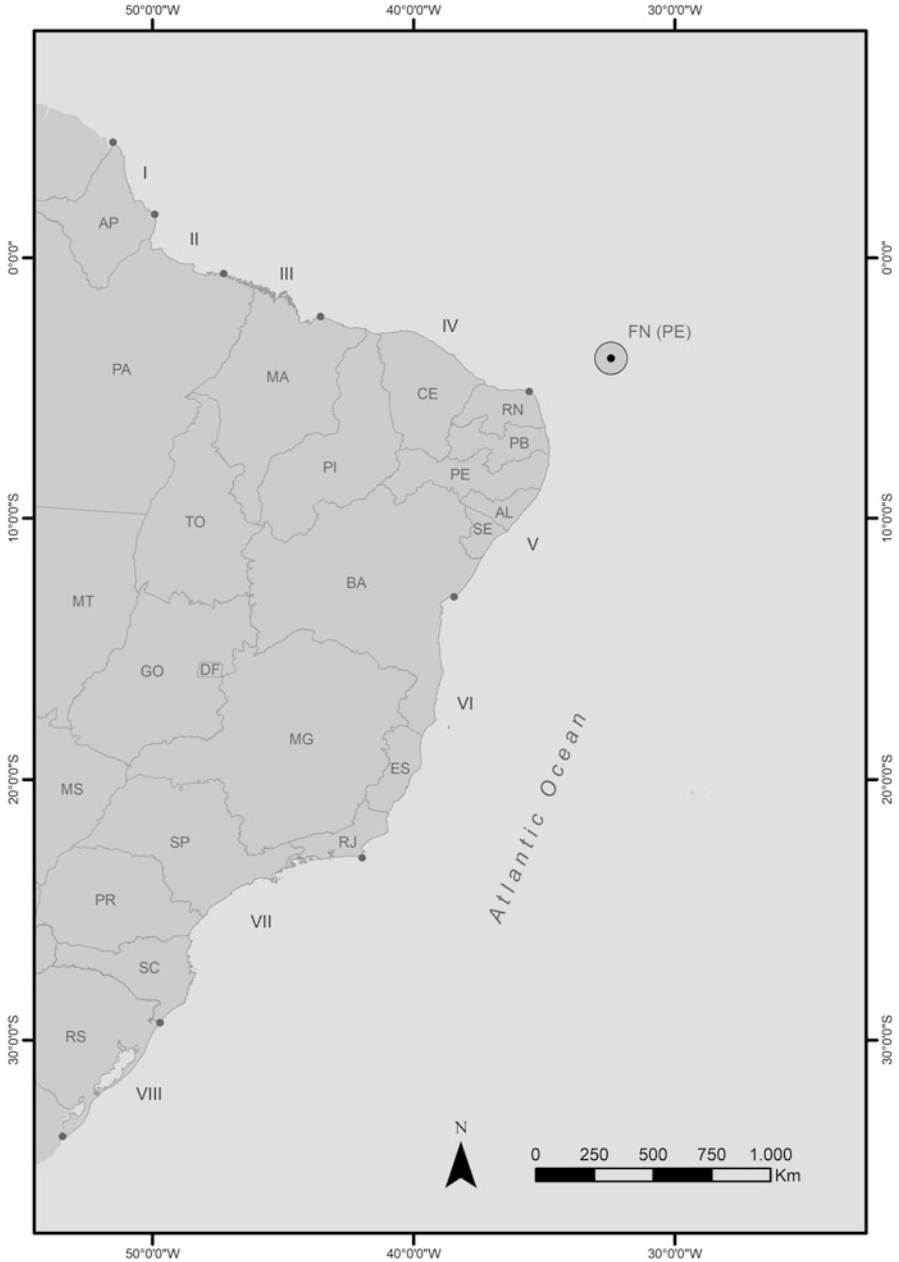
Fig. 3.1 Coastal segments proposed in Schaeffer-Novelli et al. (1990), divided by dots: I – Cape Orange (04°30′N) to Cape Norte (01°40′N), II – Cape Norte to Ponta Curuçá (00°36′S), III – Ponta Curuçá to Ponta Mangues Secos (02°15′S), IV – Ponta Mangues Secos to Cape Calcanhar (05°08′ S), V – Cape Calcanhar to Recôncavo Baiano (13°00′S), VI – Recôncavo Baiano to Cabo Frio (23° 00′S), VII – Cabo Frio to Torres (29°20′S), and VIII – Torres to Chuí (22°35′S)

including the resulting mangrove development (structure; see Table 3.1). That method was summarized by Schaeffer-Novelli et al. (2016).

Within seven out of the eight coastal segments (Table 3.1), mangroves occupy landforms that bear the signature of past legacies of dominant formative processes (Rovai et al. 2018) (Fig. 3.2). Geographic partitioning is a common tool for supporting spatial reasoning for deriving qualitative inferences from broad categories. Here, we strengthen the original mesoscale approach by incorporating the coastal geomorphology variability within each segment as originally proposed in the 1990 paper, following the elements that have been presented in Chaps. 1 and 2.

3.3   The Coastal Environmental Setting (CES) Framework

Some fifty years ago, Bruce Thom proposed a framework based on ecogeomorphology to explain ecological regularities linked to different Coastal Environmental Setting (CESs). This is the framework used in the 1990 paper. These ideas were further developed by Rovai et al. (2018) and applied to multiple-scale ecological models to explain global variations in the mangrove ecosystem's properties. Incorporating ecogeomorphic forcings into predictive models has helped to advance hypotheses that improve our understanding and capacity to foresee the effects of global changes in these ecosystems.

