Title
Mangroves in depth: long-term carbon burial across spatial scales

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Mangroves in depth: long-term carbon burial across spatial scales

A dissertation submitted in partial satisfaction of the requirements for the degree Doctor of Philosophy

in

Oceanography

by.

Matthew Thomas Costa

Committee in charge:

Professor Octavio Aburto-Oropeza, Co-Chair
Professor James J. Leichter, Co-Chair
Professor Elsa Cleland
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2019

The Dissertation of Matthew Thomas Costa is approved, and it is acceptable in quality and form for publication on microfilm and electronically:

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University of California San Diego

2019

DEDICATION

I dedicate this Dissertation to Everett William Molinari (1925–2011), grandfather, artist, teacher, and lover of learning. Thank you for the walks on the beach and the gift of observation.

EPIGRAPH

Much have I travell’d in the realms of gold,
    And many goodly states and kingdoms seen;
    Round many western islands have I been
Which bards in fealty to Apollo hold.
Oft of one wide expanse had I been told,
    That deep-brow’d Homer ruled as his demesne;
    Yet did I never breathe its pure serene
Till I heard Chapman speak out loud and bold:
Then felt I like some watcher of the skies
    When a new planet swims into his ken;
Or like stout Cortez when with eagle eyes
    He star’d at the Pacific—and all his men
Look’d at each other with a wild surmise—
    Silent, upon a peak in Darien.

—John Keats, “On First Looking into Chapman’s Homer”

For the Ages of Heroes and of Explorers we have come too late, and yet today we stand at the threshold of limitless discovery. Let us always direct our gaze to the horizon but never lose sight of our shared humanity and our shared home.

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ABSTRACT OF THE DISSERTATION

Mangroves in depth: long-term carbon burial across spatial scales

by

Matthew Thomas Costa

Doctor of Philosophy in Oceanography

Professor Octavio Aburto-Oropeza, Co-Chair
Professor James J. Leichter, Co-Chair

The global climate crisis has drawn attention to the carbon sequestration and storage ecosystem services performed by mangrove forests. In this dissertation, I investigate belowground carbon stocks in mangrove ecosystems and describe patterns of carbon distribution with depth belowground, across variable coastal landscapes, and from the equator to the northern limit of mangroves on the west coast of North America. The results of my research support the thesis that mangrove forest belowground carbon stocks possess significant spatial variation driven mainly by variation in the sediment column depth and that this variation are predicted by different paleoecological, geomorphological, or climatic factors on the local, landscape, and regional scales. Chapter 1 discusses mangrove distributions, adaptations, ecology, and ecosystem services; describes the state of scientific knowledge on mangrove blue carbon; and introduces three investigations into mangrove carbon stocks which I performed as my doctoral research. Chapter 2 describes a coring study of the sediments of four mangrove sites in Baja California Sur, Mexico. I demonstrate the accumulation of peat only below the zone of root growth and find carbon density does not decline with depth and age even in 5,000-year-old peat deposits, though there is a loss of nitrogen and a shift in microbial diversity and $\delta^{15}N$ indicating microbial nitrogen turnover. In chapter 3, I document over an order of magnitude of variation in carbon stocks along the coasts of the Galapagos. I test the roles of coastal geology and wave exposure in driving this variation and find that carbon stock variance is greater among lava sites than sites with soil. In chapter 4, I gather data from cores collected at 80 sites from the Galapagos, the Pacific and Caribbean coasts of Panama, and the Baja Peninsula to compare mangrove sediment carbon density and depth regionally. Carbon density is relatively invariable and does not increase with annual rainfall, while highly variable sediment depth increases with relative sea-level rise rate, and the relationship between sediment depth and coastal slope becomes less positive with increasing relative sea-level rise. Chapter 5 discusses the implications of these results for the study and management of mangrove ecosystems.

CHAPTER 1

Introduction to mangrove ecosystems, ecosystem services, and blue carbon research

Mangrove Ecosystems

The coasts and tidal estuaries of the tropics and subtropics are inhabited by mangroves, woody plants capable of colonizing the intertidal zone in places protected from intense wave energy (Chapman 1976). These trees frequently form dense forests, characterized by intertidal zonation, abundant biomass, rapid productivity, and thriving communities of organisms dependent on mangroves as physical habitat and detrital food sources (Lugo and Snedaker 1974, Walsh 1974, Odum and Heald 1975). These environments (termed "mangrove forests" or simply "mangroves") have been objects of study in Western civilization since the Classical Age, with the observations by the Greeks dating to 325 B.C.E.[1] Since surely even earlier and continuing to today, mangroves have served as ethnobotanical resources for coastal peoples around the world, providing timber, fuel, tannins, and diverse food products derived from mangrove fauna (Walters et al. 2008). Today, the utility of mangroves for human communities is formally recognized and studied in the context of their "ecosystem services," the ecological processes that occur in these systems that generate value for humans (Costanza et al. 1997). This area of research is growing in urgency, as mangroves suffer rapid rates of loss globally due to

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[1] The 2nd-century C.E. Greek historian Arrian records in his work *Indica* the account of Nearchus, captain of the fleet of Alexander the Great, of Alexander's anabasis (i.e. journey from the coast upstream) of the Indus Valley and of the fleet's return west through the Persian Gulf, from 325 to 323 B.C.E. (Brunt 1983). Nearchus makes observations of "great trees" in marshlands on the Indus, though it is unclear whether these are saline wetlands. More unambiguous are his comments on thick forests on the edges of a tidal channel in what is now the Straight of Hormuz.

excessive exploitation, heedless coastal development, and climate change (Valiela et al. 2001). The need to address the global crisis of climate change has drawn the attention of mangrove researchers to the service of carbon sequestration performed by these ecosystems (Mcleod et al. 2011), as well as the emissions caused by their destruction due to the release of long-held sedimentary carbon stores (Pendleton et al. 2012). In this dissertation, I investigate spatial variation in belowground mangrove carbon stocks and test the thesis that this variation can be predicted by different factors as the spatial scale of study is increased. In pursuit of this goal, I uncover patterns of carbon distribution with depth belowground, across variable coastal landscapes, and from the equator to the northern limit of mangroves on the west coast of North America. This chapter discusses mangrove taxa and distributions, physiological adaptation, ecology, and ecosystem services; describes the state of scientific knowledge on their carbon cycling; and introduces three investigations into mangrove carbon stocks which I performed as my doctoral research.

Diversity and Distribution

Though exact delineations are debated, Duke (1992) counts among the mangroves sixty extant species, scattered across nineteen taxonomic families, most of which are mainly comprised of non-mangrove taxa. The saline, flooded, anoxic, and nutrient-limited sediments of these forests present severe physiological challenges. Adaptations for survival in this environment have arisen from many disparate branches of the plant kingdom, and the similarities in form, physiology, and ecology among mangrove lineages offers a striking example of convergent evolution under strong environmental selection (Hogarth 1999). These relatively few species dominate a biome that is spread over 137,760 km^2 in 118 countries, though more than

50% of this area is distributed in just six: Indonesia, Australia, Brazil, Mexico, Nigeria, and Malaysia (data from the year 2000; Giri et al. 2011). Parallel to the patterns seen in other tropical marine ecosystems (Briggs 1999), the Indo-West Pacific is the most diverse mangrove bioregion (Duke 1992). It is hypothesized that mangroves first evolved in the Indo-West Pacific as early as 69 million years ago and spread westward to Africa and through the Neotropics (Duke 1995, Hogarth 1999). During the Cenozoic Era, during which the plant families containing extant mangrove species diversified, this westward spread was gradually restricted by the closure of the Tethys Sea and the expansion of the Atlantic Ocean. As a result, modern mangrove biogeography has since the late Miocene Epoch been divided into Indo-West Pacific and Atlantic-East Pacific provinces. The mangrove community in the northern hemisphere of the Americas, where I conducted by doctoral research, is dominated by *Rhizophora mangle*, *Laguncularia racemosa*, and *Avicennia germinans*.

Physiological Adaptation

Tidal flooding exerts major physiological stressors on mangroves. Slow-moving and poorly aerated saltwater bathes their sediments, which, dominated by microbial decomposition, are typically anoxic, reducing, and acidic (Boto 1984). These edaphic conditions both deprive roots of oxygen needed for cellular respiration and expose them to toxic sulfides. Salinity represents a perhaps even greater challenge to mangrove trees than does sediment anoxia. Though surrounded by water, mangroves paradoxically face physiologically dry environmental conditions, as their roots must work against the osmotic gradient between the sediment and their internal tissues to take up water (Odum 1974). A general lack of light limitation, due to tropical sunshine and little canopy shading (Janzen 1985), result in rapid uptake of nutrients by productive mangrove trees. Mangroves also compete for nutrients with fast-growing populations of sediment bacteria (Alongi 1988). As a result, mangrove growth is frequently macronutrient-limited (Feller et al. 2002, McKee et al. 2002), with most nitrogen and phosphorus bound up in sediment organic matter (Alongi and Sasekumar 1992).

Many of the adaptations that mangroves have developed in response to anoxic, salty, and nutrient-limiting conditions are manifested in their distinctive root systems. In response to oxygen starvation, mangrove trees possess elaborate systems of above-ground roots and air-conducting vasculature for gas exchange. The extensive aerial prop roots of the characteristic mangrove genus *Rhizophora* are pocked on their exteriors with gas exchange pores called "lenticels" (Hogarth 1999). *Avicennia* typifies a different root plan, with cable roots extending radially underground, sending up vertical woody root segments called "pneumatophores" out of the mud at intervals to provide gas exchange for the underground network of roots. In both these and other mangrove genera, a significant portion of the root interior is given over to hollow channels of tissue called "aerenchyma" that conduct oxygen gas to the portions of the roots buried in the mud and carbon dioxide into the aerial roots to be released to the atmosphere. To accommodate sediment salinity, mangroves invest energy in active transport of water and partial salt exclusion (Scholander et al. 1962). Salt not excluded is transported into vacuoles, and the cytoplasm protected from low turgor pressure by the production of osmolyte compounds (Parida and Jha 2010). For the uptake of scarce macronutrients, mangrove roots proliferate the production of fine rootlets in hotspots of nutrient availability, usually decaying root detritus (McKee 2001), constituting a measurable increase in sediment elevation by the ingrowth of root volume (McKee et al. 2007). Given the centrality of specialized root adaptations to survival in tropical, soft-sediment, intertidal environments, it is not surprising that root structural patterns are one of the clearest demonstrations of convergent evolution among phylogenetically far-flung mangrove taxa (Figure 1-1). This dependence on root-based adaptations may also explain the generally higher root-to-shoot biomass ratios in mangroves than in other plants (Clough and Attiwill 1979), especially as physiological stressors increase (Sherman et al. 2003). Root biomass production is also the central mechanism by which mangroves generate long-term carbon stocks.

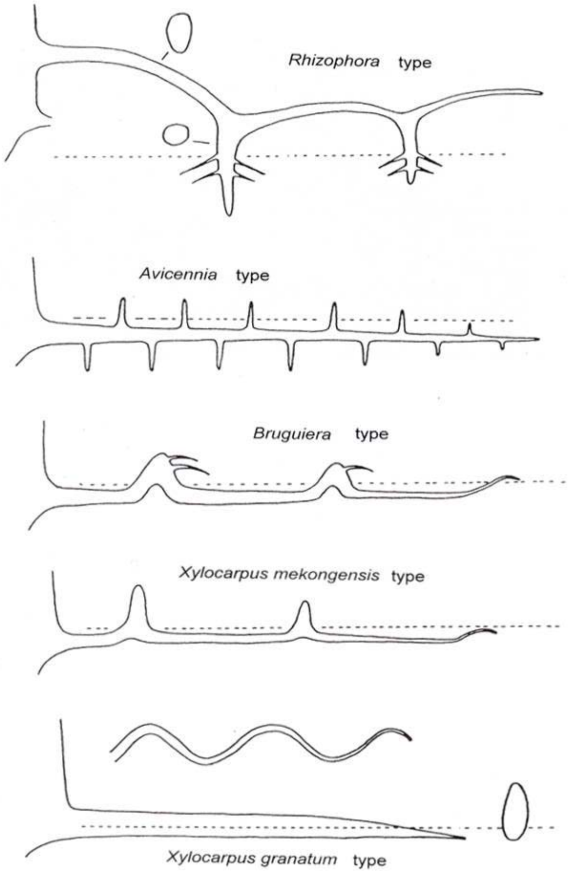

Figure 1-1: Root structures from mangrove taxa from three different taxonomic orders of plants demonstrate convergence on extensive root systems with significant aerial surface area (from Hogarth 1999).

Ecology

Mangrove forests form a distinct ecological zone at the boundary of land, air, and sea, accommodating unique biological communities and facilitating many pivotal trans-ecosystem fluxes and interactions. Here, animal populations from the neighboring terrestrial and nearshore marine environments overlap along with mangrove specialists (Nagelkerken et al. 2008). In this physiologically challenging habitat, the diversity of mangrove trees themselves is rather low, with just one to four species likely to be found in any one location in the Neotropics. The few trees that can survive here however form the foundation of an ecosystem that supports diverse and productive assemblages of fish, birds, crustaceans, mollusks, and many other animals, as well as epiphytes, fungi, and a diversity of microbial life only now beginning to be fully documented (Alongi and Sasekumar 1992, Andreote et al. 2012). The intensity of biological activity in mangrove forests depends in large part on these ecosystems' high primary productivity. Taking advantage of abundant tropical sunlight, nutrient recycling and regeneration (Alongi et al. 1992), and regular or pulsed freshwater flux from riverine or groundwater flows (Urquidi-Gaume et al. 2016), mangroves fix 218±72 TgC (mean±S.E.) per year globally (13.6±4.5 MgC/(ha×year) on average assuming a global areal extent of mangroves of 160,000 km^2), producing a vast quantity of woody material, leaves, roots, and DOC (Bouillon et al. 2008). Leaf litter, in particular, is a source of nutrition for a wide range of invertebrates and micro-organisms, and a detritus-based food web is considered responsible for the high rates of animal productivity in these systems (Odum and Heald 1975). A large amount of organic carbon is exported as POC, at rates as high as 10 kgC per hectare per day (Boto and Bunt 1981). This excess production helps support consumers in nearshore marine environments (Chong et al. 2001). Nutrients released by the breakdown (often mediated by grapsid crabs) and decomposition of mangrove organic matter support phytoplankton in mangrove estuaries (Werry and Lee 2005). This primary production in turn supports a pelagic component of the mangrove-dependent food web, though the relative importance of mangrove outwelling to nearshore food webs continues to be debated (Nagelkerken et al. 2008).

The position of mangrove forests at the land-ocean-atmosphere interface fosters these exchanges of nutrients, organic matter, and organisms across landscapes and on smaller scales the establishment of strong gradients of temperature, salinity, oxygenation, and nutrient availability that make their sediments biogeochemical hotspots (Valiela et al. 2001). Mangrove ecosystem boundaries that have received significant research attention include the sediment-water boundary, e.g. in the measurement of gas and solute fluxes (Alongi et al. 2004), or the inshore-offshore boundary in the study of the export of detritus or juvenile animals (Nagelkerken et al. 2008). The phenomena explored in this dissertation mainly take place at a less well-studied ecosystem boundary, that between the live root zone in mangrove sediments and deeper peat deposits formed from the root detritus of past mangrove plants. Understanding the processes at work at this hidden ecosystem interface is valuable not only for mapping and managing the carbon sink dynamics of these forests, but also for addressing a conceptual ecological problem posed by the idea of long-term net carbon sinks. Fifty years ago, Eugene Odum described a model of ecosystem development in which systems transition over time from early colonization to a mature or climax state (1969). In the model presented by this seminal paper, several variables increase along the ecosystem development trajectory, including the complexity of species interactions, the stability and predictability of the system, and total living and dead biomass, i.e. carbon. These variables increase asymptotically, with essentially no additional biomass increase over time once maturity is reached. This model of ecosystem development has left its mark on subsequent ecological thinking, but the idea of long-term net carbon sinks in ecosystems does not fit the model, as these systems must continuously increase their carbon content over time, with a linear, rather than saturating, carbon curve over time. As I discuss below, the formation of peat deposits from root detritus below the zone of live root growth in mangrove sediments is a primary mechanism by which these ecosystems store carbon over the long term. The subsequent chapters of this dissertation report on my investigations of patterns and processes in mangrove sedimentary carbon burial and preservation. In the conclusion, I again address the problem of net carbon sinks in mangrove ecosystems over time. I postulate that, if downward flux of carbon across the belowground boundary between mangrove ecosystems and peat deposits is included in a carbon budget, then these forests can retain constant biomass at maturity.

Ecosystem Services

The importance of mangrove forests extends beyond supporting biodiversity and enhancing the productivity of neighboring ecosystems (Nagelkerken et al. 2008). The ecological functions of mangroves translate into valuable services to humans. For instance, yellow snapper (*Lutjanus argentiventris*) are an important part of the Gulf of California's fisheries, and, though they are caught offshore on rocky reefs, they rely on mangroves as critical nursery habitats during their first year (Aburto-Oropeza et al. 2009). In fact, Aburto-Oropeza et al. (2008) found that one hectare of fringe mangrove in the Gulf of California produces 37,500 US$ of added fisheries value each year. Penaid shrimps, which in many regions comprise the most economically productive fisheries, include species that rely on mangrove habitat and productivity (Primavera 1998). Coral reef fishes, known for their ecological value on reefs and exploited in many locations for food, have also been shown to depend on nearby mangroves (Mumby et al. 2004). In addition to supporting fisheries, mangroves produce timber, fuel, and other high-value products, improve the water quality of terrestrial run-off, and provide other services for coastal people (Ewel et al. 1998, Walters et al. 2008). By absorbing the physical energy of waves, mangroves also reduce loss of life and property in coastal communities struck by cyclones and tsunami (Das and Vincent 2009, Kathiresan and Rajendran 2005). Mangrove roots trap sediment and prevent shoreline erosion, altering the coastal landscapes on which they stand (Gilman et al. 2007). In light of the projected increase in sea level and frequency of major storms expected with worsening atmospheric carbon pollution (Ciais et al. 2013), mangrove forests' role as coastal defenses will take on even greater importance in the coming decades.

Carbon Sequestration and Storage

One ecosystem service that mangroves—along with salt marshes and seagrass beds, the other "blue carbon" ecosystems—provide on a global scale is their contribution to the carbon cycle (Nelleman et al. 2009). The high rates of primary productivity that these forests exhibit convert large amounts of CO_2 from the atmosphere into plant biomass every year (Bouillon et al. 2008). The trees respire only a fraction of the carbon they fix, and many heterotrophic animals and other organisms feed on and respire some of this net primary productivity. Another fraction is exported as leaf and seedling litter, POC, and DOC to the coastal ocean and is eventually consumed by the marine food web and respired. And yet, with all these fixed carbon removal processes taken into account, mangroves still show net positive ecosystem carbon balance (Duarte and Cebrián 1996). Other forests, such as upland tropical rainforests, are capable of similarly high productivity rates (Dixon et al. 1994), but they typically possess shallow soils in which detritus is quickly respired, while about 10% of net primary production in mangroves becomes buried in the sediments (Bouillon et al. 2008).

Mangroves are generally accretionary systems, accumulating inorganic sediment, whether brought downstream by rivers or up by ocean waves and tides (Woodroffe 1992). Networks of channels and mangrove roots impede water flow, causing suspended sediment to settle out, building land vertically over time in some geological settings. This constant accumulation of material aids in the burial of mangrove primary production. So much organic matter is buried, in fact, that the vertical accretion of mangrove forests is frequently due, not just to sedimentation, but to the growth of subsurface layers of sediment almost entirely composed of organic matter, also known as peat.[2] The same physiologically challenging conditions to which mangrove trees must adapt to survive also cause their sediments to preserve mangrove detritus so effectively. Anoxic conditions and low nutrient availability outside of organic or mineral complexes severely reduces the rate of detrital decomposition (Kristensen et al. 2008, Alongi et al. 2004, Sánchez-Carrillo et al. 2009). This organic matter, especially mangrove root detritus (McKee and Faulkner 2000), is eventually deposited below the rooting zone into which some oxygen and bioturbation are able to reach and accumulates in layers of peat reaching meters deep (McKee et al. 2007, Ezcurra et al. 2016).

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[2] The word "peat" is often used specifically to refer to soils composed of *Sphagnum* moss, sedges, and other non-woody wetland plant material in high-latitude bogs and fens. First appearing as the Latin *peta* in 13th-century Scotland, it may descend from an ancient Pictish word meaning "piece" (Celtic root *pett-*), suggesting that the inhabitants of northern Europe have been cutting pieces of peat to use for fuel for at least eight centuries (Fenton 1997). As is the case with many old words employed as technical terms, the definition of "peat" is mired in ambiguity. The U.S.D.A. Soil Taxonomy Manual states that sedimentary material composed of > 20% organic matter "has been called peat or muck" (Soil Survey Staff 1999), with peats characterized as fibric (consisting of plant fibers), and mucks as sapric (containing little plant fiber). I use "peat" in the broad sense, meaning a sedimentary deposit composed largely of fibrous organic matter.

Figure 1-2: Mangrove peat from Baja California Sur, Mexico (photo: Paula Ezcurra). The entire mass is composed of compacted, undecomposed root fibers.

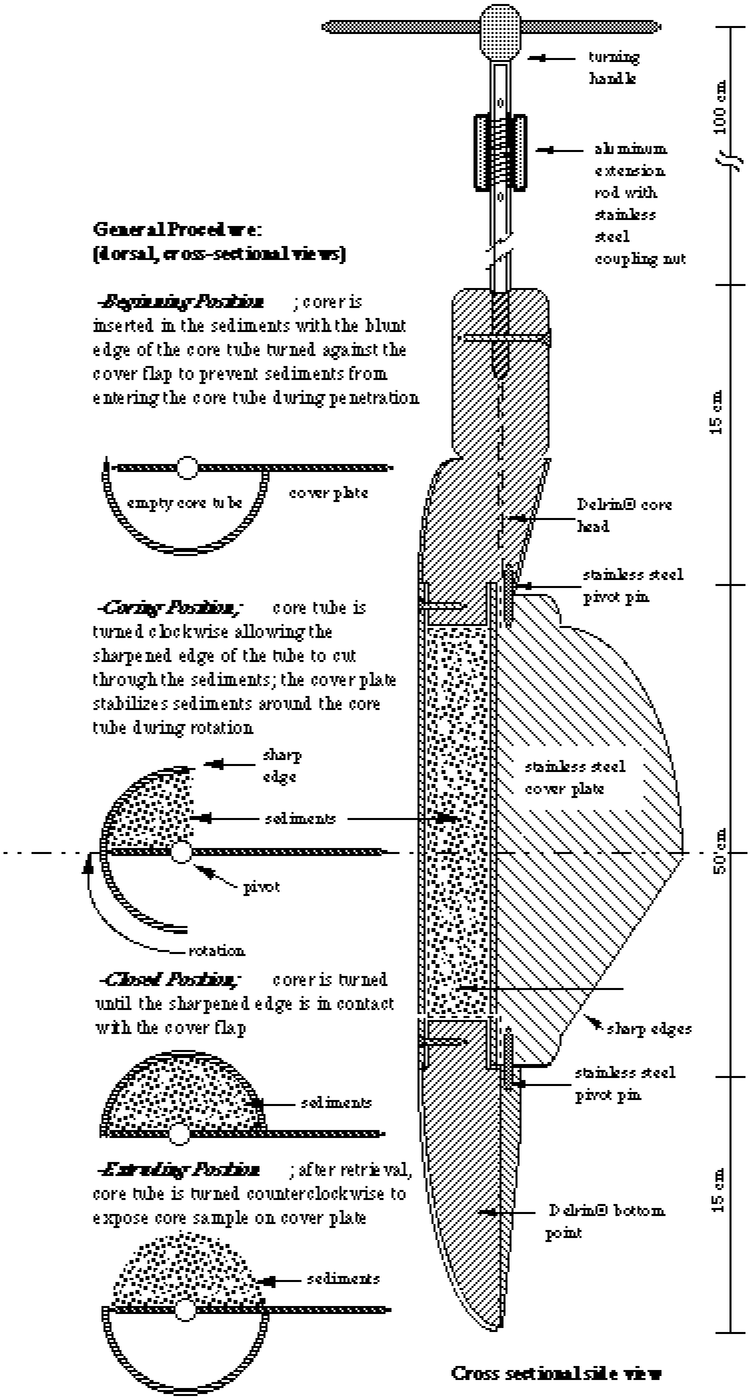
Globally, mangroves cover only about 0.03% of the area of the Earth, but their peat deposits give mangroves disproportionate importance to the biosphere's stock of organic carbon. While some studies focus on aboveground biomass (Hutchison et al. 2013), what sets mangroves and other blue carbon ecosystems apart is their long-term storage of carbon in sediments (Mitra et al. 2005). It is this component of mangrove carbon stocks that I investigate in this dissertation. Mangroves store more carbon per unit area than almost any other ecosystem on Earth, including on average the other blue carbon ecosystems of salt marshes and seagrass beds (Pendleton et al. 2012). The study of Donato et al. (2011) in Indonesia showed that mangroves far exceed other forest types in carbon storage, mostly due to belowground organic matter (1,000 MgC/ha). In the context of the ocean, mangroves store twenty times more carbon per unit area than the top meter of marine sediments averaged worldwide (Ciais et al. 2013). Estimates of the total amount of carbon stored by mangroves range from 3 PgC (Hutchison et al. 2013) to 20 PgC (by the estimate of Donato et al. (2011) of 1,000 Mg/ha). Taking into account the global areas of mangrove forests, that of the entire ocean, and the ocean sedimentary carbon pool, 0.1–1% of the carbon stored in marine sediments is contained in the tiny fringe of mangroves along the edges of the tropical oceans. Global mangrove carbon stocks are not well constrained, however, and in fact may be much higher. Duarte and Cebrián (1996) estimate that mangroves provide 17% of the ocean's carbon storage. Given this range of global mangrove carbon stock estimates and a conservative estimate for the social cost of releasing stored carbon of 37 US$ per MgC (Interagency Working Group on Social Cost of Carbon 2013), the value of the remaining global mangrove carbon stock climbs to the hundreds of billions to tens of trillions of dollars, not including the value of ongoing sequestration nor of the many other ecosystem services that they provide.

Despite growing appreciation for the economic value of mangroves, these forests are severely threatened. Currently about 1% of the world's mangroves are destroyed each year (Duarte et al. 2013). Unsustainable coastal forestry, agriculture, aquaculture, and urbanization, along with increasing sea level and intensifying heat waves, have already resulted in an estimated loss of more than 35% of global mangrove cover (Valiela et al. 2001). The use of the ecosystem service concept to place explicit economic value on the functioning of natural ecosystems holds promise as a framework to motivate biodiversity and ecosystem conservation (Turner et al. 2007). The storage of organic carbon in blue carbon ecosystems is gaining recognition in the scientific and policy communities as valuable strategy for mitigating anthropogenic carbon pollution (Thomas 2014). As global stakeholders begin to leverage the carbon storage potential of natural systems, mangrove research can provide the information necessary to map, to value, and to manage mangrove carbon stocks.

Sampling Mangrove Sediments

Belowground mangrove carbon can be investigated through sediment coring techniques (Kauffman and Donato 2012). In the research presented here, I sampled using a Russian peat corer (Aquatic Research Instruments; Figure 1-3; Belokopytov and Beresnevich 1955), which is used primarily to core in relatively soft peat sediments. This style of sediment corer possesses several advantages over other corers, providing relatively undisturbed and uncompressed cores which yield accurate estimates of bulk density and other physical characteristics (Jowsey 1966, Pitkänen et al. 2011). As illustrated in Figures 1-3 and 1-4, the corer takes vertical, semi-cylindrical sections of sediment 5 cm in diameter and up to 50 cm in length. By adding extension rods, one can then resample the same hole and obtain successively deeper 50 cm deep sections of sediment. If this process is repeated to rejection, when the core tip hits a hard substratum underlying the sediment, the entire sediment column has been sampled, representing the time span from the initiation of wetland sedimentation to the present day. This approach captures temporal variation, i.e. variation with depth, in detail without addressing spatial variation.

Sedimentology as a discipline has long been influenced by the principle that sediments are distributed in uniform, laterally continuous layers that vary principally with depth (Steno 1669). Guided by this axiom, one or a few cores can be used to describe a large area. This approach is highly pragmatic considering the difficulty of obtaining cores and is commonly employed in studies of mangrove sediments (Donato et al. 2011, McKee 2011). However, mangrove sediments are shaped by more processes than just the slow and even settling of suspended particles. In addition to riverine and tidal sediment delivery, shifting sand bars, tidal creek channels, and depressions alter the sediments over time (Thom 1967). Mangrove biomass production also varies along environmental gradients across individual mangrove forests (Feller et al. 2002). These processes generate lateral discontinuity in the mangrove landscape. Still, limited local spatial core sampling is the norm in studies in this field, including most of the work in this dissertation. Capturing belowground spatial variation on the forest scale remains an uncharted frontier for blue carbon research.



General Procedure:
(dorsal, cross-sectional views)

-Beginning Position; corer is inserted in the sediments with the blunt edge of the core tube turned against the cover flap to prevent sediments from entering the core tube during penetration

-Coring Position; core tube is turned clockwise allowing the sharpened edge of the tube to cut through the sediments; the cover plate stabilizes sediments around the core tube during rotation

-Closed Position; corer is turned until the sharpened edge is in contact with the cover flap

-Extruding Position; after retrieval, core tube is turned counterclockwise to expose core sample on cover plate

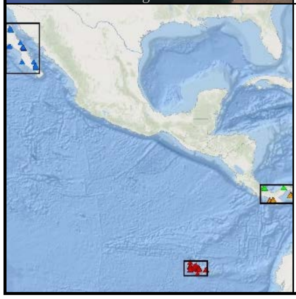
Figure 1-3: A Russian peat corer, showing the specifications and detailing the way in which semi-cylindrical core sections are obtained (Aquatic Research Instruments).

Figure 1-4: A core section, from 50 cm to 100 cm depth, taken using the Russian peat corer at La Dispensa on Isla Espiritu Santo in Baja California Sur, Mexico in July 2014. Mangrove peat is visible from 50 cm to 75 cm depth.

Mangrove Carbon across Spatial Scales

This dissertation is organized so as to explore variation in belowground mangrove carbon stocks across spatial scales, from variation with depth in individual cores to that across the northern American mangrove bioregion (Table 1-1). Chapter 2 examines patterns of carbon, nitrogen, their stable isotopes, and radiocarbon age with depth as indicators of decomposition processes in peat deposits at several sites in Baja California Sur, Mexico. In this chapter colleagues and I also characterize the diversity and community composition of bacterial and archaeal life in these core samples with depth. This paper tests the hypotheses that microbial communities vary in accordance with sediment type and peat age; that microbial diversity and nitrogen density decreases with peat age as carbon sources become more recalcitrant, as does carbon density due to slow organic matter remineralization; and that stable isotopes of carbon and nitrogen increase, indicating preferential loss of the light isotopes in microbial remineralization processes. Chapter 3 documents the first study of blue carbon in the Galapagos, in which, as part of a larger expedition, I lead a collaborative effort to measure belowground carbon stocks in the mangrove forests of the archipelago. This study included an assessment of inter-site variability, showing more than an order of magnitude of variation in carbon stocks, driven mainly by sediment depth. The hypotheses that this inter-site variation is predicted by geological or oceanographic stressors are tested. Finally, chapter 4 compiles core sample data that I collected with the help of several collaborators from eighty sites across four areas of the New World mangrove distribution: the Galapagos, the Pacific and Caribbean coasts of Panama, and the Baja Peninsula. This work considers separately the two constituents of belowground carbon stocks, sediment carbon density and depth, across the varying climatic and geological conditions prevalent in these different areas. We tested the hypotheses that sediment carbon density increases with annual rainfall and that sediment depth is predicted by the interaction of coastal slope and rate of relative sea-level rise. Chapter 5 summarizes the findings of these studies and makes recommendations for the future of blue carbon research.

Table 1-1: This dissertation explores variation in belowground carbon stocks in mangroves on a range of spatial scales: with depth in the sediment column, across variable coastal landscapes, and spanning the distribution of mangroves in the New World from the equator to 29 °N.

	Spatial Scale	Question	Hypotheses
 Paula Ezcurra	Sediment Column	How do microbial community and nitrogen and organic carbon content vary with depth and age in peat deposits?	Microbial community varies with sediment properties; microbial diversity, C_{org}, and N decrease with depth; and $\delta^{13}C$ and $\delta^{15}N$ increase.
 © Maxar Technologies	Landscape	How does belowground carbon respond to heterogeneity across mangrove landscapes?	Carbon stock variance is associated with coastal geology and wave exposure. Sediment depth constrains carbon stocks.
	Region	Do sediment carbon density and depth vary with regional climate, RSLR rate, and coastal slope patterns?	C_{org} increases with rainfall, and sediment depth and its sensitivity to coastal slope increase with RSLR.

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CHAPTER 2

Baja California Sur mangrove deep peat microbial communities cycle nitrogen but do not affect old carbon pool.

Abstract

Mangrove forests provide important ecosystem services including fisheries nursery habitat, coastline protection, runoff purification, and other local benefits. Of global import is their ability to store carbon in organic peat belowground for thousands of years, with more carbon per unit area than terrestrial tropical forests. Mangrove carbon storage relies in part on their high primary productivity, but essential to the large and long-lived nature of this storage is the slow rate of microbial decomposition of buried mangrove peat. In this study, we ask how carbon and nitrogen contents and microbial community composition vary with peat age and describe the formation of these mangrove peat deposits over time. At four peat-containing mangrove sites in the area of La Paz, B.C.S., Mexico, we cored the sediments until rejection with a Russian peat corer and from these cores obtained 5 cm samples at 20 cm intervals. In these samples we measured organic carbon, nitrogen, and ^{14}C age. We observed high carbon densities ($3.4\times10^{-2}\pm0.2\times10^{-2}$ g/cm^3) and C_{org}:N ratios (42±3) in peat samples and inter-site difference in C_{org}:N that reflect differing preservation conditions. Recalcitrant organic matter sources and anaerobic conditions create a strong imprint on peat microbial communities. Microbial community composition and diversity was strongly driven by depth gradients and variation in sediment biogeochemistry variables, including C_{org}:N ratio and radiocarbon age. Carbon dating allowed us to reconstruct the accumulation of organic matter over the last 5,029±85 years. Even

over these long time scales, though microbes evidently have continuously cycled the peat nitrogen pool, carbon stocks remain effectively untouched over time. Future work examining the roles of distinct microbial taxa and metabolisms in the slow turnover of peat carbon, nitrogen, and other elements would shed further light on biological basis of mangrove belowground carbon preservation.