Ecology has made great strides since the 1980s when the 1990 paper was conceived; new notions, tools, and concepts have been developed and are taking increasingly important roles in expanding observational windows in quality and scope, furthering interpretation, and reinterpretation of data and previous analyses. These new tools and notions have interacted catalytically to broaden ecological knowledge greatly in time and space. Understanding and dissemination of knowledge now have achieved global scales and we now can speak of global or macroecology as a discrete research field. The beneficiary community has expanded as well, and now includes scientists, educators, resource managers, and large stakeholder communities. New tools have also become available such as remote sensing instruments including global positioning systems (GPS) and inexpensive portable sensors. Increasing computational power and progressively easier access to distant places and real-time communications among researchers has propitiated a revolution in ecology that is still taking place and continues at an increasing pace. Furthermore, there are now more universities, scientists, and engineers than ever before in history. More importantly, complex environmental issues are part of the public sphere or social spaces nowadays. Thus, there is an increased demand for scientific communication to nonprofessionals to promote greater public understanding and engagement by educated constituencies.

The 1990 paper's perspective remains relevant as an appropriate level of observation for revealing mesoscale order as a starting point for a triadic approach that pays attention to events that take place at other levels: the focal level, the next higher level, and the level immediately below (Salthe 1985). Here we will demonstrate that

Table 3.1 Eight coastal segments proposed in Schaeffer-Novelli et al. (1990)

Segment	Description
I	From Cape Orange (04°30′N) to Cape Norte (01°40′N), at the northern limit of the mouth of the Amazon River. It is characterized by homogeneous forests dominated by the *Avicennia*. Mangroves colonize coastal rivers, extending to considerable distances inland. The genus *Rhizophora* occupies the estuarine portion of the rivers, where the marine influence is direct. In these areas, *Montricardia* and *Laguncularia* occupy the inner parts of the forests.
II	From North Cape (01°40′N) to Ponta Curuçá (00°36′S). Mangrove development and cover are sparse in this segment due to the influence of the fluvial discharge of the Amazon River. The forests are mixed, with freshwater mudbanks dominating the northern part of the Amazon River mouth. The mangroves are mostly formed by the genus *Avicennia* at sites of low elevation and low salinity, while the *Rhizophora* occurs at sites with more significant marine influence or periodically inundated by tides.
III	From Ponta Curuçá (00°36′S) to Ponta Mangues Secos (02°15′S). The genus *Rhizophora* dominates the forest fringes. The higher ground behind the fringes is colonized by *Avicennia* and *Laguncularia*. Low-energy, depositional environments are colonized by *Spartina*. The genus *Conocarpus* is found in transition zones to upland.
IV	Ponta Mangues Secos (02°15′S) to Cape Calcanhar (05°08′S). Mangroves are poorly developed along this stretch of coast due to the lack of freshwater input associated with prolonged dry seasons. High salt concentrations limit mangroves to river mouths.
V	Cape Calcanhar (05°08′S) to Recôncavo Baiano (13°00′S). Due to the high energy of this section of the coast, mangroves develop in sheltered areas, associated to estuaries and coastal lagoons. *Rhizophora* and *Laguncularia* appear as pioneers. In the inner parts of the forests, *Avicennia* and *Laguncularia* form mixed forests.
VI	From Recôncavo Baiano (13°00′S) to Cabo Frio (23°00′S). Relatively extensive mangroves are commonly found behind *restingas*. All three genera of mangroves are found, either mixed or in monospecific stands. In the Todos os Santos Bay, *Laguncularia* is dominant, colonizing sandy-clay soils. *Rhizophora* is found predominantly on the margins, forming a narrow strip on the fringes. When dominant, they form monospecific stands frequently flooded by the tides. *Avicennia* and *Laguncularia* may also form mixed marginal forests.
VII	From Cabo Frio (23°00′S) to Torres (29°20′S). The tallest mangrove trees border estuaries, channels, and some river downstream. Forests can be monospecific or mixed of the three genera. Recent sediments of barrier islands may be colonized by *Spartina*, forming saltmarshes completely flooded by high tides. *Rhizophora* colonizes muddy sediments with large amounts of organic matter, while *Avicennia* is found in higher deposits forming extensive forests. Landward transitional zones are often colonized by *Hibiscus*, *Crinum,* and *Acrosthicum*. The latitudinal limit for real mangrove species is on the coast of Santa Catarina, at 27°30′S (*R. mangle*) and 28°30′S (*A. schaueriana* and *L. racemosa*).
VIII	From Torres (29°20′S) to Chuí (33°45′S). This stretch of coastline is formed by extensive beach deposits, associated with dune ridges and sandy ridges. Abundant lagoons, isolated from the ocean by multiple barriers, result from successive transgressive and regressive geologic events. Low winter temperatures and a wide temperature range inhibit the growth of typical mangrove species, promoting the development of salt marshes.

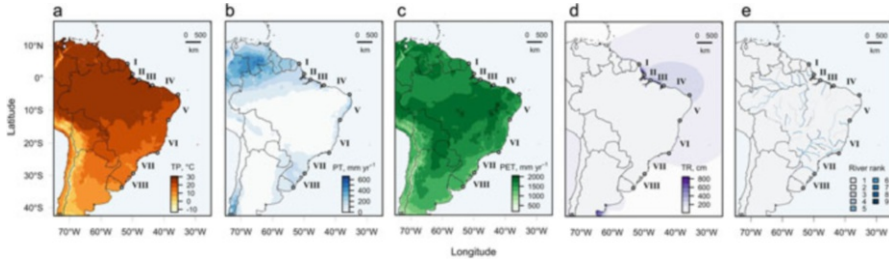Adapted from Schaeffer-Novelli (1999)