Introduction

Mangrove forests have been recognized for decades as productive ecosystems that support detritus-based food webs (Odum and Heald 1975). Situated on tropical and subtropical coasts around the world (Duke 1992), these coastal wetlands also contribute to the productivity of adjacent nearshore ecosystems such as coral reefs through the outwelling of excess production (Alongi 1990). This ecological function of mangroves is made possible by their high rates of primary productivity (Bouillon et al. 2008), exceeding the capacity of local grazers, and of physical exchange with neighboring environments due to tides. As sources of food and shelter, mangroves have been shown repeatedly to function also as nursery habitats for a wide range of marine and other animals (Nagelkerken et al. 2008). These functions in many cases translate into valuable ecosystem services (Costanza et al. 1997), and in recent decades a surge of research effort has been devoted to documenting and economically valuing the services mangroves provide for humans, driven by the alarming 2% global loss of mangrove area annually (Valiela et al. 2001). Mangroves produce timber and other plant products, filter terrestrial run-off, and stabilize coastlines from erosion (Ewel et al. 1998), even mitigating the impact of severe events such as tsunami (Kathiresan and Rajendran 2005). Their nursery habitat function exports fish and invertebrates consumed by people, producing as much as 37,500 US$/ha each year for coastal fisheries (Aburto-Oropeza et al. 2008). Thus, both in terms of the export of detrital plant matter and of entire organisms, mangrove research has documented the ways in which these ecosystems are sources of production and productivity to the larger environment.

More recently, a different aspect of mangrove productivity has gained attention in the literature. In addition to mangroves producing and exporting organic carbon, they also act as carbon sinks (Twilley et al. 1992). Though leaf litter and propagules are consumed by detritivores or exported by the tides, woody material including roots can remain unconsumed for long periods of time (Middleton and McKee 2001). Some of this production is buried in vertically accumulating peat deposits, where anoxic conditions and metabolic recalcitrance help preserve organic matter for millennia (McKee et al. 2007). As a result, mangroves and other coastal wetlands globally possess exceptionally high rates of carbon sequestration (Chmura et al. 2003), and soil carbon stocks in these systems surpass those in other types of forests several times over (Donato et al. 2011). The recognition in the last decade of the disproportionately high contribution of mangroves, as well as salt marshes and seagrass beds, to global carbon storage has added a new prong to the study of their ecosystem services, the quantification of the "blue carbon" contained in these ecosystems (Nelleman et al. 2009). Using carbon stock estimates to drive economic investment in the preservation of mangroves has gained attention as a potential tool to mitigate anthropogenic carbon dioxide pollution (Thomas 2014). Though researchers have raced to quantify mangrove carbon stocks around the world (Donato et al. 2011; Adame et al. 2013; Alongi et al. 2016), understanding of the processes that control belowground mangrove carbon stocks is far from complete.

Decades of research on estuarine carbon cycling has explored the role of micro-organisms in these ecosystems and their functioning. Early work focused on the role that microbes play in breaking down mangrove primary production or moving it up the food chain to be consumed by animals. Fell et al. (1975) cultured phycomycete fungi from mangrove leaf litter and tested their impact on its degradation, enriching the material in nitrogen relative to carbon and thus facilitating its use by invertebrate consumers. In a temperate salt marsh/seagrass system, microbial abundance varied significantly with depth, and to a lesser extent with the physical characteristics of the sediment (Ferguson and Murdoch 1975). In the North River mangrove system in Florida, Odum and Heald (1975) discussed the role that microbes' partial consumption and attachment to leaf litter particles play in the forest's detritus-based food web. Sediment bacterial densities and productivity rates were shown to possess high spatial and seasonal variability in mangroves of northeastern Australia, where it was estimated that a large part of ecosystem production passes through the bacterial community (Alongi 1988). Bacterial densities also vary between forest types, with greater densities in large deltaic systems than smaller fringe or riverine forests, with productivity rates correlated with availability of DON and DOC (Alongi and Sasekumar 1992). Though sediment microbes and mangrove trees interact biogeochemically, bacterial densities and growth rates vary with edaphic conditions, rather than the species of nearby trees (Alongi et al. 1993). More recent research has shifted attention toward the functional role of microbes in mangrove ecosystems. Sediment microbes fix nitrogen from the atmosphere and immobilize it from the dissolved pool, consume and transform organic carbon, and solubilize phosphorus, making it available for nutrient-limited mangrove growth (Holguin et al. 2001). Balanced methane production by microbes and subsequent oxidation in the sediment (Giani et al. 1996), as well as microbial solubilization of mineral phosphate (Vazquez et al. 2000), have both been measured in a mangrove lagoon in Baja California Sur, Mexico, with implications for the carbon balance and productivity of these forests. More recently, researchers have begun the study of microbial diversity in mangrove sediments using genetic sequencing methods (Andreote et al. 2012), making it possible to map out the biogeochemical potential of mangrove soil communities.

Here, we examine variation in sediment carbon, nitrogen, and microbial community composition with depth and age of accumulated sediment. We hypothesized that microbial community composition varies with sediment composition, reflecting a specialized community associated with peat in these forests. Furthermore, we hypothesized that deeper, older peat contains lower densities of organic carbon and enrichment in $\delta^{13}C$ and $\delta^{15}N$ due to carbon and nitrogen remineralization by these microbes over time. We also hypothesized that, with increasing peat age, the microbial community shifts toward lower taxonomic richness and increased dominance by specialized taxa that can consume refractory organic matter under anoxia.

Methods

Field sites

The Bahia de la Paz on the eastern coast of Baja California Sur lies near the northern limit of mangroves on the Pacific coast of North America and experiences arid, subtropical conditions, with less than 200 mm/year of precipitation (Rebman and Roberts 2012). Despite relatively low productivity in this extreme mangrove environment (López-Medellín and Ezcurra 2012), these forests are still capable in some geomorphic settings of storing large carbon stocks in deep peat deposits thousands of years old (Ezcurra et al. 2016). We sampled these peat deposits to probe the role of belowground microbial communities in the slow decomposition of persistent buried organic matter. We chose four sites expected from previous sampling in the area to contain deep peat deposits (Figure 2-1). Only one core was taken at each site. In the large mangrove system at the southern tip of Isla San José, we cored at two sites: San José A, near a tidal creek in the center of the forest in a low intertidal site dominated by *Rhizophora mangle*, and San José B, in an area where the high intertidal steeply abuts a supratidal berm and where all three local mangrove species (*Avicennia germinans*, *Laguncularia racemosa*, and *R. mangle*) are present. The San Gabriel core was taken in a sandy coastal lagoon on Isla Espíritu Santo, in a location dominated by *L. racemosa* and *R. mangle*. The core at El Mérito was taken at the high intertidal edge of a small, geomorphically constrained mangrove bay, in a zone currently inhabited by dwarf *A. germinans* trees.

Figure 2-1: The four sites sampled in this study, in the Bay of La Paz area of the Gulf of California: El Mérito, San Gabriel, and San José (containing two sites).

Field Methods

We sampled mangrove sediments using a Russian peat corer (Aquatic Research Instruments), taking vertical, semi-cylindrical sections of sediment 5 cm in diameter and up to 50 cm in length. By adding extension rods, we then returned to the same hole to obtain successively deeper 50-cm sections of sediment. We repeated this process to rejection, when the core tip hit a hard substratum of rock or gravel, capturing the entire sediment column. Each core section was photographed and subsampled every 20 cm with depth and just above any apparent change in horizon, using a knife and a measuring tape to obtain samples of a uniform 5 cm in vertical extent. Each horizon was visually identified as falling into one of the following sediment types: calcite, clay, peat, or sand. Samples for carbon analysis were taken adjacent in the core to samples taken for microbial analysis. Microbial samples were removed from the core using tools sterilized with a 1:1 solution of bleach and ethanol.

Carbon and Nitrogen Analysis

We placed each sample for sediment analysis in a drying oven at 60 °C until dry (≥ 24 hours). In cases when it was not possible to dry the samples immediately, we kept them on ice until they could be dried. We weighed the dried samples and then homogenized them using an automatic grinder and mortar and pestle until they passed through a 500-µm sieve. To remove $CaCO_3$, the samples were HCl-fumigated following the method of Ramnarine et al. (2013) before analysis, so that the only carbon remaining was organic. From each sample, 6–9 mg were precisely weighed into a tin envelope and analyzed by CG-MS (Carlo Erba NA 1500 elemental analyzer), yielding percent carbon and nitrogen by mass as well as $\delta^{13}C$ and $\delta^{15}N$. Percent carbon (or nitrogen) multiplied by the measured bulk density of the sample gives the mass of carbon (or nitrogen) per unit volume.

Individual pieces of mangrove root tissue were picked out of the dried samples for radiocarbon analysis at the KCCAMS radiocarbon facility at UC Irvine following standard procedures. Radiocarbon estimates of the fraction of modern carbon in each sample are corrected for isotopic fractionation using $\delta^{13}C$ measurements at the Keck AMS facility and calibrated using the OxCal tools to estimate the predicted calendar age ranges (Ramsey 2008), given 95% confidence intervals (CI).

For the purpose of constructing carbon and nitrogen budgets for the deep peat deposit at El Mérito, we combined the data on the peat samples from that site in this study with those from two cores taken at the same site (within 10 meters of the coring location used in this study) in a sampling expedition in 2014 in which soil nitrogen and organic carbon were measured with depth (carbon data in Ezcurra et al. 2016). Using the linear relationship found between depth and radiocarbon age in the peat samples from El Mérito in this study (linear regression, slope = $4.27\pm0.50\times10^{-2}$ cm/year, intercept = 17.1 ± 19.2 cm, $t = 8.6$, $p < 0.001$), we ascertained the age of the peat samples from the nearby cores as a function of their depths. Combining these data provided an n of 19, rather than just the 10 samples from the core in this study. Assuming that the loss of nitrogen or carbon with age from peat would follow a simple exponential decay, we plotted the natural log of these sediment constituents against age and tested for a negative linear relationship.

Data analysis was conducted using the software R (R Core Team 2016).

DNA Extraction, Quantification, and Barcoded Amplicon Sequencing

The 16S ribosomal RNA gene (16S rRNA) was analyzed to classify the diversity and community composition of archaea and bacteria present in the sediment samples. To do so, sediment from each sampling point in each core underwent DNA extraction, and the 16S genes from these DNA extracts were amplified using PCR, purified, and then sequenced.

Samples for molecular analysis were stored at -20 °C and transferred with dry ice until they were brought to UC Riverside, where they were analyzed. Microbial DNA was extracted using a MO BIO PowerSoil DNA Isolation kit (MO BIO Laboratories Inc., Carlsbad, CA, U.S.A.) following the manufacturer's instructions and using a PowerLyzer® 24 bench top bead-based homogenizer sold by Mo Bio Laboratories, Inc. A NanoDrop 2000/2000c UV-Vis spectrophotometer (Thermo Fisher Scientific, Wilmington, DE, U.S.A.) was used to quantify the DNA in soil extracts. PCR for bacteria and archaea was performed using primers that target the 16S V3 and V4 regions (S-D-Bact-0341-b-S-17 and S-D-Bact-0785-a-A-21; Klindworth et al. 2013) of the 16S rRNA gene. Microbial genomic DNA (2.5 µL) was combined with forward and reverse primer (5 µL each), and 2x KAPA HiFi HotStart ReadyMix (KAPA Biosystems, Wilmington, MA, U.S.A.) (12.5 µL). A Bio-Rad MJ Research PTC 200 Thermocycler was used to amplify all samples at one time with the following program: 95 °C for 3 minutes; 25 cycles of 95 °C for 30 seconds, 55 °C for 30 seconds, and 72 °C for 5 minutes; and hold at 4 °C. AMPure XP beads (Beckman Coulter Genomics, Danvers, MA, U.S.A.) were used to purify the 16S amplicon of primers and primer dimers. Dual indices and Illumina sequencing adapters were attached to the amplicon using the Nextera XT Index Kit (Illumina, San Diego, CA, U.S.A.). Amplicon DNA (5 µL) was combined with 2x KAPA HiFi HotStart ReadyMix (25 µL), Index 1 and 2 primers (5 µL each), and PCR-grade water (10 µL). The same thermocycler was used with the following program: 95 °C for 3 minutes; 8 cycles of 95 °C for 30 seconds, 55 °C for 30 seconds, 72 °C for 30 seconds, and 72 °C for 5 min; and hold at 4 °C. A second bead cleanup was used to purify the final library before quantification. The samples were verified with gel electrophoresis after every step and then quantified in duplicate using the Quant-iT PicoGreen dsDNA assay kit (Life Technologies, Grand Island, NY, U.S.A.). All samples were pooled in equimolar concentrations and then sequenced with an Illumina MiSeq instrument.

Sequence Analysis

Quantitative Insights into Microbial Ecology (QIIME; Kuczynski et al. 2012) was used to quality filter the sequences and determine taxonomic identity against the Greengenes reference databases using 97% similarity. Using QIIME, we performed alpha diversity analyses and generated a list of microbial taxa (operational taxonomic units, or OTUs) that compose the core microbiome shared across all samples or across the subset of samples consisting of peat.

Analysis of prokaryotic community diversity was conducted in R using the “vegan” package to assess community composition (R Core Team 2016). Biodiversity of the microbial community was quantified using the form of Simpson’s diversity index equal to $1 - \Sigma^{R}_{i=1} p_i^2$, where R is the total number of OTUs sequenced in a sample and p_i is the proportional abundance of the i^{th} OTU. This index increases with the richness or evenness of the abundance distribution of OTUs.

To examine microbial community variation and to determine the relationships between community composition and depth and other sediment variables, we used a PERMANOVA analysis of microbial community data using Unifrac dissimilarity and the adonis function in the vegan package of R (Anderson et al. 2008; Oksanen et al. 2012). First, we investigated the relationships between microbial community composition and both site and a set of sediment variables. We included sediment depth, bulk density, C_{org} and N densities, $\delta^{13}C_{org}$, $\delta^{15}N$, and radiocarbon age in our PERMANOVA analyses to examine whether variation in these environmental variables was associated with the variation observed in microbial community composition across samples. Next, to remove the effect of variation across sediment types (calcite, clay, peat, and sand), we restricted the PERMANOVA only to test against permutations of data from within each of the four sediment types separately. Then, to remove the effect of intersite variation across cores, we restricted the PERMANOVA only to test against permutations of data from within each of the four sites separately.

We used non-metric multidimensional scaling (NMDS) with Unifrac to visualize microbial taxonomic variation with the measured sediment variables. Observing significant shifts in community composition with depth or age of peat would support the hypothesis that a particular microbial community is associated with deep, long-preserved carbon in these mangrove peat deposits.

Results

Core Description

The cores obtained from each site were qualitatively distinct from one another (Figure 2-2). San José A, the *R. mangle*-dominated, low intertidal fringe site possessed muddy peat from the surface to a depth of 94 cm and from 94 cm to the bottom of the core at 119 cm course sand interspersed with mud and peat fragments. In contrast, the sediment column at the high intertidal site at San José B was composed of peat from the surface to the bottom at 191 cm, with the section from 131 to 191 cm depth also containing some clay. The sandy San Gabriel core did not extend very deep, with muddy sand from the surface to 30 cm, peat from 30 to 54 cm, and muddy sand from 54 to the core bottom at 59 cm. At El Mérito, the top 70 cm of the core is a layer of gray-green clay interspersed with occasional *A. germinans* roots. Beneath this clay is a deep layer of peat from 70 to 278 cm. Beginning at 278 cm was a found a basement layer composed of a limestone gravel with interstitial mud and rare root fragments.

Organic Carbon

Peat samples had relatively high densities of organic carbon, with an average of $3.4 \pm 0.2 \times 10^{-2}$ g/cm^3 (mean ± standard error, throughout), compared to that of all other sediment types, $1.0 \pm 0.2 \times 10^{-2}$ g/cm^3. The subsequent analyses of carbon and nitrogen are specifically on the peat samples, unless otherwise specified. Peat organic carbon density does not vary consistently with depth across all sites (Figure 2-2), though inter-site differences in peat stratigraphy make complicate statistical comparison. For instance, peat extended from 30 to 54 cm depth at San Gabriel, completely non-overlapping with the 70–278 cm peat deposit at El Mérito. However, patterns with depth and among sites can still be described, especially in the two cores with vertically extensive peat deposits, San José B and El Mérito. In the case of organic carbon density, neither of these sites' peat deposits varied with depth, and there was no significant difference between the mean C_{org} densities of the two sites (Welch's t-test, $t = -1.6$, $p > 0.1$).

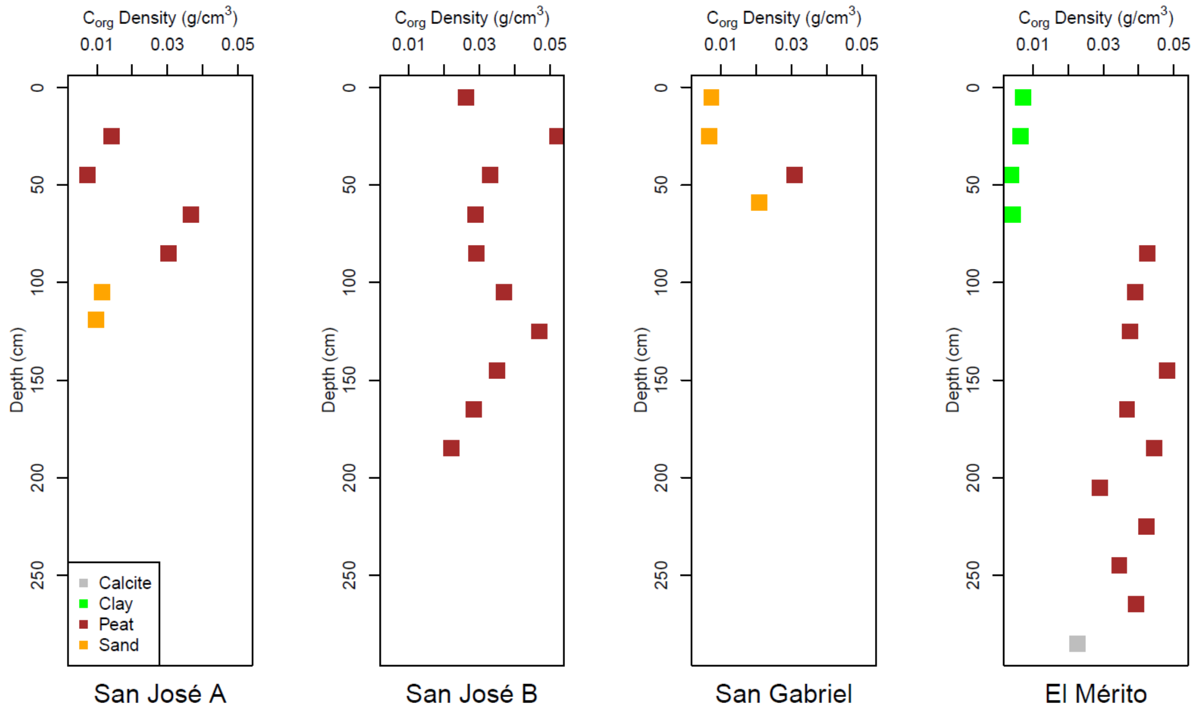

Figure 2-2: Depth profiles of organic carbon density (g/cm^3) in each core from the four study sites. Sediment type is marked with color, as shown in the legend at bottom-left.

Nitrogen

The nitrogen content of the peat averaged 8.6±0.7×10^{-4} g/cm^3, and that of other sediment types 5.1±0.5×10^{-4} g/cm^3. Peat nitrogen density appears to decrease with depth, though, as with organic carbon, this apparent overall trend is caused by inter-site differences (Figure 2-3). At San José B, nitrogen density seems to decrease with depth (least-squares fit: slope = -2.3×10^{-6} g/cm^4, intercept = 1.2×10^{-3} g/cm^3). The nitrogen density of El Mérito's peat samples does not present as clear a decrease with depth as San José B, and their mean value of 6.8±0.3×10^{-4} g/cm^3 is lower than that from San José B, 9.8±0.7×10^{-4} g/cm^3 (Welch's t-test, $t = 3.9$, $p < 0.002$). One of the most notable differences among the sites' profiles is seen in the ratio of organic carbon to nitrogen (Figure 2-4). C$_{org}$:N ratios are steady with depth but vary by site between San José B and El Mérito (Welch's t-test, $t = -7.7$, $p < 0.001$), with an average ratio of 35±2 at San José B and one of 58±2 at El Mérito.

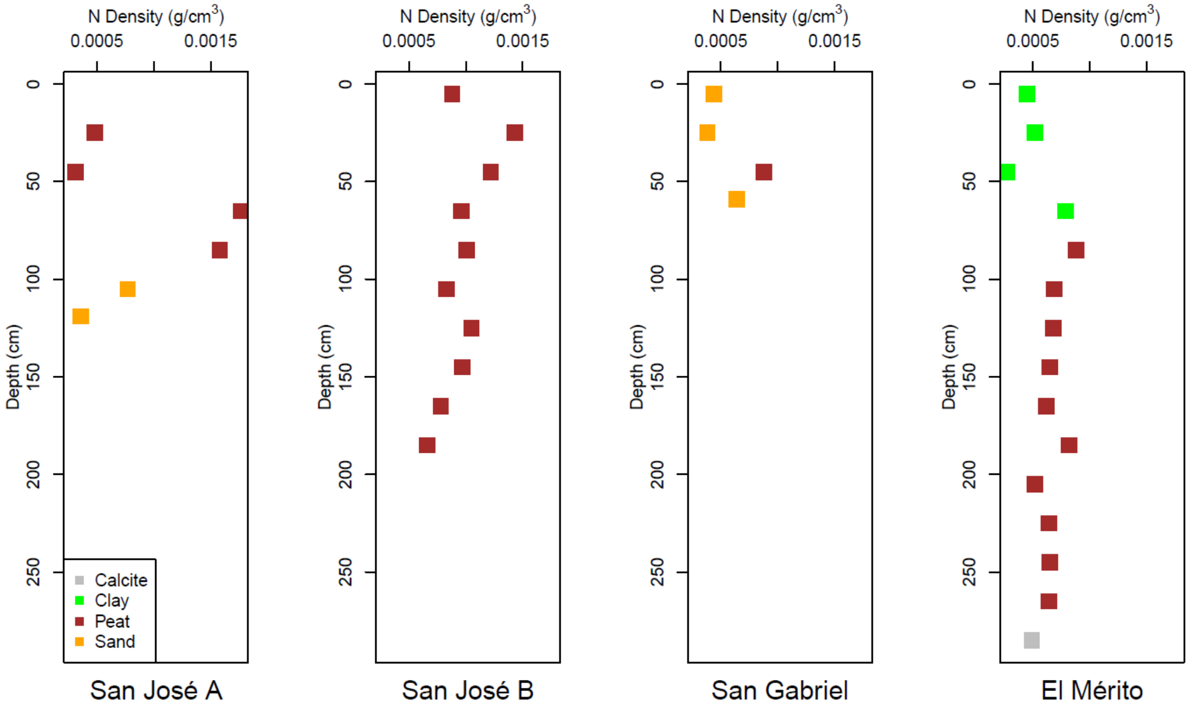

Figure 2-3: Depth profiles of nitrogen density (g/cm^3) in each core from the four study sites. Sediment type is marked with color, as shown in the legend at bottom-left.

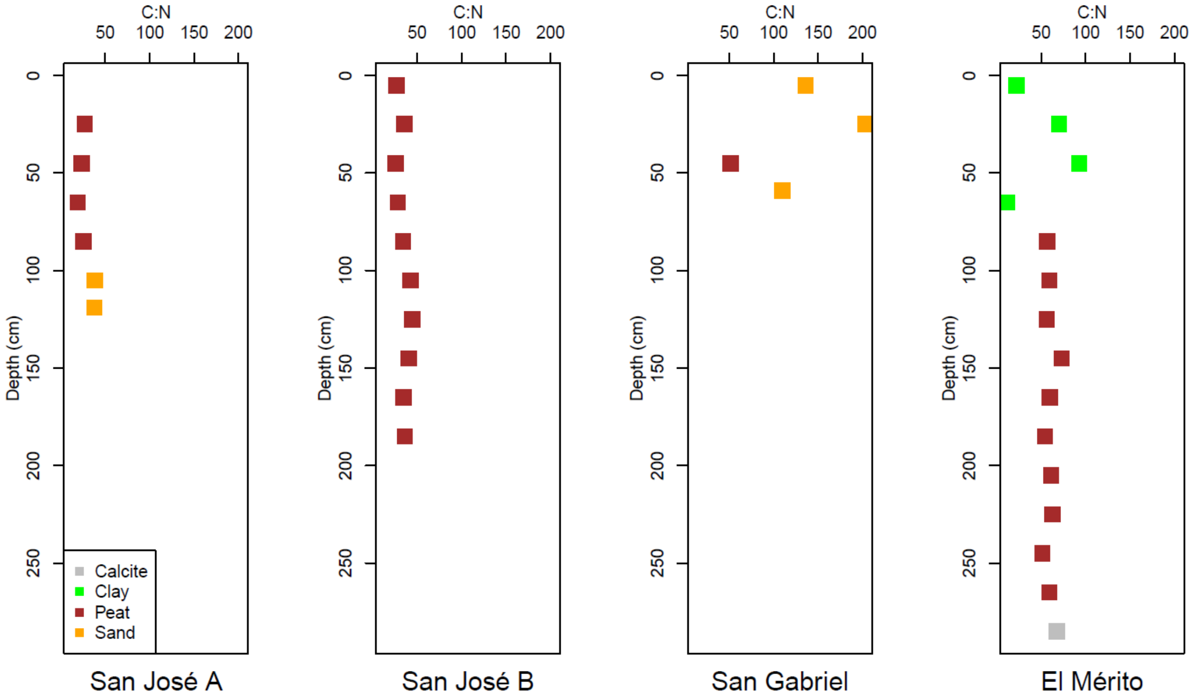

Figure 2-4: Depth profiles of the C_{org}:N ratio in each core from the four study sites. Sediment type is marked with color, as shown in the legend at bottom-left.

$\delta^{13}C$ and $\delta^{15}N$

The average $\delta^{13}C$ composition of peat deposits across all sites was -25.1±0.2 (Figure 2-5). Those from the two major peat deposits at San José B and El Mérito do not appear to vary consistently with depth. However, the sample from 40 to 45 cm depth in San José B had an anomalously high $\delta^{13}C$ value of -22.1 (> 1.5 × the interquartile range from the median value). San José B's peat samples had an average $\delta^{13}C$ ratio of -24.6±0.3, significantly greater than that of El Mérito, -25.6±0.1 (Welch's t-test, $t = 3.2$, $p < 0.008$), regardless of whether this outlier was included.

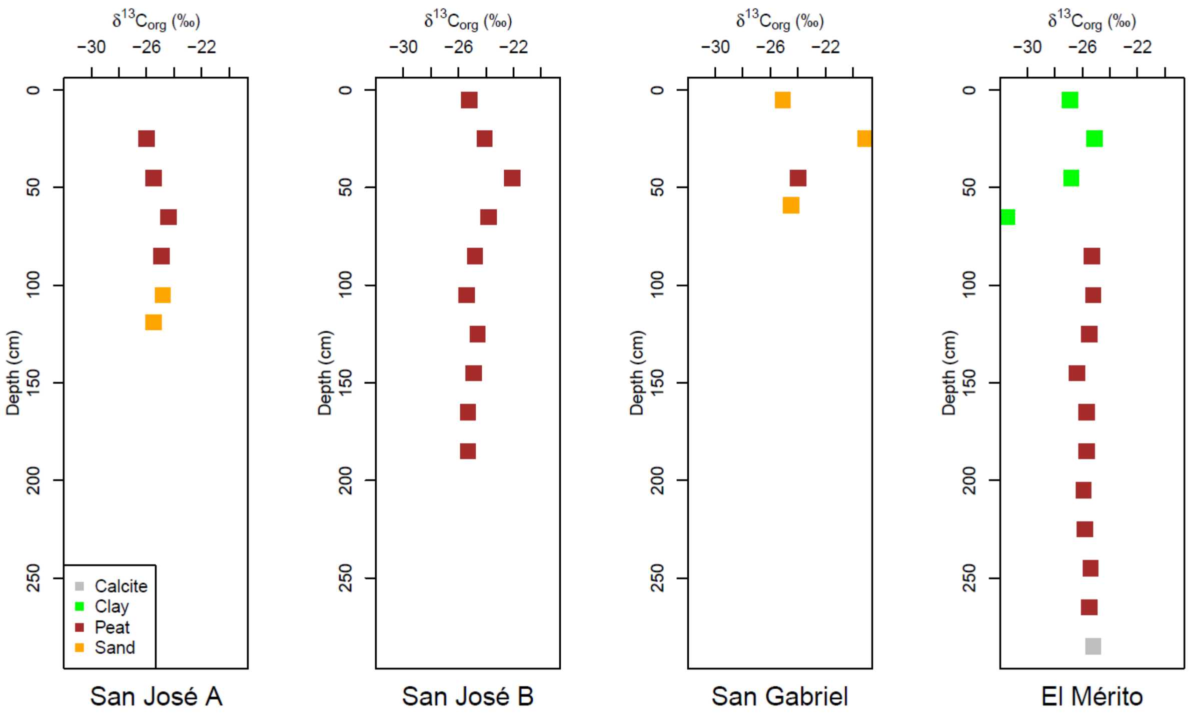

Figure 2-5: Depth profiles of δ^{13}C in each core from the four study sites. Sediment type is marked with color, as shown in the legend at bottom-left.

The δ^{15}N ratio of peat deposits averaged 5.0±0.2 across sites and appears to increase with depth when combining data from across all sites, though, again, there are inter-site differences (Figure 2-6).

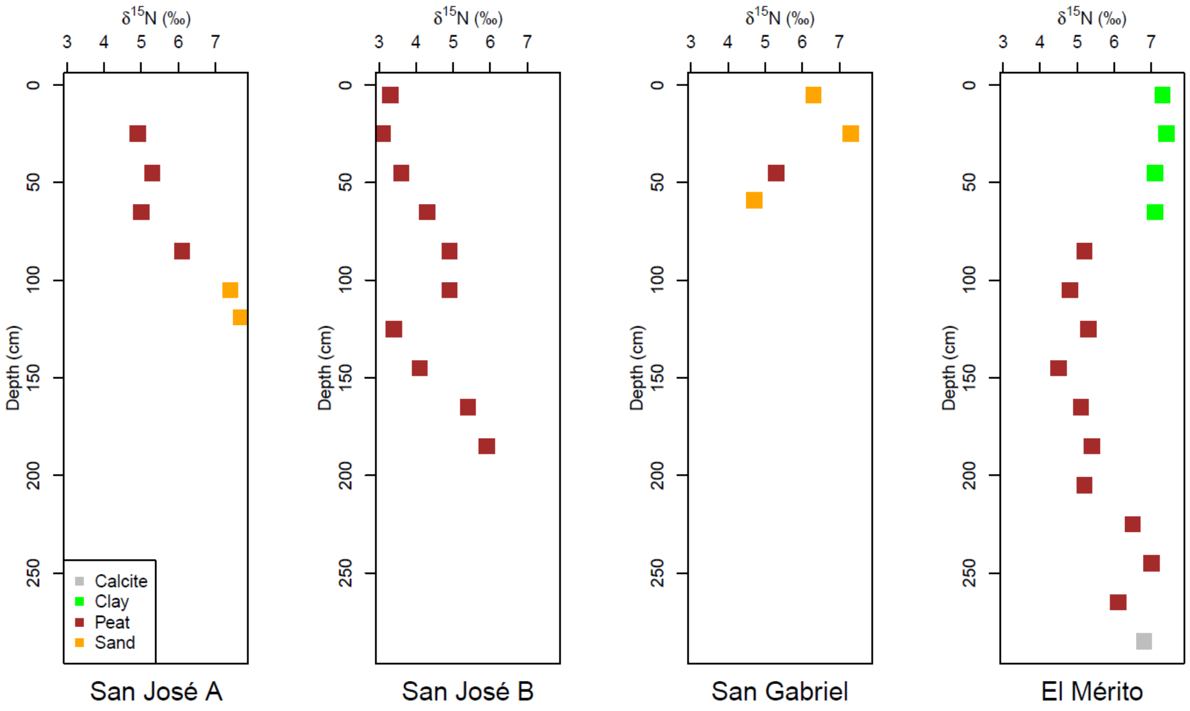

Figure 2-6: Depth profiles of δ^{15}N in each core from the four study sites. Sediment type is marked with color, as shown in the legend at bottom-left.

Radiocarbon Dating

As peat accumulates vertically over time, the age in years before present (BP) of the root tissues making up the peat deposits increases with depth. Inter-site differences are noteworthy (Figure 2-7, ranges represent 95% confidence intervals (CIs)). At San José A and B, the peat layer beginning from the sediment surface is of consistently modern age (from since 1950 B.C.E.) extending downward to at least 85 cm depth at San José A and to at least 45 cm at San José B. Beyond these depths, the peat increases in age with depth indicating successive accumulation over time. San Gabriel's shallow subsurface peat deposit from 30 to 54 cm depth is not modern, but dates to 754±18 years BP. At El Mérito, the surface clay layer that extends down to 70 cm is consistently modern down to the 60–65 cm sample, the age of which is

5,243±122 years BP, matching that of the calcite beneath the underlying peat deposit, 5,263±124 years BP.