Fig. 3.2 Coastal segments proposed in Schaeffer-Novelli et al. (1990) highlighting dominant environmental forcing's and climate-driven threats. Mangroves are present in segments I–VII, salt marshes are predominant at segment VIII. (**a**) TP-mean annual temperature, (**b**) PT-mean annual precipitation, (**c**) PET-mean annual potential evapotranspiration, (**d**) TR-mean tidal range, and (**e**) River order rank. Sources: TP and PT data from Hijmans et al. (2005), PET from Title and Bemmels (2018), TR from Vestbo et al. (2018), and river order rank from Patterson and Kelso (2018)

the CES framework[1] provides the most obvious and tangible ground for improvement in spatial resolution, accessing constraints, and moving toward higher fidelity scales. All ecological processes and structures are multiscales (Allen and Hoekstra 1992). We provide a reanalysis of mangrove structural (biomass) and functional (primary productivity, carbon sequestration) attributes discussed in the 1990 paper. We used global compilations on climatic and oceanographic variables to predict mangrove ecological traits at a continental scale, expanding models proposed in our original 1990 paper from a conceptual to an empiric perspective. Particularly, we explored how the relative contribution of rivers, tidal range, along with regional climate, shapes distinct CES, reflected in substrate conditions to which plants respond (Thom 1982; Woodroffe 1992; Twilley et al. 2018) (Fig. 3.3). Distinct CES, for example, deltas, estuaries, and lagoons, are formed by the relative contribution of geophysical variables (e.g., river discharge, tidal amplitude, wave energy). Along with regional climatic drivers, these geophysical forcings constrain carbon partitioning among ecosystem compartments (soil, above- and belowground biomass). CES types include large rivers, small deltas (grouped as deltaic by Thom 1982), tidal systems (estuaries, bedrock as defined by Thom 1982), lagoons (including composite settings as defined by Thom 1982), carbonate coastal settings, and arheic or dry coastlines.

The following brief, yet comprehensive overview on dominant global types of CES was originally summarized by Rovai et al. (2018). However, we suggest consultation of the original sources (Thom 1982; Woodroffe 1992) for additional information. One of the major factors defining the different CES is sediment source (i.e., river-borne), which represents a combination of geophysical processes and

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[1]The term Coastal Environmental Settings (CESs) refer to a typology of mangrove-occurring localities that share certain composed by geophysical, geomorphic, and biologic characteristics.
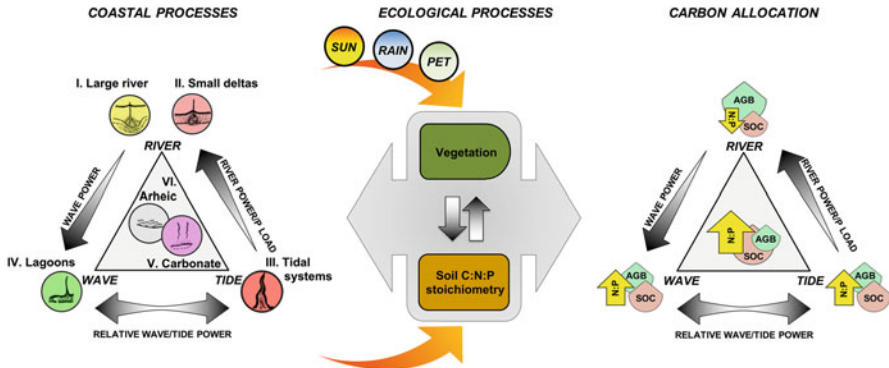
Fig. 3.3 Coastal ecogeomorphology conceptual framework, showing how bidirectional fluxes between abiotic and biotic components control nutrient stoichiometry and carbon storage in mangroves. CES types: I – large rivers; II – small deltas; III – tidal systems; IV – lagoons; V – carbonate coastal settings; and VI – arheic, or dry coastlines. PET: potential evapotranspiration; C:N:P: carbon-to-nitrogen-to-phosphorus ratio. Adapted from Twilley et al. (2018)

local geology influencing mangrove dynamics (Thom 1982; Woodroffe 1992; Woodroffe 2002).

The CES framework provides an alternative to the latitude gradient paradigm, and its use has advanced our capacity to predict mangrove ecological attributes such as aboveground biomass (Rovai et al. 2016), litterfall production (Ribeiro et al. 2019), and soil organic carbon (Rovai et al. 2018) at larger scales with a high confidence level. This is particularly useful for coastlines that lack such information. Here, we focus on the variability of mangrove aboveground biomass (AGB), litterfall (NPP$_L$, or Net Primary Productivity Litterfall), and soil organic carbon (SOC) along the Brazilian coastline, as these ecosystem attributes constitute the largest long-term (>100 years), perennial carbon pools in mangrove forests. However, a pressing need remains for generating estimates of belowground biomass (roots) and productivity as these are significant components of ecosystem-level C stock and budget, respectively. CESs provide an ecological/terrain conceptual unit for management that is easily geographically defined.

3.4 Aboveground Biomass

Previous attempts to predict continental-scale mangrove aboveground biomass (AGB) include latitude (Saenger and Snedaker 1993; Twilley et al. 1992) and climate-based models (Hutchison et al. 2014). Although latitude-based models can indirectly encompass critical climatic and geophysical variables, their individual contribution to explain AGB value spatial patterns is unknown, since their explanatory power is not explicitly weighted in the statistical analysis. Although a climatic modeling approach explicitly includes climate variables such as temperature and
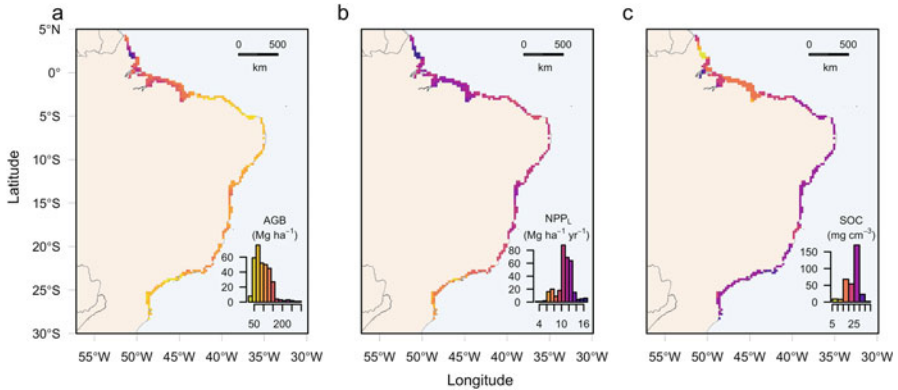
Fig. 3.4 Predicted mangrove aboveground biomass (**a**) (AGB in Mg ha^{-1}), litterfall productivity (**b**) (NPP$_L$ in Mg ha^{-1} year^{-1}), and soil organic carbon density (**c**) (SOC in mg cm^{-3}) in Brazilian mangroves. Histograms depict the frequency of modeled values for each mangrove attribute. AGB data extracted from Rovai et al. (2016), NPP$_L$, from Ribeiro et al. (2019), and SOC from Rovai et al. (2018)