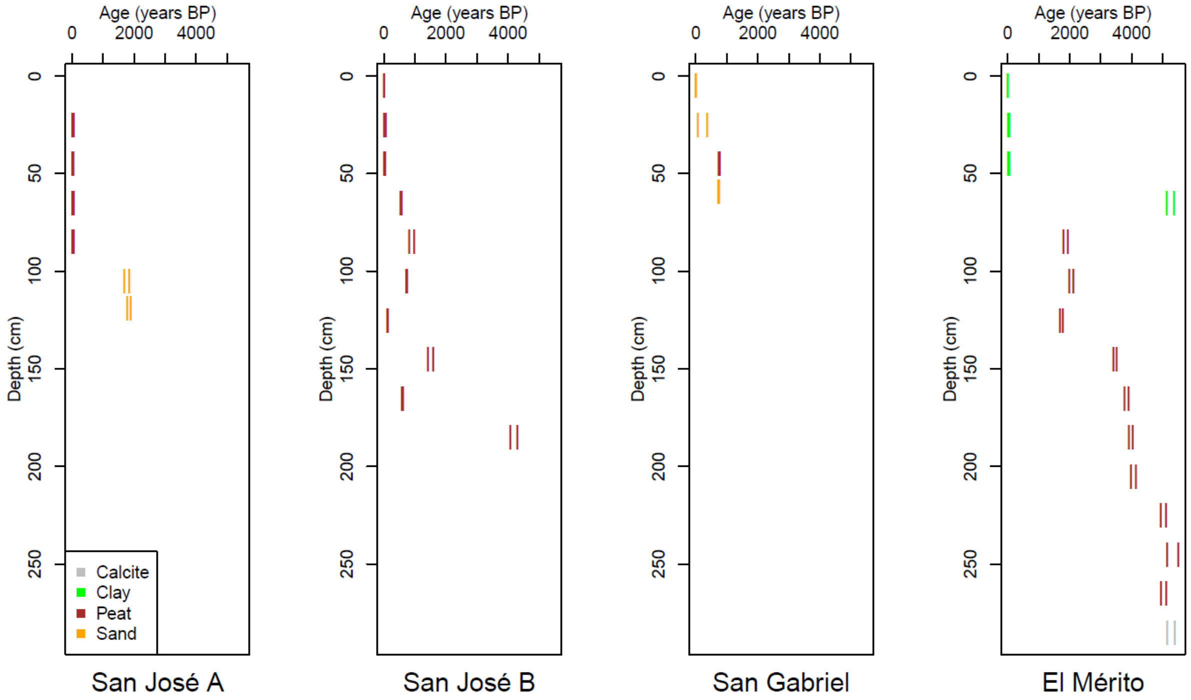

Figure 2-7: Depth profiles of calendar age in years BP of root tissue in each core from the four study sites. Sediment type is marked with color, as shown in the legend at bottom-left. Age ranges plotted represent 95% CIs.

Microbial Communities

Microbial community composition varied with depth (PERMANOVA, $p < 0.001$), site ($p < 0.001$, Figure 2-8), and sediment type (calcite, clay, peat, or sand; $p < 0.001$; Figure 2-9). Simpson's diversity index decreased with age in peat samples (linear regression, slope = -2.10±0.27×10^{-6} year^{-1}, intercept = 0.998, t = -7.7, R^2 = 0.72, $p < 0.001$, Figure 2-10). To reveal the roles of factors that may covary with sediment type, we removed the effect of sediment type from the PERMANOVA and found that depth ($p < 0.001$), radiocarbon age ($p < 0.001$), C_{org}:N ratio ($p < 0.001$), and $\delta^{15}N$ ($p = 0.006$) were significant factors predicting variation in microbial community composition. Similarly, when we removed the effect of inter-site variation from the PERMANOVA, we found that depth ($p < 0.001$), radiocarbon age ($p < 0.001$), C_{org}:N ratio ($p < 0.001$), and $\delta^{15}N$ ($p = 0.008$) were again significant factors, while in addition bulk density ($p < 0.001$) and organic carbon density ($p = 0.025$) were also significant factors, suggesting that these factors underlie the effect of site on the microbial community.

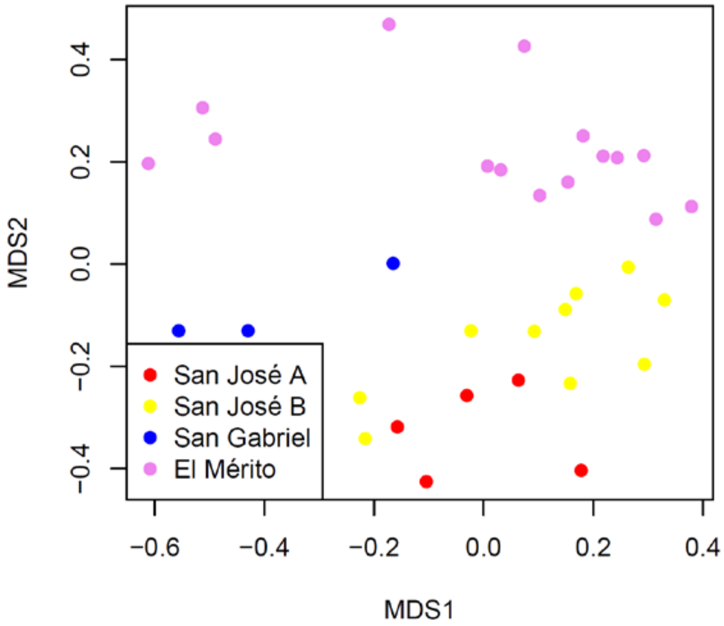

Figure 2-8: Nonmetric multidimensional scaling (NMDS) plot of 16S sequencing results from all samples, showing bacterial and archaeal community variation across sites. Point colors indicate sites, and more closely-clustered points indicate greater similarity among the samples' communities.

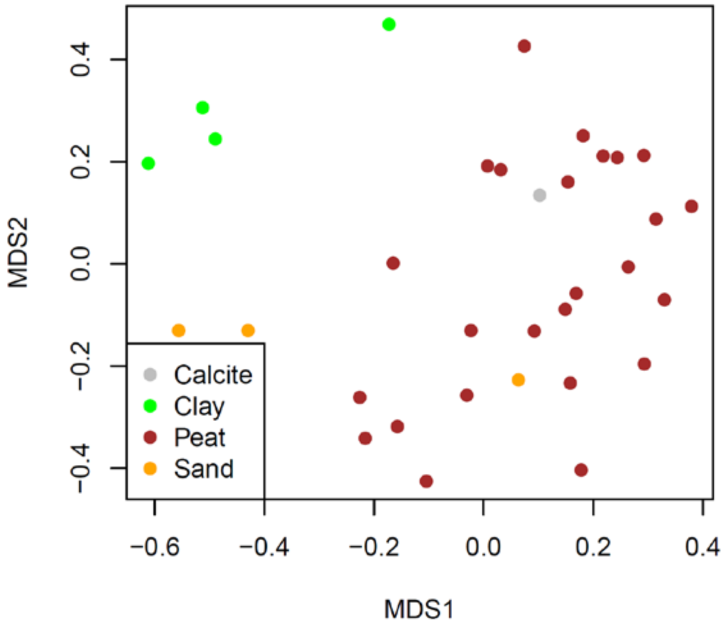

Figure 2-9: Nonmetric multidimensional scaling (NMDS) plot of 16S sequencing results from all samples, showing bacterial and archaeal community variation across sediment types. Point colors indicate sediment types, and more closely-clustered points indicate greater similarity among the samples’ communities.

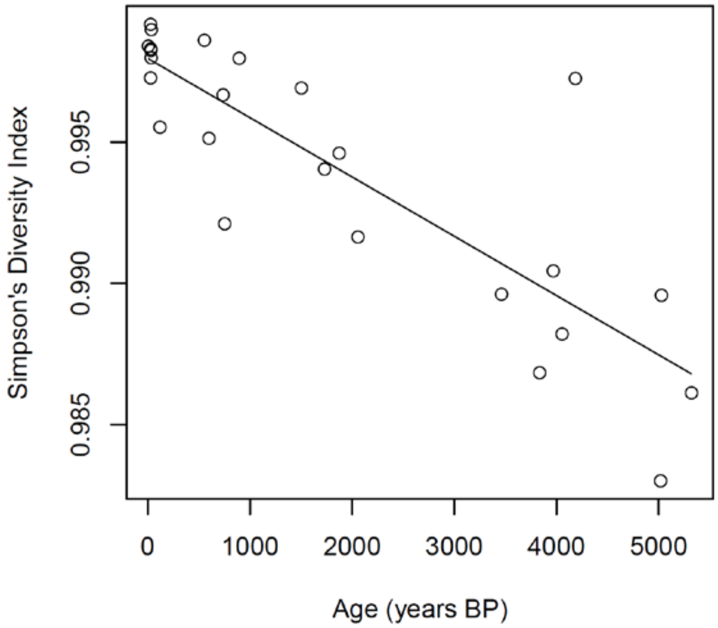

Figure 2-10: In peat samples, Simpson's diversity index—a measure of bacterial and archaeal OTU richness and evenness—is plotted against increasing radiocarbon age (linear regression, slope = $-2.10\pm0.27\times10^{-6}$ year^{-1}, intercept = 0.998, $t = -7.7$, $R^2 = 0.72$, $p < 0.001$).

Discussion

Peat Formation at Each Mangrove Site

Inter-site variability in core stratigraphy in this study reveals how environmental setting influences the formation and evolution of mangrove peat deposits. San José A, on a low-intertidal creek fringe dominated by *R. mangle*, seems to represent a young stage of mangrove deposit development, with about one meter of peat of modern age overlying an older sandy layer (Figure 2-7). The fact that the entire surface meter of peat was of undistinguishable 20th-century age highlights an important point for the interpretation of these data. Peat deposits formed from the roots of mangrove trees are not "sediment," i.e. their source material does not settle in defined layers above marginally older material. Rather, roots of live trees spread downward into the sediment matrix and subsequently die, becoming part of the peat deposit at whatever depth they had reached, imparting the age signature of the time that they grew upon the peat that they form. As a result, the temporal records of organic matter age in mangrove peat deposits can be vertically mixed over a depth interval equivalent to the depth range within which mangrove roots grow. In *R. mangle*, most fine roots are distributed within a few cm of the surface, preventing the passage of surface detritus into the belowground zone where peat is formed (Covington and Raymond 1989). Ezcurra et al. (2016) discuss the role that species differences in root growth patterns can play in the formation of peat and employs a model of peat formation that occurs belowground in the rooting zone. In this study, the roughly a half-meter of surface peat of apparently uniform modern age seen at both San José sites (followed at the older B site by an increase in peat age with depth), further supports the idea that there is a surface peat formation zone in which live roots grow among dead plant material. As the sediment surface accretes upward, as does the depth range of root growth, material from the bottom of this zone is added to the peat deposit, forming a temporal sequence now visible in the radiocarbon record. Much of the physical compaction of the peat likely occurs at this early stage of deposition, as the mixed, actively growing surface peat can be much less consolidated than the deeper part of the peat deposit. For instance, the two most shallow samples from the San José A core have much lower organic carbon density values than the deeper peat samples from that core due to their much lower bulk densities (mean bulk density of 0.055 and 0.553 g/cm^3 respectively; Figure 2-2).

San José B's peat record contains two samples of anomalously young age at 120–125 and 160–165 cm depths (Figure 2-7). These samples break the pattern of sequentially older peat with depth, suggesting that occasional live mangrove roots may penetrate deep enough to offset the apparent overall age of the peat at that depth. This observation makes clear that taking a single radiocarbon date to characterize the history of accretion in a mangrove peat core creates a risk of inaccurate interpretations. In this core, having the data on the older samples above and below the anomalously young ones allows a fuller picture of peat formation at this site that a single date at depth would not have afforded. Specifically, estimating carbon accumulation using just an anomalously young sample would yield a lower accumulation rate estimate than is possible using the full age profile.

At San Gabriel, the mangrove area sampled was near the sandy mouth of a lagoon. Though deeper peat cores had been obtained from nearby (Ezcurra et al. 2016), this physically high-energy and temporally dynamic setting likely contributed to the very limited peat deposit observed, only extending from 30 to 54 cm depth. Though rarely acknowledged in the literature, variation in mangrove peat deposits across a single, small estuary appears to be the norm rather than the exception, at least in the isolated mangrove environments of B.C.S. (Costa 2014). The considerable variation distinguishing the four sites in this study, separated by only a few tens of kilometers, underscores this point.

The deep peat deposit at El Mérito presents a relatively simple case of peat accumulation, without any anomalously young peat radiocarbon dates. In fact, the age of the deepest peat sample in his core, 5,029±85 years BP, is the oldest mangrove peat core measured in the region. This site possesses the interesting feature of a capping layer of clay above the peat, from which it is distinctly demarcated. The 5,243±122 years BP age of the bottom of this clay layer suggests that it has lain atop the growing peat deposit for millennia, further supporting the conception of these peats as forming fully belowground, rather than accreting from the surface (see Ezcurra et al. 2016). In this site, it appears that clay sediment has gradually been added from the surface, while belowground the mangrove peat deposit expanded upward. The 1875±72 year BP age of the top of the peat deposit suggests that at this location peat stopped accumulating almost two millennia ago. The dwarf *A. germinans* trees currently growing at this location apparently are contributing to the minor fraction of organic matter in the clay layer, as their roots reach about half a meter down into the clay, seen in the modern organic matter dates from the clay samples from the surface to 40-45 cm depth (Figure 2-7). But they apparently do not reach through the bottom of the clay into the established peat deposit, of much greater age.

Recognizing both the anomalies in peat age with depth seen in the San José B core and the overall variation in peat stratigraphy across sites provide rationale for the adoption of finer-resolution coring and analysis to study these dynamic estuarine environments. Unfortunately, coring fieldwork and radiocarbon analysis represent large investments of time and money relative to the amount of data produced, presenting a challenge for researchers to obtain broadly significant results with limited resources. The sedimentary variation underlying mangrove forests should not be ignored however. In this study, capturing the variation among sites made it possible to infer the different stages and extent of peat formation that has occurred at these sites. Uncovering this variability also made it difficult to draw general, statistical conclusions across sites, however. Future studies of mangrove peat should take into account the possibility of significant natural variation both with depth and across sites as observed here.

Carbon and Nitrogen Pool Characterization

Carbon densities do not appear to decrease with depth. Though it was hypothesized that deeper, older peat samples exposed for a longer time to microbial decomposition, would possess decreased carbon densities. The lack of a pattern of carbon density with age suggests that, if such a loss of carbon is occurring, it must be so slow as to be undetectable in the noise of random variation among samples. There is, however, a negative relationship between peat deposit nitrogen density and depth, especially at San José B, suggesting that peat nitrogen may be more sensitive to microbial processes than carbon, but within-site replication is required to confirm this trend.

The most salient difference among sites can be seen in the ratio of organic carbon to nitrogen in the two sites with peat deposits of significant depth, San José B and El Mérito (Figure 2-4), whose ratios are 35±2 and 58±2 respectively. The markedly higher C_{org}:N ratio in peat samples at El Mérito than at the other sites might seem to suggest a difference in the stoichiometry of the source. Mangrove detritus can vary in C:N ratio, with *R. mangle* detritus tending to be have higher C:N ratios than that of *A. germinans* (Twilley et al. 1996). The coring site at El Mérito is, at least today, dominated by *A. germinans* to a greater extent than any of the other sites in this study, where *R. mangle* is more prevalent. This potential difference in source C_{org}:N would cause the opposite difference from what is observed however, as El Mérito's peat has a higher, not lower, C_{org}:N ratio than that from San José B. In any case, even the C_{org}:N value of 35±2 found at San José B is already a relatively high value for mangrove detrital material. In addition, the δ^{13}C ratios of the peat from San José B and El Mérito are not very different, -24.6±0.3 and -25.6±0.1 respectively, thus not signaling a drastically different source material.

Instead of deriving from variation in source stoichiometry, the higher C_{org}:N ratio of the El Mérito peat may indicate preservation conditions distinctive to this site. The lack of a trend in this ratio with depth at any of the sites is evidence against a mechanism whereby nitrogen is slowly lost relative to organic carbon over time. Therefore, if this difference is due to a characteristic of the peat preservation environment, it must work via a mechanism that is active as soon as the peat is formed, such as during the near-surface zone of active root growth described above. The presence at El Mérito layer above the peat of clay which has likely been present there for the entirety of the peat deposit's history is the most obvious trait of the El Mérito core not shared by the others. Due to its finer particle size, clay impedes diffusion more effectively than other sediment types such as sand. The formation of a peat deposit rich in organic matter causes rapid consumption of dissolved oxygen in porewater. Though oxygen concentrations are low in most peat deposits (evidenced by the sulfidic smell of most of the peat samples obtained in this study), a peat deposit formed under a layer of clay impeding the diffusion of oxygen from the surface would experience lower oxygen concentrations. Lack of oxygen affects carbon and nitrogen biogeochemistry in several ways, both slowing microbial remineralization of organic carbon in general and favoring the loss of remineralized nitrogen from the system via anaerobic nitrogen metabolisms (Cornwell et al. 1999). The remineralization of detrital nitrogen and subsequent uptake by bacteria in mangrove sediments is an important mechanism whereby nutrients are internally recycled in these productive ecosystems (Alongi et al. 1992). In low-oxygen environments, however, nitrogen loss processes such as denitrification or anammox may happen quickly enough to break this cycle, removing some fraction of remineralized nitrogen from the system. It is possible that the clay layer above the peat-forming zone encouraged a greater rate of nitrogen loss from the peat than in the other sites. The remaining organic nitrogen contained in the El Mérito peat at a lower ratio to carbon than in other deposits may be comprised by a set of nitrogen-containing compounds that are more difficult to break down by peat microbes and thus less readily remineralized in the first place. These results suggest that the physical conditions prevalent near the surface may influence the material that passes into long-term storage beneath the zone of peat formation.