precipitation to explain mangrove AGB at the global scale (Hutchison et al. 2014), this analysis is limited not only by the number of climatic variables included in the model but also by the lack of other environmental variables that directly influence mangrove structural and functional properties at regional and local scales (Twilley 1995; Twilley and Rivera-Monroy 2009).

A literature review to assemble a global dataset containing information on published mangrove AGB and forest structure data is summarized in a review by Rovai et al. (2016). The inclusion of other geophysical variables in the climatic-geophysical model significantly improves AGB estimates at the latitudinal scale as demonstrated for the neotropics. As in the conceptual model proposed in the 1990 paper, the review by Rovai et al. (2016) shows that at continental scales, higher tidal amplitudes contributed to high forest biomass associated with warm temperatures, abundant rainfall, and low potential evapotranspiration (Figs. 3.1a–c and 3.3a). For the Brazilian coast, this model corroborates the mangrove forest structural development described for each segment proposed in the 1990 paper (see Chaps. 4 and 6), with higher AGB values predicted for low latitude, deltaic and macrotidal coastlines (Segments I–III, Fig. 3.1; Table 3.1), and lower values along increasingly austral latitudes, tide- and wave-dominated, or dry coastlines (Segments IV and VII, Table 3.1; Fig. 3.4a).

Mangrove AGB values in Brazil range from 25.3 to 284.8 Mg ha^{-1} (mean = 95.8 Mg ha^{-1}), within the range estimated for the neotropics (16.6–627.0 Mg ha^{-1}, mean = 88.7 Mg ha^{-1}) (Rovai et al. 2016). Using a biomass-to-carbon conversion factor of 0.475 (Hamilton and Friess 2018) and a mangrove forest cover of 7675 km^2 (Hamilton and Casey 2016), the total C stored in mangroves' AGB in Brazil is estimated at 0.04 PgC, which corresponds to 7.3% of global C stocks in mangrove AGB (Rovai et al. 2016).

Rovai et al. (2016) show that CES represents a major determinant on mangrove wetland development, configuration, and realized maximum biomass, particularly considering the diversity of mangrove geoecological settings and associated dynamics (Thom 1982; Woodroffe 1992; Twilley 1995). This energy signature is strongly influenced by the local tidal range and river discharge, critical geophysical variables explaining a significant percentage of the AGB total variance (Rovai et al. 2016). Indeed, tidal amplitude, a component of the hydroperiod regime in coastal regions, significantly influenced mangrove structural development. Higher tidal amplitude promotes nutrient exchange and aeration of soil layers, which reduces sulfide production and accumulation, allowing higher growth rates and forest development (Lugo and Snedaker 1974; Castañeda-Moya et al. 2013).

3.5 Net Primary Productivity – Litterfall (NPP$_L$)

Ribeiro et al. (2019) provided the first model that accounts for continental-scale variability in mangrove Net Primary Productivity [Litterfall] (NPP$_L$) in response to climatic and geophysical variables combined. Their results advance the current understating of mangrove NPP$_L$ variability across latitudinal and longitudinal gradients, considering that previous studies did not account for the role of geophysical forces in driving large-scale NPP$_L$ variability. Instead, correlations were usually performed using absolute variation in latitude degrees as a predictor of mangrove primary productivity (e.g., Twilley et al. 1992; Saenger and Snedaker 1993; Bouillon et al. 2008).

The model by Ribeiro et al. (2019) addresses a core question in mangrove macroecology, clarifying the role of factors that control mangrove NPP$_L$ at larger spatial scales. The authors show that mangrove NPP$_L$ is controlled by a combination of climatic (temperature and precipitation) and geophysical forces, such as tidal range. Here we used the model results by Ribeiro et al. (2019) for the neotropics to estimate NPP$_L$ for Brazilian mangroves (Fig. 3.4b). The predicted NPP$_L$ values for Brazilian mangroves ranged from 3.79 to 16.97 Mg ha^{-1} year^{-1} (mean = 10.92 Mg ha^{-1} year^{-1}), and the range reported for the neotropics is 1.66–28.81 Mg ha^{-1} year^{-1} (mean = 10.25 Mg ha^{-1} year^{-1}) (see Ribeiro et al. 2019 for details). Using a biomass-to-carbon conversion factor of 0.475 (see Hamilton and Friess 2018), the predicted mean NPP$_L$ for Brazilian mangroves corresponds to 5.5 Mg C ha^{-1} year^{-1}. Using Hamilton and Casey's (2016) estimative for Brazilian mangrove forest cover of 7675 km^2, the annual rate of C removed from the atmosphere by mangrove NPP$_L$ in the country is estimated at 4 Tg C, which corresponds to 30% of total NPP$_L$ in the neotropics (Ribeiro et al. 2019).

Higher NPP$_L$ rates were predicted for mangrove forests influenced by large river systems, such as along the Amazon River coastline. These patterns of high NPP$_L$ rates predicted for river-dominated coastlines are consistent with observed values reported for other deltaic coastal settings in the neotropics such as in the San Juan River delta (Colombia), Orinoco River delta (Venezuela), and Essequibo River

(Guyana) (see Ribeiro et al. 2019 for details). These regions with high NPP_L are located in tropical regions subjected to low annual variability in temperature, high rates of rainfall (>2000 mm year^{-1}) (Hijmans et al. 2005), and macrotidal regimes (Carrère et al. 2012). Conversely, the low rates of NPP_L in Brazil were predicted for mangroves subjected to lower winter temperatures, reduced tidal amplitude (i.e., Segment VII, Table 3.1; Fig. 3.2), as well as reduced annual precipitation and reduced river discharge (Segment IV, Table 3.1; Fig. 3.2), which altogether constrain high primary productivity and forest development.

Ribeiro et al. (2019) showed that the interaction between precipitation and temperature accounted for most of the variability in mangrove NPP_L across the neotropics. Temperature and precipitation regimes have long been described as important drivers of mangrove NPP_L (Pool et al. 1975; Twilley 1995; Day et al. 1996; Feher et al. 2017). Temperature affects plants' vital processes from photosynthesis and respiration to reproductive success and carbon storage (Duke 1990; Lovelock 2008). Similarly, rainfall also influences mangrove growth and primary production (Day et al. 1996; Twilley et al. 1997; Agraz-Hernández et al. 2015). Lower primary production has been reported for mangrove forests along dry coastlines, whereas the highest NPP_L rates were related to areas with rainfall regimes over 2000 mm year^{-1} (Hernández and Mullen 1975; Félix-Pico et al. 2006; Lema and Polanía 2007). The synergism between temperature and precipitation regimes plays a major role in determining mangrove development and distribution (Spalding et al. 2010; Osland et al. 2016; Feher et al. 2017).

The results in Ribeiro et al. (2019) also highlighted the role of tidal regimes in mangrove NPP_L variability at larger scales. These findings support previous studies that show a strong positive influence of tidal amplitudes in primary production (Cintrón and Schaeffer-Novelli 1981; Alongi 2002). Tides are an energy subsidy to mangroves' primary production (Odum et al. 1982) and as this energy increases, so is the amount of organic matter exchanged between mangroves and adjacent environments (Twilley et al. 1986, 1992). Periodic tidal inundation promotes nutrient exchange and soil aeration, which reduces the accumulation of toxic substances (e.g., sulfides) and enhances forest development (Lugo and Snedaker 1974; Castañeda-Moya et al. 2013). In addition, earlier studies have shown tides to be a major driver of carbon allocation between above- and belowground compartments in mangrove forests. For instance, higher tides are frequently associated with well-developed mangrove forest stands (Cintrón and Schaeffer-Novelli 1981; Twilley 1995; Rovai et al. 2016). Conversely, mangrove root biomass was found to be higher in sites subjected to infrequent inundation (Castañeda-Moya et al. 2011; Adame et al. 2017). Similarly, higher soil organic carbon stocks have been negatively correlated with tides (Rovai et al. 2018). Also, the tidal amplitude is an important component of hydroperiod influencing mangrove species zonation (Crase et al. 2013) as well as the vertical range of suitable environment for mangrove establishment (Hutchings and Saenger 1987).

Although not selected as a significant term in the model by Ribeiro et al. (2019), potential evapotranspiration (PET) has been acknowledged as one of the major climatic factors determining the distribution of life zones on Earth (Holdridge

1967). PET represents the amount of water that could potentially be used by plants, but it is transferred back to the atmosphere through evaporation, thus, being an important regulator of forest water balance (Holdridge 1967). The interaction between PET and precipitation is especially important for mangroves, due to soil water content and salinity balance (Clough 1992; Wolanski et al. 1992). Indeed, PET has been shown to play a major role in the continental-scale variability of above-ground biomass and soil organic carbon stocks in mangroves (Rovai et al. 2016, 2018).

In equatorial climates, where temperatures are constantly high throughout the year, precipitation rates are moderate to high and the ratio between precipitation and PET is low, so mangrove forests can allocate more energy to their aboveground biomass and thus are better developed (Schaeffer-Novelli et al. 1990; Clough 1992). Where PET exceeds rainfall, the water deficit leads to decreased soil moisture, and consequently higher soil salinities, water stress on mangrove trees, and restricted forest development (Schaeffer-Novelli et al. 1990; Day et al. 1996; Castañeda-Moya et al. 2006). Moreover, the upper limit of distribution and survival of particular mangrove species is very often determined by soil salinity and soil water content, which are regulated by the conjunction of PET, rainfall, and tidal amplitude (Wolanski et al. 1992; Castañeda-Moya et al. 2006).

Furthermore, the influence of river discharge on mangrove ecosystems functioning is also indubitable. Nevertheless, excessive freshwater discharges act as a constraint by promoting competition by glicophytes that limits mangrove colonization. This is true in the Amazon estuary as well as south of Laguna (28°30′S) where freshwater habitats prevail displacing mangroves and favor freshwater marsh development. Overall, rivers are responsible for most of the freshwater input in mangroves, acting as a source of nutrients (phosphorus) and decreasing interstitial salinity (Pool et al. 1975; Castañeda-Moya et al. 2013). Riverine mangroves are characterized by optimal structural growth, with high values of aboveground biomass and NPP_L resulting from high nutrient availability, abundant freshwater drainage, and reduced soil salinity levels, which are controlled by river discharge (Cintrón et al. 1978; Castañeda-Moya et al. 2006). River discharge is particularly important in dry (or arheic) coastlines such as in Northeast Brazil (see Chap. 1). In these dry climates, evapotranspiration exceeds the moisture supplied by precipitation, and river discharge becomes an important source of freshwater that controls salinity within limits that are not stressful for mangrove survival, forming extensive hypersaline flats (or "apicuns").