The $\delta^{13}C$ ratios of peat samples were consistent across sites and did not appear to vary with depth. The -25.1±0.2 average value is within the range of $\delta^{13}C$ values observed in C3 plants, a group that includes the local mangrove taxa (Andrews et al. 1984). The anomalously high $\delta^{13}C$ value of -22.1 at 40–45 cm depth at San José B may indicate that the organic matter in this section of the peat record contained a significant component of algal biomass, typically higher in $\delta^{13}C$. In general, there is no evidence of a shift toward higher $\delta^{13}C$ with depth caused by preferential remineralization of isotopically light carbon, contrary to our hypothesis.

As discussed above, the cycling of nitrogen between organic and mineral forms is central to the maintenance of productivity in mangrove ecosystems. It is likely for this reason that the $\delta^{15}N$ record seems to be more sensitive to processes of microbial turnover than that of $\delta^{13}C$. Mangrove biomass $\delta^{15}N$ has been shown to drop in response to nitrogen-limitation (McKee et al. 2002), introducing variation in source material that could be mistaken for a diagenetic signal. However, research conducted in mangroves of the Gulf of California on phosphate solubilization by microbes (Vazquez et al. 2000) and on whole-estuary carbon, nitrogen, and phosphorus budgets (Sánchez-Carrillo et al. 2009) suggests that the mangroves of this region are generally phosphorus-limited. In our study, $\delta^{15}N$ is much more variable than $\delta^{13}C$, and, combining the samples from the two cores with significantly deep peat deposits, $\delta^{15}N$ has a negative linear relationship with age (linear regression, slope = $4.6 \pm 0.7 \times 10^{-4}$ ‰/year, intercept = 3.9±0.2‰, $t = 6.2$, $R^2 = 0.68$, $p < 0.001$; Figure 2-11), supporting our hypothesis. The y-intercept of this fit, indicating the $\delta^{15}N$ composition of organic matter at the time of burial, is 3.9±0.2‰, similar to reported values for mangrove detritus and surface sediment (Reis et al. 2017). Over time in the sediment, the relative abundance of ^{15}N in the peat increases, likely due to microbial activity. Bacterial growth on mangrove detritus enriches the material in bacterial nitrogen, which tends to have higher δ^{15}N than that in plant-derived biomass (Alongi et al. 1992). In addition, nitrogen is isotopically fractionated when it undergoes microbe-mediated turnover processes including anammox and denitrification, resulting in the preferential release of ^{14}N as gas and the retention of ^{15}N in organic matter (Reis et al. 2017).

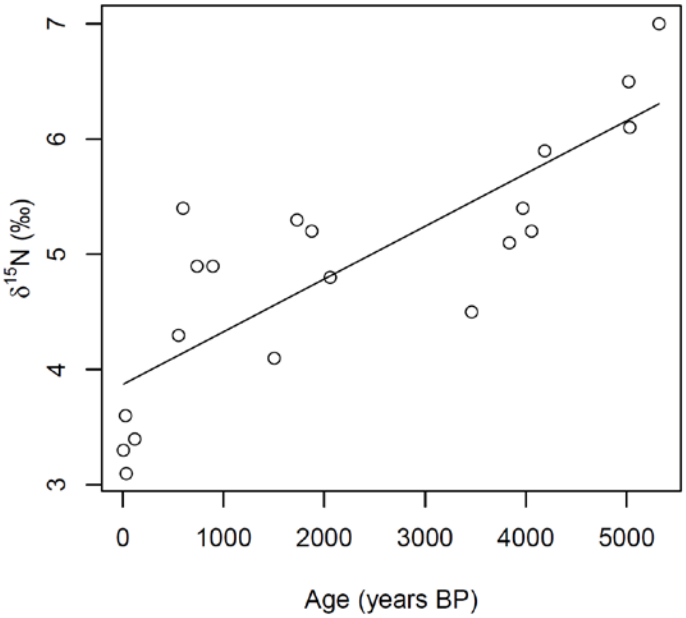

Figure 2-11: The δ^{15}N of peat samples from San José B and El Mérito *versus* the calendar age of those samples. A linear regression is also plotted (slope = 4.6±0.7×10^{-4} ‰/year, intercept = 3.9±0.2‰, $t = 6.2$, $R^2 = 0.68$, $p < 0.001$).

Microbial Community Variability

We uncovered measurable structure in the bacterial and archaeal community in the sediments of the mangrove forests under study. Community composition varied significantly with depth and by site and sediment type (Figures 2-8 and 2-9). This result supports the hypothesis that different sediment materials vary in their microbial communities in these mangroves. Given the particular cores taken in this study, some sediment types are exclusively or predominantly found in only some sites, requiring further analysis to disentangle the statistical effects of these factors. In a PERMANOVA in which the effect of sediment type was removed, C_{org}:N ratio emerged as a significant predictor of community composition. As discussed above, C_{org}:N is significantly different between the large peat deposits of San José B and El Mérito, so this factor captures important differences between sites. The effects of sediment stoichiometric factors such as C_{org}:N on the microbial community are likely the proximate drivers of the detected site effects. Sediment type however has the ability to influence microbial community directly via the physical and chemical conditions it establishes. In a PERMANOVA removing the site effect, bulk density and organic carbon density emerged as significant predictors. These two factors are among the most obvious differences between peat and other sediment types in this study, with peat showing lower bulk density and higher carbon content. Other effects of sediment type on microbial communities may be important, as, for instance, sandy sediment has greater relative pore volume than clay, effecting habitat characteristics and the diffusion of oxygen, organic matter, and nutrients.

Depth is also associated with variation in the microbial community, along with radiocarbon age and δ^{15}N. Age increases with depth in peat, and, as has been shown (Figure 2-11), δ^{15}N increases with peat age, so all three of these factors show collinear behavior in this dataset. Thus, these results do not reveal separate effects of depth, age, and δ^{15}N on the microbial community. Rather, the latter two variables reflect physical changes to the peat environment over time of which depth is a proxy. Specifically, we hypothesize that the microbial community shifts with peat age in response to the gradual change in the character of the peat-derived organic matter substrate. Peat δ^{15}N increases with age, reflecting ongoing microbial nitrogen processing in which nitrogen is repeatedly broken down and reassimilated into microbial biomass, with the remineralization and loss processes incurring an isotopic fractionation in favor of ^{14}N. The decrease in Simpson's diversity index with peat age reflects a decrease in taxonomic richness and evenness as peat ages. In still-forming, modern peat near the surface of peat deposits, as seen at San José, we hypothesize that there exists a broader array of microbial functional groups capable of consuming organic matter over a range of lability in a more spatially complex and bioturbated environment with potentially some patch availability of oxygen and inorganic nutrients. Deeper in the peat, only a community of specialists in this environment, including slow-growing sulfate-reducers and consumers of recalcitrant organic matter, are able to dominate, reducing microbial diversity. These hypotheses could be further tested by measurements of the activities of specific microbial metabolic processes across the peat-age-associated gradients revealed in this study.

Carbon and Nitrogen Pool Dynamics

Attempts to estimate budgets of carbon, nitrogen, or other constituents into or out of mangrove ecosystems have generally used proxies of mangrove productivity such as leaf litterfall rate and derived estimated of ecosystem burial efficiency (Bouillon et al. 2008, Duarte and Cebrián 1996), direct measurements of fluxes of gases or solutes across sediment, water, and air boundaries (Alongi et al. 2004), and measurements of soil composition and surface sediment accretion measured by sedimentary radioisotopes (Chmura et al. 2003). These approaches are limited for several reasons. The biology of mangrove root growth, exudation, and turnover is understood in very little detail (Bouillon et al. 2008), but these processes are of central importance given the fact that mangrove peat deposits are mainly composed of dead fine roots (McKee et al. 2007). In addition, gas and tidal flux measurements are necessarily snapshots of growth and decomposition processes that play out over centuries and likely miss the spatio-temporal patchiness of mangrove gas fluxes due, for instance, to the hotspots of respiration associated with mangrove aerial roots and crab burrows (Kristensen et al. 2008). Finally, studies of burial based on the well-constrained estimates of the decay of heavy radioisotope activity downcore from the surface are only capable of estimating material that enters the sediment via sedimentation, not the significant subsurface accretion due to the ingrowth of mangrove roots, capable of adding biomass to the soil and height to the sediment column (McKee et al. 2007). The fact that the top 45 to 85 cm of peat in the San José cores from this study are well mixed with regard to organic carbon age implies that measuring carbon burial and sediment accretion from the surface down would lead to an underestimate of carbon accumulation rate by decreasing the slope of the age-depth relationship. This relatively uncompacted zone of root growth and bioturbation is in a state of active exchange with the atmosphere, and thus its organic carbon is of uniformly modern age (Figure 2-7). Long-term burial of carbon begins at the bottom margin of this zone, deeper than the depths to which many sedimentation studies core. In contrast, measuring the composition and radiocarbon profile of the sediment to its maximum depth allows for the estimation of fluxes of material into and out of the peat deposit. Given that long-term storage on the centuries- to millennia-scale is in fact what sets apart mangroves and other blue carbon ecosystems (Mitra et al. 2005), creating budgets of carbon, nitrogen, et c. for their deep peat pool is of great relevance to the study of their role as carbon sinks.

In the peat deposit at El Mérito, there is a statistically significant negative relationship between ln(N density) and age (linear regression, slope = $-7.13 \pm 3.04 \times 10^{-5}$, intercept = -6.95 ± 0.11, $t = -2.3$, $R^2 = 0.24$, $p = 0.031$; Figure 2-12). Exponentiating the intercept gives the inferred density of nitrogen in sediment at the time of burial, 9.6×10^{-4} gN/cm^3 (95% CI: $8.6 \times 10^{-}$

^{4}–1.07×10^{-3} gN/cm^{3}). This value, multiplied by the linear accretion rate of peat measured at this site of 4.74×10^{-2} cm/year, gives the rate of nitrogen burial per year over the course of this deposit's formation, 4.1×10^{-5} gN/(cm^{2}×year), equal to 4.1×10^{-3} MgN/(ha×year) (95% CI: 3.7×10^{-3}–4.6×10^{-3} MgN/(ha×year)). The exponential decay equation $N = N_0(1 - e^{d/t})$ gives the amount of nitrogen that is lost from the peat deposit per year, where N_0 is the depth-integrated nitrogen pool of the deposit, d is the exponential decay rate, and t equals 1 year. Integrating nitrogen density with depth across the peat samples at El Mérito from this study gives a value of N_0 of 0.0312 gN/cm^{2}, and the slope of the regression of ln(N Density) against age gives a value of d of -7.13±3.04×10^{-5}/year. Using these values in the exponential decay equation gives an annual loss of nitrogen from the deposit of 2.2×10^{-6} gN/(cm^{2}×year), equal to 2.2×10^{-4} MgN/(ha×year) (95% CI: 1.3×10^{-4}–3.2×10^{-4} MgN/(ha×year)). This loss of nitrogen and increase in δ^{15}N with age (Figure 2-11) suggests that microbial cycling of nitrogen derived from organic matter in these peat deposits results in the gradual release via gas evolution or leaching of remineralized nitrogen or DON, with an isotopic preference for the retention of ^{15}N.

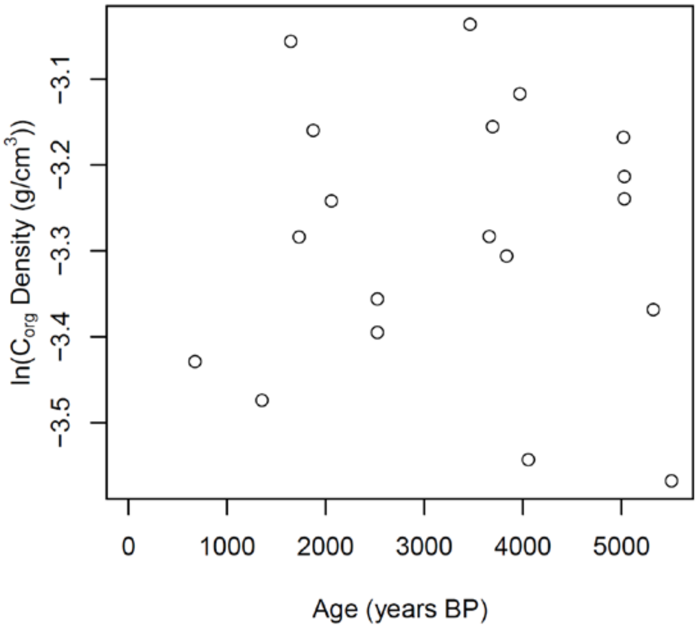

Figure 2-12: In peat samples from El Mérito, the natural log of sediment nitrogen density (g/cm^3) is plotted against calendar age of peat (linear regression, $R^2 = 0.24$, slope = $-7.13\pm3.04\times10^{-5}$, intercept = -6.95 ± 0.11, $t = -2.3$, $R^2 = 0.24$, $p = 0.031$). The dotted line indicates the extrapolation to the intercept, when age = 0 years BP, to infer the density of N of sediment at the time of burial.

Unlike for nitrogen, ln(C_{org} density) shows no significant linear relationship with age (linear regression, $t = -0.12$, $p > 0.1$; Figure 2-13). Though we observed a significant exponential decay in peat nitrogen but not in carbon with age, this decoupling is extremely slow, as can be seen from the apparent stability of the C_{org}:N ratio of the peat deposits at San José B and El Mérito with depth (Figure 2-4). The lack of a detectable change in peat composition inferred from these stable C_{org}:N ratios even after thousands of years reinforces the conception of mangrove peats as highly effective carbon sinks, where the decomposition rate is slowed virtually to zero. With the loss of organic carbon from this system apparently negligible, we can only estimate the annual gain of carbon via burial. This burial rate is estimated by the product of the mean carbon density of the peat deposit, $3.93\pm0.17\times10^{-2}$ gC_{org}/cm^3, and the accretion rate,

4.27×10^{-2} cm/year, equal to $1.7\pm0.1\times10^{-3}$ $gC_{org}/(cm^2\times year)$, or $1.7\pm0.1\times10^{-1}$ $MgC_{org}/(ha\times year)$. Because this deposit is no longer accumulating peat (see Figure 2-7, where the youngest peat's age is 1,875±72 years BP), this rate refers to the annual burial during the time period when peat was forming at the location cored in this study, from 5,029±85 to 1,875±72 years BP.

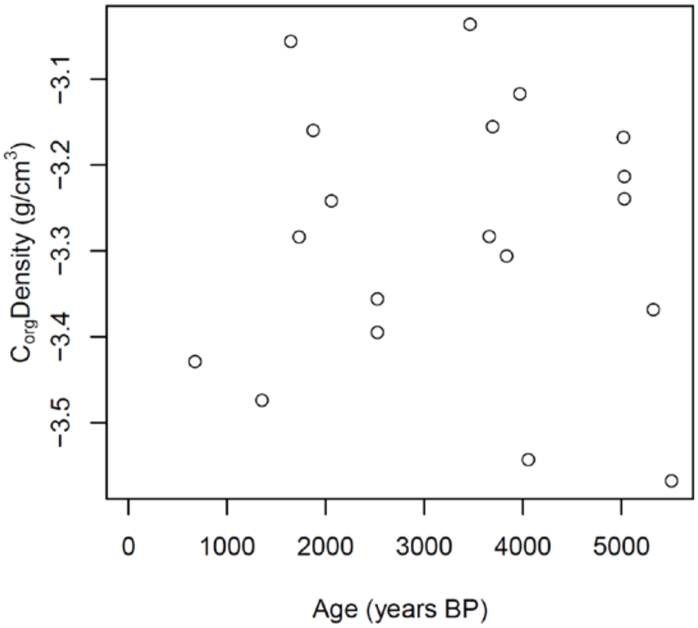

Figure 2-13: In peat samples from El Mérito, the natural log of sediment carbon density (g/cm^3) is plotted against peat age.

As with other methods of estimating fluxes of carbon or nitrogen into or out of mangrove systems, this approach has limitations, the most important of which is that it assumes constant carbon and nitrogen composition and static rates of peat accumulation and decomposition over time. There is no evidence that the species or general climatic conditions of mangroves in this region have deviated significantly over the late Holocene, so large changes in the composition of peat material buried are not expected. The assumption of static accumulation is supported by steady rates of SLR reported in Toscano and Macintyre (2003) and Ezcurra et al. (2016) during recent millennia, in addition to the rate estimated in this study. There are not measurements of peat decomposition rates over comparably long timescales, so it is difficult to hypothesize what the temporal variability of decomposition rates in steadily accumulating peat deposits should be. Given the apparent recalcitrance of the organic matter, slow course of change in the nitrogen pool and microbial community with age, and apparent isolation from surface processes of this peat, it is reasonable to assume that decomposition rates do not fluctuate considerably in this kind of steadily-accumulating deposit.

We note that the rate of accretion and thus inferred SLR measured in this study at El Mérito of 0.43±0.05 mm/year does not agree with that of 0.70±0.07 mm/year estimated in Ezcurra et al. (2016), even though they were estimated from mangrove peat deposits in the same region. Further work to measure accretion rates in other coastal environments on the Baja Peninsula would provide insight on whether sedimentation has generally tracked relative SLR in a consistent manner in this tectonically active region.

Implications and Future Work

Though these results provide insight on the microbial diversity and carbon and nitrogen cycling of mangrove peats, in-depth understanding of the biogeochemical processes underlying mangrove peat preservation will be aided by further research. One barely-explored frontier in the microbial ecology of mangrove sediments is the role of fungi (Fell et al. 1984). Though some studies of the distribution of fungi on the surfaces of mangroves, litter, and sediment have been done (Ulken 1983, Kohlmeyer et al. 1987), and the ability of fungi to contribute to leaf litter enrichment (Fell et al. 1975) and phosphorus solubilization (Vazquez et al. 2000) has been documented, there is still barely any understanding of their role in mangrove carbon cycling

(Alongi and Sasekumar 1992). Even less is known about the distributions and activities of mangrove fungi belowground, where the growth of fungi has been thought to face limitations due to high tannin concentrations (Walsh 1974) and low oxygen availability (Holguin et al. 2001). The belowground environment is, however, precisely where their role in peat carbon cycling could be especially important given that these taxa normally take on the role of the degradation of lignin, a component of mangrove sediment organic matter that confers much of its metabolic recalcitrance (Dittmar and Lara 2001). Bringing to bear modern molecular methods on the study of the role, or lack thereof, of fungi in belowground mangrove carbon cycling holds promise for illuminating this long-neglected component of mangrove ecosystems.

We have shown that sediment microbial communities vary with depth and sediment characteristics in peat deposits, with diversity trends reflecting a community response to organic matter age. These descriptions are only the beginning, however. Mangrove ecosystem science has for decades gathered organismal distribution pattern data but will only progress by engaging in more process-based studies (Alongi and Sasekumar 1992). The increasing availability of molecular tools to examine patterns of microbial diversity in mangroves and other ecosystems brings with it opportunities for direct or indirect measurements of rates of bacterial heterotrophic production, nitrogen and carbon remineralization, and other processes. Though performing experimental manipulations of these microbial processes in mangrove ecosystems and detecting their effects poses challenges, results from such studies could provide the mechanistic understanding necessary to use this information for the protection and management of mangrove ecosystems.

Microbe-plant-soil interactions have been recognized for their influence on fluxes of carbon and nutrients in mangroves (Alongi 1988, Alongi et al. 1993), and the goal of elucidating these mechanisms takes on clear practical value in light of the urgent need to maintain or even to increase natural carbon sinks under climate change. Even beyond carbon sequestration, capturing the functional role of microbes in mangrove ecosystems has implications for other important functions of these forests. The outwelling of mangrove leaf litter has long been considered a major source of carbon for coastal food webs (Odum and Heald 1975), while recent research suggests that mangrove POC and DOC may be much more important in that role (Young et al. 2005, Kristensen et al. 2008). Microbial metabolism strongly effects the nutritional quality of litter exported (Odum and Heald 1975, Holguin at el. 2001), in addition to providing the major conduit of mangrove carbon into the particulate and dissolved pools. In addition to their long-recognized food web roles, mangrove sediment microbes have now been shown to accomplish the breakdown of microplastics in the environment (Auta et al. 2018), a topic of growing concern in marine ecosystems.

A complex interplay of physical environmental dynamics, microbial community development, and plant biomass growth, death, and decay set the conditions for burial of carbon in mangrove peat deposits. This work shed light on several of the phenomena at play in this process. The radiocarbon profiles at San José demonstrated that actively-forming mangrove peat deposits are well-mixed with regard to carbon accumulation (the quantity of interest for blue carbon) in the top 45 to 85 cm due to active root growth. It is only below this point that “dead” peat accumulates successively beneath the root zone, left behind as the live roots shift upward with vertical peat accumulation. The role of subsurface root growth in influencing elevational changes in mangroves is further demonstrated at El Mérito, where radiocarbon dating of the peat and overlying clay suggest that belowground root and peat layers had expanded vertically independent of surface fine sediment accretion for millennia until mangrove peat formation ceased. These observations demonstrate that realistic carbon accumulation rates can be calculated based on carbon and age measurements specifically over the range of depths over which peat age increases with depth, not simply starting from the surface. Alternative approaches to estimating the budget of carbon, nitrogen, or other constituents of wetland sediments can be constructed from deep, high-resolution sampling as done in this study. In this case we detected no loss of carbon from the peat over more than 3,000 years but did estimate a slow loss of nitrogen, 2.2×10^{-4} MgN/(ha×year) (95% CI: 1.3×10^{-4} – 3.2×10^{-4} MgN/(ha×year)). Thus, integrative analysis of peat biogeochemistry and microbial ecology with depth in mangrove sediments offers valuable opportunities for understanding the ecology and ecosystem services of these ecosystems.

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CHAPTER 3

Storage of blue carbon in isolated mangrove forests of the Galapagos' rocky coast

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ORIGINAL PAPER

Storage of blue carbon in isolated mangrove forests of the Galapagos' rocky coast

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Abstract Threatened globally, mangrove forests provide many ecosystem services, including blue carbon storage. These forests, and the services that they provide, are distributed across spatio-temporally variable coastal landscapes and a range of environmental conditions, though this variability is underappreciated in the blue carbon literature. The Galapagos, Ecuador, presents the opportunity to explore spatial variability in carbon storage. This volcanically active archipelago features rocky shores and arid conditions at low elevations (< 500 mm/year), with patchy forests under far from optimal conditions. At 29 mangrove sites, we cored from the sediment surface down to basement rock, and samples were dried, weighed, and analyzed for their carbon content by GC–MS. Belowground carbon stocks range from < 50 Mg/ha to > 500 Mg/ha, i.e. from practically no carbon to values typical of lush, productive mangroves. This variability is driven principally by variation in sediment depth, with high inter-site variance associated with underlying lava substrate. The first to measure mangrove blue carbon in the Galapagos, this study reveals the spatial heterogeneity of the islands' patchy mangroves. These results underscore the importance of local ecosystem constraints and natural variability in ecosystem service valuation for conservation prioritization.

Keywords Blue carbon · Carbon storage · Ecosystem service · Galapagos · Mangrove · Spatial variability

Introduction

Mangroves forests are highly productive (Bouillon et al. 2008), at the base of rich detritus-based food webs that support diverse marine and terrestrial fauna (Odum and Heald 1975). These systems provide numerous valuable services to local people, from shoreline stabilization and run-off purification to the provisioning of fisheries stocks (Ewel et al. 1998; Aburto-Oropeza et al. 2008), and one mangrove ecosystem service of global impact is their role as carbon sinks (Chmura et al. 2003). Mangroves store more carbon than most other forest types, mostly in

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accumulated layers of peat (Donato et al. 2011). Mangroves and other coastal vegetated ecosystems, including salt marshes and seagrass beds, are now known to play an important role as carbon sinks by fixing and trapping in their sediments disproportionately large amounts of long-lived organic matter, referred to as "blue carbon" (Nelleman et al. 2009). Mangroves and other blue carbon ecosystems have garnered considerable recent interest for their potential contribution to the mitigation of anthropogenic CO_2 pollution (Thomas 2014).

Mangroves are generally characterized as inhabiting sedimentary environments in tropical coastal areas (Hogarth 1999). Much study of these systems, including prominent blue carbon research, has been done on humid, tropical coasts, river deltas, and protected bays with high rates of sedimentation, freshwater fluxes, or both (Thom 1967; Bouillon et al. 2008; Donato et al. 2011). However, mangroves are not one environment, but rather this biome encompasses a range of physical settings, including typical tropical mudflats as well as arid, subtropical coastal lagoons and equatorial, volcanic islands (Duke 1992). Only a few carbon storage studies have yet been conducted in mangroves from across a broader set of environmental conditions. McKee et al. (2007) studied mangroves on small islands off Belize, not connected to any riverine sources of freshwater or sediment, which have accreted peat deposits vertically for millennia, keeping pace with Holocene sea level rise. Dwarf, subtropical desert mangroves in Baja California Sur, Mexico, also possess deep deposits of stored carbon in some geomorphological settings (Ezcurra et al. 2016). Results such as these cast doubt on the assumption that conditions favorable to high mangrove productivity are necessary for large belowground carbon stocks and underscore the need for extensive, deep core sampling and analysis to quantify this sizeable, variable, and invisible pool of organic matter.

The Galapagos Archipelago, located 1000 km west of mainland Ecuador, imposes harsh and variable physical conditions and extreme isolation on its biota. Arid conditions prevail near sea level (mean annual rainfall < 500 mm), with freshwater only reaching the coast through spatially heterogeneous groundwater sources (d'Ozouville et al. 2008; Trueman and d'Ozouville 2010). A lack of freshwater in combination with coastlines often consisting of bare, volcanic rock and exposure to oceanic waves create challenging conditions not normally associated with mangrove establishment and survival (INGALA et al. 1989). As a result, the presence of mangroves here is barely mentioned or completely omitted in fundamental texts on mangrove flora or recent overviews of mangrove ecosystems (Chapman 1976; Hogarth 1999; Rivera-Monroy et al. 2017). However, mangroves are found distributed across the Galapagos Archipelago, usually in isolated patches and often in dwarf growth form, on all the large islands in the archipelago (Moity et al. 2019), with ecological significance for wildlife (Dvorak et al. 2004). The islands' mangrove communities are comprised by the species *Avicennia germinans*, *Conocarpus erectus*, *Laguncularia racemosa*, and *Rhizophora mangle*, with the former two species typically found at the landward edge of the intertidal and the latter two, especially *R. mangle*, dominating the coastal fringe (Wiggins and Porter 1971).

In April 2015, we conducted the first study of mangrove blue carbon in the Galapagos, quantifying belowground carbon stocks by measuring the sediment depth and organic carbon concentration. Most of the carbon in mangrove ecosystems is stored belowground as peat (Donato et al. 2011), which, unlike shorter-lived aboveground biomass, often remains undecomposed for millennia (McKee et al. 2007; Ezcurra et al. 2016). For this reason, we chose only to measure belowground carbon, representing long-term storage of relevance to the time-scale of climate change. We investigated the spatial variability of belowground carbon and explored some of the factors that may predict this variability across the archipelago. The Galapagos are exposed to oceanic swell with prevailing directionality, frequently from the south or southwest. Because greater exposure to incident wave energy should discourage sedimentation and mangrove growth and biomass accumulation, we hypothesized that mangrove carbon stocks vary depending on the direction in which each site is exposed to open water. Also, where the Galapagos' variable and evolving coast consists of young lava rock *versus* more developed soil, the flow of groundwater to the ocean may be inhibited (Trueman and d'Ozouville 2010). Thus, we hypothesized that coastal geology would also predict inter-site variation in belowground carbon stocks. Though this kind of variability is often ignored in blue carbon studies due to inherent data limitation, this first exploration of the Galapagos' mangrove carbon addresses this spatial variation, an approach capable of generating realistic ecosystem service estimates and identifying conservation priorities.

Methods

We visited 29 sites across the six largest islands in the Galapagos, covering almost all the major mangrove areas in the archipelago. At each of our 29 sites, at least one sediment core was taken, while in some cases multiple cores were obtained to capture fine-scale variability. To prevent impact on terrestrial environments, we accessed all the mangrove sites by small boat, limiting our coring to the coastal fringe, dominated by *R. mangle* and, to a lesser extent, *L. racemosa*. Given that the steep, rocky coast of the Galapagos mostly precludes the formation of large basins extending inland, this sampling strategy is representative of the archipelago's mangroves in general.

We sampled mangrove sediments using a Russian peat corer (Aquatic Research Instruments), taking vertical, semi-cylindrical sections of sediment 5 cm in diameter and up to 50 cm in length. By adding extension rods, we then returned to the same hole to obtain successively deeper 50-cm sections of sediment. We repeated this process to rejection, when the core tip hit a hard substratum of rock or gravel. Each core section was photographed and subsampled every 25 cm with depth and just above any apparent change in horizon, using a knife and a measuring tape to obtain samples of a uniform 2 cm in vertical extent. We placed each sample in a drying oven at 60 °C until dry (at least 24 h). In cases where field circumstances prevented quick access to a drying oven, we kept the samples on ice until they could be dried. We weighed the dried samples and then homogenized them using an automatic grinder and mortar and pestle until they passed through a 500-µm sieve. From each sample, 6–9 mg were precisely weighed into a tin envelope and analyzed by CG–MS (Carlo Erba NA 1500 elemental analyzer), yielding percent carbon by mass and $\delta^{13}C$. Inorganic carbon must be excluded from estimates of blue carbon, but calcium carbonate ($CaCO_3$) sand is mostly absent from the sediments of the mangroves on these rocky, volcanic islands. There were however four sites with some $CaCO_3$ sand in the sediment (Puerto Grande I, Roca Fuerte, Poza Sardina, and Garrapatero). For the 9 samples from these sites in which sand was present, the samples were HCl-fumigated following the method of Ramnarine et al. (2011) to remove $CaCO_3$ before analysis, so that the only carbon remaining was organic. An inspection of $\delta^{13}C$ values confirms the lack of $CaCO_3$ in the samples, as all $\delta^{13}C$ values were $< -20‰$, typical of the organic matter comprising mangrove peat. Percent carbon multiplied by the measured bulk density of the sample gives the mass of carbon per unit volume, which, integrated over the depth interval of each sediment horizon and summed for each horizon throughout the entire sediment depth, gives the total belowground carbon per unit area, in tons of C per hectare (Mg/ha).

We measured the cardinal direction in which the mangrove sites are exposed to open water to approximate their exposure to prevailing wave energy and tested differences in carbon storage across these levels using the Kruskal–Wallis test. We identified the type of substrate along the coast at each mangrove site as either soil or bare lava rock using mapping and data in Trueman and d'Ozouville (2010) and INGALA et al. (1989). We tested for differences in median carbon stock between these substrate types with the Wilcoxon rank sum test and the variance in these stock estimates with an F test.

Results

Carbon storage values vary greatly across the Galapagos archipelago (Fig. 1, Supplement). Measured values of belowground carbon per hectare from each site ranged from 16 to 679 Mg/ha, with a median of 169 Mg/ha.

The direction in which mangrove sites are exposed to open water, and thus prevailing wave energy, was not a significant predictor of carbon storage (Kruskal–Wallis test, $\chi^2 = 5.5$, $p > 0.1$). In a comparison of sites by substrate, soil or lava rock, median belowground carbon storage values are indistinguishable (Kruskal–Wallis test, $\chi^2 = 0$, $p > 0.1$; Fig. 2), though the variance in carbon storage is greater among lava sites ($N = 9$) than soil sites ($N = 20$; $F = 2.9$, $p = 0.05$).

The average sediment organic carbon concentration across sites was 0.0426 ± 0.0183 g/cm^3 (mean ± SD), with a coefficient of variation of 0.429. The

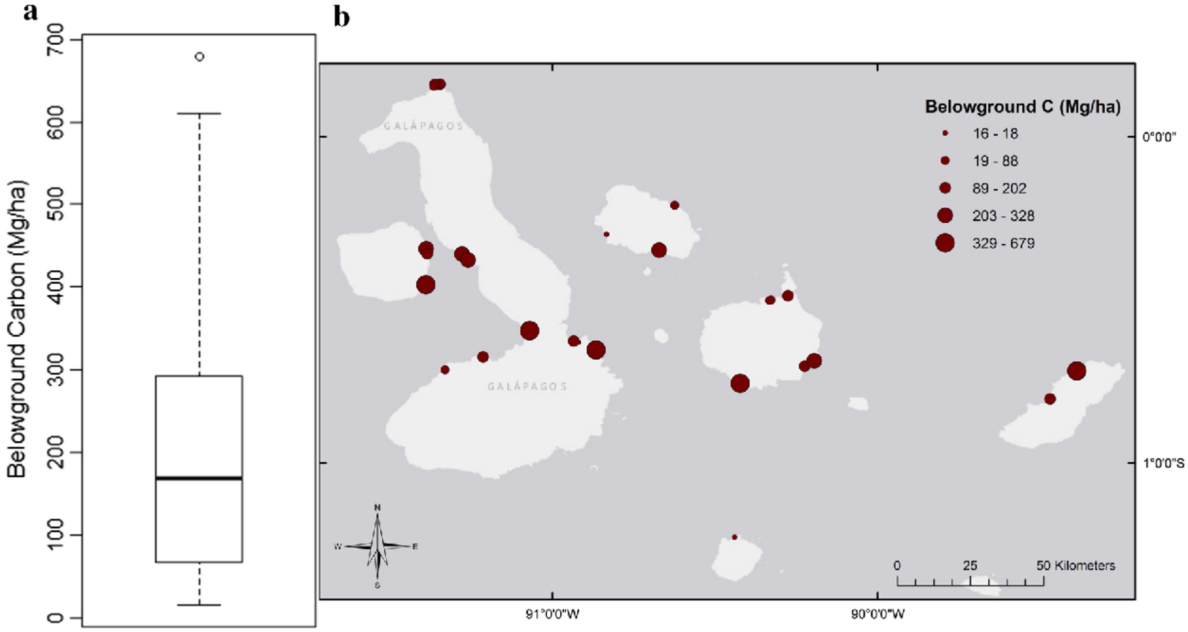


Fig. 1 **a** Belowground organic carbon storage at 29 mangrove sites across the Galapagos Archipelago. The box marks the median and 1st and 3rd quartiles, and the whiskers include all points within 1.5 × the interquartile range. **b** In the site map, the size of the circles indicate the amount of belowground carbon per hectare

total depth of the sediment profile was highly variable: 50.2 ± 40.1 cm, with coefficient of variation of 0.799 (Fig. 3).