The *apicum* (in singular) is a spatial-temporal ecogeomorphic feature of the mangrove ecosystem; it is a morphoclimatic hydrosere, a dynamic feature of the high intertidal zone, and technically a high salt marsh feature. The high salt marsh is influenced by precipitation, runoff, or seepage (Costa and Davy 1992; Hadlich et al. 2010). In dry coastlines with minor river discharge, massive mangrove diebacks can occur triggered by inland droughts, multidecadal fluctuations in sea level such as the 18.6-year Metonic Cycle (Munk et al. 2002), reductions in rainfall, and abnormally high air temperatures (Duke et al. 2017; Lovelock et al. 2017). During these events, only mangroves fringing estuary channels and upstream riverine stands remained healthy and mostly intact (Duke et al. 2017).

3.6   Soil Organic Carbon (SOC) Stocks

In the present work, we include a new mangrove ecological feature not covered in the 1990 paper, the continental-scale variability of Soil Organic Carbon (SOC) stocks in response to climatic and geophysical drivers. Mangroves have long been recognized for their potential role as a significant global carbon sink that may mitigate atmospheric CO_2 enrichment (Twilley et al. 1992). They were recently recognized as the most carbon-dense forests in the tropics (Donato et al. 2011), culminating in an increase in research papers reporting mostly on local and regional carbon stocks. Few studies have attempted to deliver global mangrove carbon budgets (Chmura et al. 2003; Bouillon et al. 2008). Only recently have specific models been developed to account for global variation in mangrove SOC stocks (Jardine and Siikamäki 2014; Atwood et al. 2017; Rovai et al. 2018). Attention has been driven to SOC stocks, because most of the carbon in mangroves ecosystems is stored in this compartment (Twilley et al. 1992; Hamilton and Friess 2018), where it remains stable for much longer compared to AGB.

Rovai et al. (2018) demonstrated how local and regional estimates of SOC linked to CES can render a more realistic spatial representation of global mangrove SOC stocks. They combined 107 published and unpublished studies conducted worldwide to yield a dataset consisting of depth-integrated (top meter) mangrove SOC density values, reporting on 551 sites from 43 countries. In contrast to previous studies (e.g., Jardine and Siikamäki 2014; Atwood et al. 2017), this dataset included exclusively soil profiles that were at least 0.3 m in depth (which were then normalized to a depth of 1 m), and mangrove SOC density values obtained from elemental analyses or chemical determination (i.e., wet oxidation). Rovai et al. (2018) showed that the diversity of CESs can contribute to the global integration of complex geomorphological, geophysical, and climatic responses that explain the contribution of mangroves to global carbon sequestration. Their approach improved our capacity to predict the global contribution of coastal systems such as mangroves to carbon dynamics in the Earth system. Although their global mangrove SOC budget estimate was similar to early ones, for example, 2.3 PgC (Rovai et al. 2018) and 2.6 PgC (Atwood et al. 2017), they showed that mangrove SOC stocks vary markedly across different types of CESs, increasing from river- to tide/wave-dominated to carbonate coastlines. For example, a global estimate, recently provided by Atwood et al. (2017), used a country-level mean mangrove SOC stock of 283 Mg C ha^{-1} based on values from 48 countries to extrapolate global patterns for the remaining 57 countries that lack data on mangrove SOC. Results in the study by Rovai et al. (2018) indicate that for those countries, many of which comprise mostly carbonate CESs, the global mean reference value of mangrove SOC stocks suggested by Atwood et al. (2017) is about 50% lower than values based on distinct CESs. Moreover, their analysis showed that the CES framework has the potential to resolve unexpected patterns observed between carbonate and river-dominated coastal landforms identified in former global mangrove SOC budgets (Jardine and Siikamäki 2014). They showed that mangrove SOC stocks have been underestimated by up to 44%

(a difference equivalent of roughly 200 MgC ha^{-1}) and overestimated by up to 86% (around 400 MgC ha^{-1}) in carbonate and deltaic settings, respectively, likely due to the omission of geomorphological and geophysical drivers in accounting for the large-scale variability of mangrove SOC stocks.

Here we used Rovai et al. (2018) results to compute estimates of SOC for Brazilian mangroves (Fig. 3.4c). Lower SOC density values were predicted for deltaic and macrotidal (Segments I–III, Table 3.1; Fig. 3.2) and arid (Segment IV, Table 3.1; Fig. 3.2) CESs. Higher SOC values were consistent along tide- and wave-dominated coastlines (Segments V–VII, Table 3.1; Fig. 3.2). Mangrove SOC stocks in the soil top meter in Brazil ranged from 72.1 to 388.3 MgC ha^{-1} (mean = 240.4 MgC ha^{-1}), within the global range of 33.8 to 464.1 MgC ha^{-1} (mean = 296.6 MgC ha^{-1}) (Rovai et al. 2018). Using the mangrove forest area of 7675 km^2 (Hamilton and Casey 2016), the total carbon stored in mangroves soils in Brazil is estimated at 0.15 PgC, which corresponds to 6.5% of global SOC stocks in contrast to the 9.3% suggested earlier (Hamilton and Friess 2018).

3.7 Advancing the CES Framework: Challenges for Mangrove Macroecologists

Tremendous advances have been made recently in terms of mapping the global mangrove forest cover. The two most recent mangrove forest cover estimates range from nearly 82,000 (Hamilton and Casey 2016) to 132,000 km^2 (Giri et al. 2011). This difference of approximately 40% in mangrove forest cover is due to different methodologies used to classify mangrove occurrence within each degree-cell. While the database in Hamilton and Casey (2016) (CGMFC-21)[2] estimates the percent cover for each degree-cell within a mangrove forest, the earlier database in Giri et al. (2011) (MFW)[3] uses a presence approach. Despite these methodological aspects, both CGMFC-21 and MFW databases have a very high resolution of approximately 900 m^2 (30 × 30 m at the equator).

The parameters on which we based most of the discussion in this chapter (that is, AGB, NPP$_L$, and SOC) were conveyed using the mangrove forest cover provided by the CGMFC-21 database but adjusted to a much lower fidelity (approximately 625 km^2 or 25 × 25 km at the equator) than the original spatial resolution. As pointed out in the original sources, we based our analyses on Rovai et al. (2016 and 2018) and Ribeiro et al. (2019).

There are essentially two main reasons that may be preventing the development of robust higher-resolution large-scale mapping of mangrove ecological attributes. First, the attempt to balance the loss of information during the trade-off process of down- and upscaling data with different resolutions (Blackburn and Gaston 2002).

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[2]CGMFC-21 (project): Continuous Global Mangrove Forest Cover for the Twenty-first Century.
[3]MFW (dataset): Mangrove Forest Cover Loss dataset.

Indeed, recent efforts in macroecology strived to consolidate a database of environmental variables that are thought to be relevant to species' ecology and geographic distribution at a reasonable spatial resolution (0.08333° or approximately 8.3 km at the equator) (Title and Bemmels 2018). Even the WorldClim database (Hijmans et al. 2005), which has over 3000 citations, has resolutions that range from 1 to 340 km^2. In this respect, some of the predictors used in the analyses we present here have a coarse native resolution, such as river discharge (0.5°). Thus, it is reasonable to work with an intermediary cell size (e.g., 0.25°) that is spatially representative of most CES domains, which the modeling framework is based on. Second, although the integration of information on mangrove typology based on local hydrology and topography (e.g., fringe vs. interior sites) would potentially allow for more robust local and global estimates, most papers in which the analyses presented here are based on do not include accurate information on hydroperiod. Accordingly, the spatial resolution of most global compilations on marine and terrestrial environmental variables (Title and Bemmels 2018) does not reflect the variability compatible with neither the CMFGC-21 nor the MFW database native resolution.

In order to perform a multiscale spatial analysis, both dependent and independent variables would have to be available at differing resolutions. Moreover, the set of environmental variables would have to hold ecological meaning across different spatial scales, which is unlikely as variables that control SOC formation in coastal wetlands differ at different scales (check Holmquist et al. 2018; Osland et al. 2018; and Rovai et al. 2018). While the scale-dependent issues discussed here are perhaps one of the major challenges mangrove ecologists will face when upscaling ecological traits from site-level observations, the CES framework resolved much of the dramatic difference in mangrove SOC estimates, particularly in terms of spatial variability with mangrove soil properties following close the energetic signature of distinct coastline types (Rovai et al. 2016, 2018; Twilley et al. 2018; Ribeiro et al. 2019).

3.8   CES Restrict the Atlantic South American Mangrove Limit

Laguna is an interesting threshold and is currently considered the southernmost limit of mangroves in Brazil (Cintrón and Schaeffer-Novelli 1981; Soares et al. 2012). However, it is attention-grabbing, because suitable habitats further south in the country seem to be present (Ximenes et al. 2018), yet mangroves as an ecosystem stop abruptly at Laguna (28°48′S). The mean sea surface temperatures here vary from 18.2 °C in summer to 16 °C in winter (Ximenes et al. 2018).

In a biogeographical terminus, this is a particularly interesting transitional zone, because it appears not only to be a limit to a species but to an ecosystem; at this geographic location, a regime or phase shift takes place. The discontinuity apparent in Laguna is a topic of great relevance to climate change research and the

understanding of the future of mangroves in the region. Rather than mangrove expansion, the region may have been experiencing a contraction due to increasing freshwater dominance that might have resulted in a freshwater barrier blockage that now limits further mangrove expansion to the south beyond Laguna (Cintrón-Molero and Schaeffer-Novelli 2019) (Map 16).

Furthermore, because of potential conflict with agricultural land use in the Patos Lagoon region, it is likely that manmade attempts to restrict saline intrusions could further limit mangrove expansion to the south in the near future. Below Laguna is the 620 km coastal tract of Rio Grande do Sul State (Map 17), which encompasses South America America's longest barrier structure, running almost uninterruptedly except near Cassino and Tramandaí inlets; the former is the inlet to the Patos Lagoon. Both are permanent openings due to the high freshwater discharges of the coastal lagoons behind the barrier.

Patos Lagoon's extensive marshes are dominated by the genera *Spartina*, *Juncus*, *Cyperus*, *Typha*, *Scirpus, Paspalum*, and *Sesuvium* (Delaney 1962), which prevail in an eminently freshwater environment promoted by abundant rainfall water ($P \approx 1500$ mm year^{-1}), reduced potential evapotranspiration, high percolation rates, seepage, river flows, and microtidal regime (Hijmans et al. 2005; Carrère et al. 2013; Cohen et al. 2013). These occupy the biogeographic changeover zone that extends to northeastern Argentina (Costa and Davy 1992). The coast of the Rio Grande do Sul State, south of 34°S, is well known to receive rain throughout the year, including the passage of Mesoscale Convective Systems (MCS) (Houze Jr 2004), severe frontal systems as well as sporadic severe hail and frost events. The larger continental landmass at 10–25°S is conducive to the development of deep convective activity fed by Amazon moisture transport by a low-level jet into the area. This makes this area the most active MCS region in the world (Nesbitt and Zipser 2003).

Mangroves are documented to persist at the latitude of 38°45′S at Westport, Australia, where the mean annual atmospheric temperature is 18 °C and the coldest is 17 °C and where humid subtropical (Cfa) and maritime (Cfb) climate prevails (Peel et al. 2007). At Corner Inlet, Australia, they are found at 38°54′S. So, the abrupt phase shift at Laguna (Brazil) is a prominent feature that merits further and more detailed attention in the context of environmental change prediction. In any case, climate change is perhaps one of the most active research areas in present times, and southeastern Brazil and mangrove ecosystem dynamics offer fruitful research possibilities that would lead to understanding how climate influences coastal vegetation.

The southern domain is an area where planetary, regional, and local processes interact but where it is realistic to locate instrumentation to provide local-level data recordings and frequent site-level vegetation and interstitial salinity monitoring. This is a region where active climatological research is taking place and where climatology is of great interest because of its impact on agriculture and the local economy. This research is bound to help support new hypotheses about the distribution and abrupt limit of mangrove occurrence in this coastal segment.

3.9   Dynamic Framing and the Three Coastal Domains

The segments described, in the 1990 paper, are embedded within three broad domains that span the whole coast; they remain relevant to serve as guiding posts for versatile back-and-forth shifting of observation scales, an approach we have designated as *dynamic framing*. The three domains we identified are (Fig. 3.5)

- The *Northernmost Domain* is highly moisture- and tide-subsidized and extends from the Guyanas and Amapá (Brazil, Cape Orange, Oiapoque River) to Cape São Roque).
- The *Central Deltaic Coast Domain* extends from below Cape São Roque to Cabo Frio, as a domain characterized by warm temperatures but strong lateral constraints due to high levels of wave/energy.
- The *Cabo Frio to Laguna Domain*, largely below the Tropic of Capricorn and increasingly influenced by cold frontal systems and the convective activity of the South Atlantic Convergence Zone. This portion of the Brazilian coast is periodically and strongly influenced by local, regional (South American Monsoon System, Robertson et al. 2005), and global forcings (e.g., ENSO).

An apparent paradox by which muddy coasts act simultaneously as outwelling sources of biological organic matter while being geological sinks is resolved by recognizing a dialectical perspective between scales. In the short term, outwelling is notable and characteristic but over long temporal scales, deposition and accumulation prevail. This suggests that the CES scale integrates equilibrial and nonequilibrial dynamics at the scale of the whole system.

3.10   Final Remarks

It is misleading to consider coastal features as static or perceive variability as a disturbing feature. Variability is representative of complexity and although it presents obstacles to generalizing and identifying clear-cut patterns in nature, it is part of it and is present at all scales driven by external and internal factors, especially climate and self-organization. The emerging awareness about mangrove systems in sequestering carbon emissions and their contribution to climate regulation increases the relevance of continued research for education, developing robust conservation policy and for suggesting future research grounded in the emerging field of complexity science.
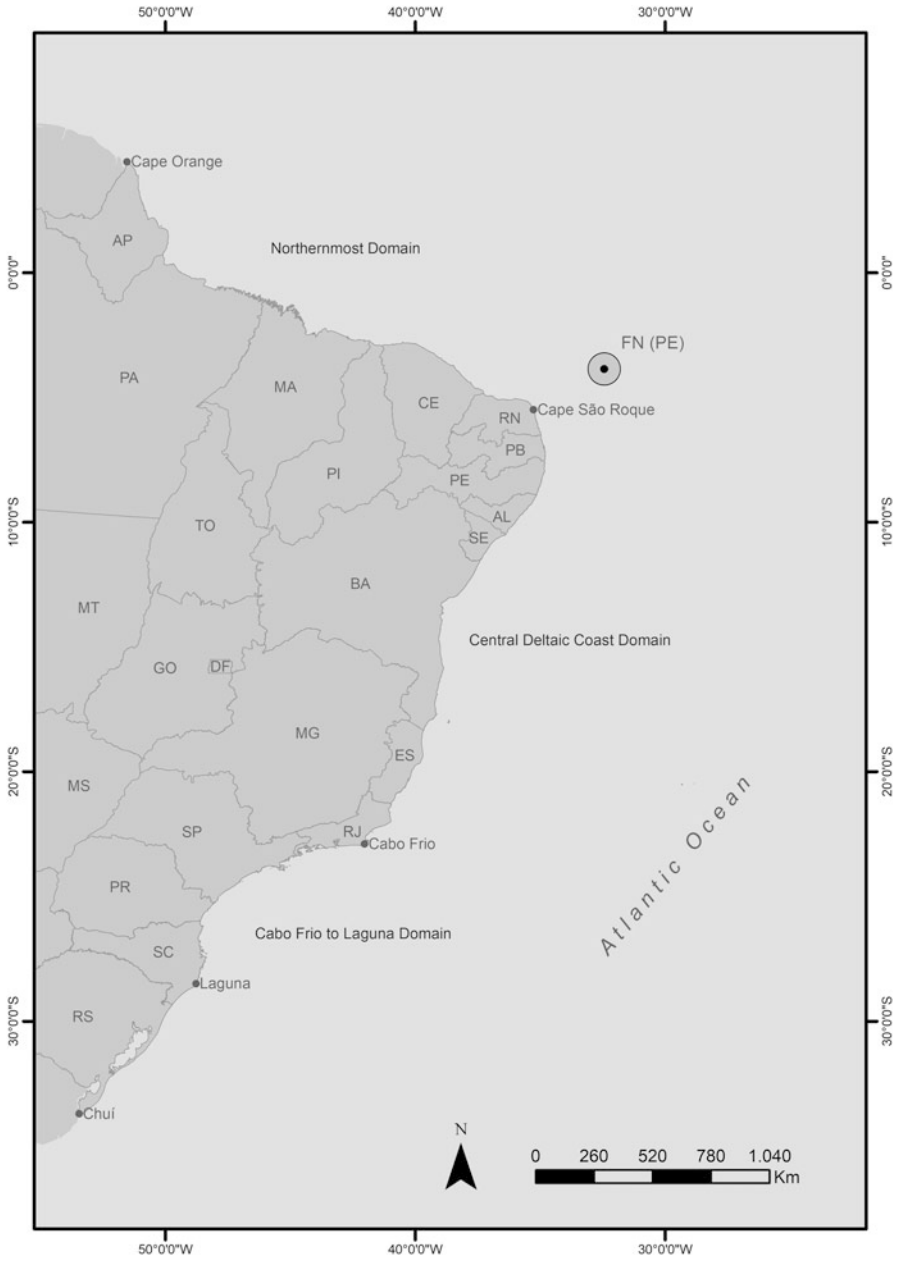
Fig. 3.5 Northernmost, Central Deltaic, and Cabo Frio to Laguna Coastal Domains

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