Discussion

Our results demonstrate the magnitude and variability of mangrove belowground carbon on the tropical volcanic islands of the Galapagos. The estimates across our 29 sites range from 16 Mg/ha to 679 Mg/ha, differing by a factor of 42. These differences arise mainly due to variation in sediment depth (Fig. 4), with some mangroves growing practically on bare rock, with just a few centimeters of sediment, and others on peat deposits more than a meter deep. The importance of variation across landscapes in physical factors constraining belowground carbon storage may be especially evident in the rocky, dynamic environment of the Galapagos, but in fact it plays a role in most mangroves. For instance, in the Mexican Caribbean, Adame et al. (2013) measured a range of soil carbon from 95 to 1166 Mg/ha across nine sites, and, in the Indo-Pacific, Donato et al. (2011) observed large, unexplained variability in carbon stocks along a transect perpendicular to shore. Due to the difficulty of sampling and the objective of attaining comparable estimates across regions, some studies have employed the assumption of 1 m of sediment depth when scaling up mangrove carbon estimates (Bouillon et al. 2008), and others considered sediment carbon concentration and not depth (Chmura et al. 2003). In a global model driven by climate and latitude, Jardine and Siikamäki (2014) estimated Ecuador's mangroves to contain 462 ± 22 Mg/ha in a meter of sediment depth. These results present interesting predictions of belowground carbon concentrations, but they fail to capture the large variation due to coastal geomorphology and other physical conditions that shape the carbon concentration and depth of sedimentary layers. In our study, the coefficient of variation of mangrove sediment depth across sites was 0.799, roughly double that of the sites' sediment carbon concentrations, 0.429. Thus, at least in the mangroves of the Galapagos, variation in the total amount of carbon buried has more to do with the volume of material buried than its concentration of carbon. Considering this depth variation and the factors that control it, rather than assuming a uniform one-meter depth, is

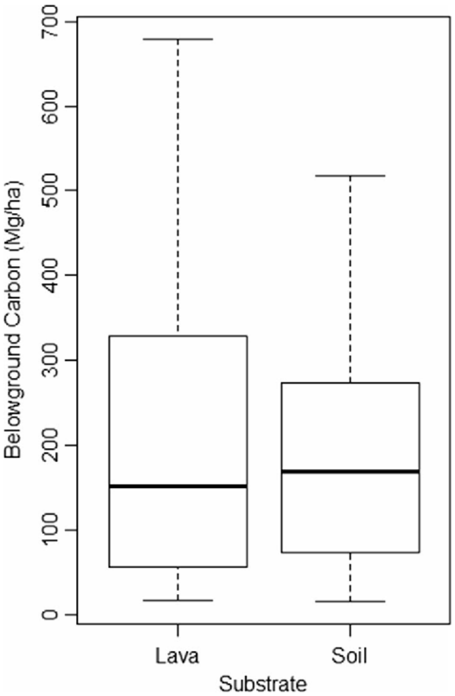


Fig. 2 Belowground carbon storage in Galapagos mangrove sites on coasts composed of lava rock (N = 9) and those on coasts with soil (N = 20). The boxes mark the medians and 1st and 3rd quartiles, and the whiskers include all points within 1.5 × the interquartile ranges (in this case, all the points)

important for capturing mangrove carbon variation across landscapes.

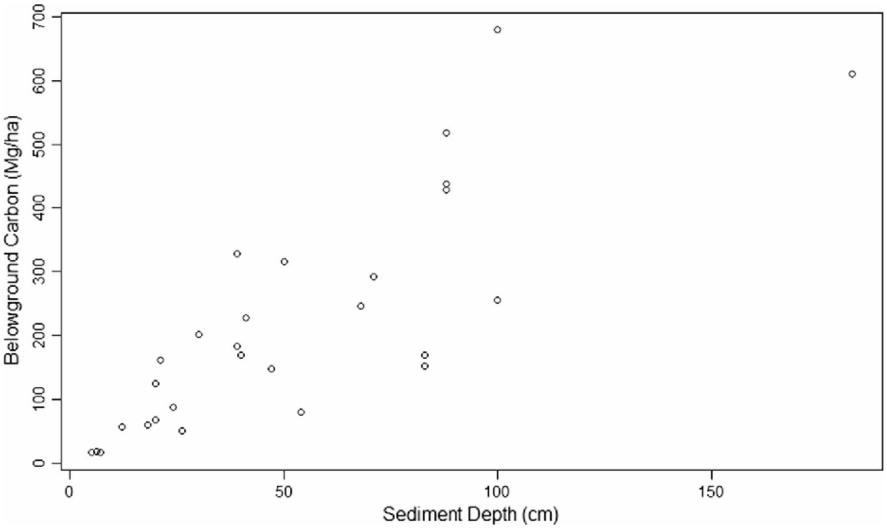
The considerable inter-site variation in belowground carbon storage uncovered in this study presents challenges for making broad generalizations. The results do raise the question of what drives such stark variability in the capacity of these mangrove forests to store carbon. The rocky, wave-washed character of the Galapagos' coasts likely inhibits mangrove production and sedimentary accumulation, but a test for a relationship between the direction in which mangroves are exposed to open water and local belowground carbon stocks yielded a null result. It is possible that patterns of coastal geomorphology and bathymetry are more important in protecting mangrove sites from physical disturbance than their orientation in the wave field. Indeed, mangroves are essentially absent on the open coasts of the Galapagos, regardless of their direction of exposure, indicating that geomorphological shelter is a prerequisite for mangrove establishment. Very little published literature explores spatial variation in mangrove sedimentation on oceanic islands, though on microatolls in the Great Barrier Reef it has been observed that local geomorphological features help shape the course of mangrove establishment (Stoddart 1980), and presumably carbon accumulation.

The Galapagos' extreme patchiness in mangrove carbon likely flows ultimately from its starkly heterogeneous coastal geology. The shores of these islands represent a patchwork of hardened lava flows ranging from millions to mere years old (Rowland 1996). The chaotic patterns with which these lava flows intersect the coast likely directs the flow of groundwater among them, with varying resistance to hydrological flow depending on geology (d'Ozouville et al. 2008). Limited freshwater flux and resultant elevated salinity are known to reduce mangrove productivity in other arid environments (Pool et al. 1977; Cintrón et al. 1978), with evidence suggesting the same pattern in the Galapagos (Song et al. 2011). Elizabeth lagoon, with one of the highest measurements of belowground carbon in this study, 610 Mg/ha, was identified by Howmiller and Weiner (1968) as featuring a surface lens of brackish water, indicating a subterranean source of freshwater to this enclosed area. This site has a narrow, silled entrance separating the deep mangrove lagoon from an outer, rocky bay, a set of characteristics observed in several of the more well-developed mangrove sites sampled in this study. We tested whether lava or soil substrates, with hypothetically different permeabilities to groundwater flow, were associated with variation in carbon stocks but did not observe a difference in mean belowground carbon storage (Fig. 2). However, we did find that, though low carbon stocks can be found under both conditions, there is greater variance among lava sites than among those with soil, with the highest carbon values found at Elizabeth and Carthago Chico III, both on Isla Isabela and situated where relatively young lava reaches the coast. However, because freshwater fluxes in the Galapagos are essentially restricted to subterranean flows, they are difficult to measure, with few data available. Increasing efforts to map freshwater flows to the intertidal across the Galapagos, for instance through hydrogeological remote sensing (d'Ozouville et al. 2008), will provide useful information for understanding and valuing its mangrove ecosystems.

Accurate, spatially explicit estimation of mangrove forest carbon stocks is essential for useful and credible ecosystem service valuations, upon which blue carbon

Fig. 3 Four cores from sites with different sediment depths. **a** At the site Punta Mangle on Isla Fernandina, sediment extended to 88 cm deep. **b** At Poza de Patillos I on Isla Fernandina, to 50 cm. **c** At one coring site at Baleado on Isla Isabela, to 31 cm. **d** At Norte III on Isla Isabela, only to 12 cm

Fig. 4 As the total belowground carbon stock is soil concentration integrated over depth, variation in belowground carbon reflects that in sediment column depth



market investment and government incentive programs depend. This work sheds the first light on the carbon stocks of the Galapagos. Hamilton and Lovette (2015) modelled Ecuador's mangrove carbon stocks but excluded the Galapagos due to their remoteness. However, the Galapagos' mangroves are uniquely valuable in terms of carbon storage, fisheries provisioning, and recreational value (Tanner et al. in press), and the global impact of carbon storage makes this ecosystem service equally relevant in remote as in high-use areas. Nevertheless, understanding these globally important carbon stocks requires local detail, given large variation across mangrove sites. Natural variability in carbon storage and other services should not be seen simply as a challenge to attempts to value ecosystems for conservation, which in most systems likely give highly conservative estimates anyway (Costanza et al. 2014). Rather, capturing real spatial variation offers the opportunity to identify conservation priority hotspots, especially in terms of co-benefits across ecosystem services. In a study of perhaps the most urgently threatened ecological role of mangroves in the Galapagos, Dvorak et al. (2004) surveyed the habitat of the critically endangered mangrove finch (*Cactospiza heliobates*), finding that this population of little more than 100 birds was found at two sites comprising only 32 ha of mangrove. These sites stand out from most Galapagos mangroves in their high canopies of 10 to 20 m; abundant dead wood and litter, in which the birds forage for insects; and relative protection from the open ocean. This setting likely makes these locations both prime finch habitat and effective carbon stores, compounding their conservation value. Thus, capturing local-scale variability in ecosystem services makes possible the identification of co-beneficial high-priority conservation sites. In light of the urgent challenges facing mangrove environments worldwide (Valiela et al. 2001), monitoring of these systems should be increased and the innovation of faster, more cost-effective methods of estimating carbon storage and other services stimulated.

This study demonstrates that, despite their harsh conditions for mangroves, with largely exposed rocky shores and little freshwater flux, the Galapagos still has the potential for large carbon stocks. Most importantly, these stocks vary by an order of magnitude across the archipelago, likely due to physical constraints on mangrove establishment, production, and detritus accumulation. Though sediment carbon concentration varies, the main contributor to inter-site carbon stock variation is the wide range of sediment depths, a factor sometimes ignored in the blue carbon literature. The rocky, wave-washed, and arid shores of the Galapagos, and other environments like them only marginally suitable for mangroves, are inherently patchy and especially poorly represented by broad-strokes modelling approaches, and yet they should not be ignored, as they can contain sites locally high in carbon storage. Though the Galapagos might represent an especially heterogeneous mangrove setting, landscape-scale variation in mangrove carbon stocks is likely much more prevalent worldwide than is reflected by the nascent blue carbon literature. Increasing spatial sampling and understanding of mangrove carbon burial, alongside other ecosystem services, will allow science-based management efforts to marshal limited resources to best effect in valuable mangrove ecosystems.

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Compliance with ethical standard

Conflict of interest The authors declare that they have no conflict of interest.

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Supplementary Material

Table 3-1: Belowground carbon estimates from sediment cores collected at 29 sites across the Galapagos Islands.

Island	Site Name	Latitude (°N)	Longitude (°E)	Exposure	Coastal Geology	Mangrove Species	Sediment Depth (cm)	Belowground C (Mg/ha)
Fernandina	Poza de Patillos I	-0.343705	-91.388415	E	Soil	*R*	50	315
Fernandina	Poza de Patillos II	-0.358760	-91.384980	E	Lava	*R*	83	152
Fernandina	Punta Mangle	-0.453435	-91.388506	E	Soil	*R*	88	428
Floreana	Baronesa	-1.227800	-90.439710	N	Soil	*R*	5	17
Isabella	Baleado^3	-0.674428	-91.212892	N	Soil	*R*	47	147
Isabella	Cañones	-0.359674	-91.277699	W	Soil	*R*	100	256
Isabella	Carthago Chico I	-0.658014	-90.863225	E	Lava	*L*, *R*	6	18
Isabella	Carthago Chico II	-0.653216	-90.868574	E	Lava	*L*, *R*	39	328
Isabella	Carthago Chico III	-0.653009	-90.865779	E	Lava	*L*, *R*	100	679
Isabella	Carthago Grande I^3	-0.625645	-90.934800	E	Soil	*L*, *R*	21	162
Isabella	Carthago Grande II	-0.629000	-90.920109	E	Lava	*L*, *R*	7	17
Isabella	Elizabeth	-0.594091	-91.069653	W	Lava	*R*	183	610
Isabella	Norte I	0.161576	-91.345364	N	Lava	*L*, *R*	20	125
Isabella	Norte II	0.160178	-91.361832	N	Lava	*L*, *R*	30	202
Isabella	Norte III	0.155076	-91.365055	N	Lava	*L*, *R*	12	56
Isabella	Punta Morena	-0.713764	-91.329592	N	Soil	*R*	26	51
Isabella	Urvina^2	-0.378029	-91.259406	W	Soil	*L*, *R*	68	247
San Cristobal	Poza Sardina	-0.717210	-89.389120	N	Soil	*R*	88	437
San Cristobal	Puerto Grande I	-0.799370	-89.468700	N	Soil	*L*, *R*	18	60
San Cristobal	Puerto Grande II	-0.803450	-89.470430	N	Soil	*R*	40	169
Santa Cruz	Garrapatero	-0.702900	-90.224860	E	Soil	*R*	83	170
Santa Cruz	Itabaca	-0.487530	-90.275920	S	Soil	*R*	39	183
Santa Cruz	Poza de Parroquiano^2	-0.755101	-90.422644	S	Soil	*L*, *R*	88	518
Santa Cruz	Roca Fuerte	-0.686420	-90.195370	E	Soil	*R*	41	228
Santa Cruz	Tortuga Negra I	-0.501860	-90.332270	N	Soil	*R*	54	80
Santa Cruz	Tortuga Negra II	-0.500392	-90.328072	N	Soil	*L*, *R*	24	88
Santiago	Laguna Azul	-0.347700	-90.672180	S	Soil	*L*, *R*	71	293
Santiago	Puerto Nuevo^2	-0.298810	-90.833280	W	Soil	*R*	5	16
Santiago	Sarten	-0.209875	-90.624115	N	Soil	*L*, *R*	20	67
					Median		40	169
					Mean		50	211

Note: Site names with ^{2} or ^{3} indicate that the sediment depth and belowground C figures reported represented the average of 2 or 3 cores, respectively, collected at that location to capture local variation. Mangrove species indicates the species found within 5 m of the coring site (*L* = *Laguncularia racemosa*, *R* = *Rhizophora mangle*).

CHAPTER 4

Sediment depth and accumulation constrain belowground carbon stocks across northern New World mangroves.

Abstract

Much recent effort has been spent estimating mangrove carbon stocks, but ecological and geological drivers of the variation in these stocks remain poorly understood. The long-term sedimentary carbon sinks of mangroves and other blue carbon ecosystems have rapidly become a focus of research and conservation attention. However, sampling coverage remains very low, with sediment cores sparsely distributed across a subset of mangrove environmental settings. We cored diverse mangrove environments to assess the limits of mangrove sedimentary carbon storage: the volcanic Galapagos, the arid lagoons of the Baja Peninsula, and the geologically and climatically distinct Caribbean and Pacific coasts of Panama. We cored entire sediment columns, subsampled with depth, and dried, weighed, and analyzed the samples for their organic carbon content. Depth integrated carbon stocks are highly variable, from < 17 to > 1,700 MgC_{org}/ha. Contrary to global models, we did not find a positive relationship between sediment carbon density and annual rainfall, though some carbon density differences across areas emerged. Variation in sediment depth, ranging from 7 to 427 cm across sites, dominated variation in carbon stock locally and across the four areas studied. This research emphasizes the role that long-term ecosystem processes play in shaping mangrove peat deposits, allowing more accurate estimation of this variable and valuable carbon pool.

Introduction

Since the Industrial Revolution, we humans have unearthed and burned millions' of years worth of plant and algal organic carbon stored via burial in shallow marine and wetland environments, i.e. fossil fuels. Oxidizing this organic carbon pool has increased the concentration of CO_2 in the atmosphere and led to a global climate crisis (Ciais et al. 2013). In recent decades, researchers have focused attention on the ecosystems that today are fixing carbon dioxide as organic matter and storing it underground, in some measure counterbalancing human greenhouse gas emissions. Highly productive and efficient at trapping and preserving plant detritus in anoxic, accumulating sediments, mangroves, salt marshes, and seagrass beds have been identified as "blue carbon ecosystems," marine organic carbon sink hotspots (Nelleman et al. 2009). Measurements of their carbon sequestration rates (Mcleod et al. 2011), the net amount of organic carbon added to the ecosystem each year, have been gathered, making possible estimates of the value in terms of future drawdown of atmospheric CO_2 of maintaining or restoring these ecosystems. In contrast, studies of the magnitudes of these ecosystems' buried carbon stocks, an integration of long-term carbon storage in soil over each site's history (Pendleton et al. 2012), elucidate the greenhouse gas emissions risk associated with their disturbance or destruction. Both aspects of blue carbon are highly relevant to climate mitigation. More than 35% of mangrove area has already been lost (Valiela et al. 2001), creating ample opportunity for restoration and sustainable management, and the ongoing rate of deforestation globally is at least 1% annually, resulting in large emissions from oxidized carbon stocks (Kauffman et al. 2017). There has been a push to map out the distribution of blue carbon stocks globally, especially to facilitate the development of national or regional blue carbon inventories for integration into national climate change mitigation plans or carbon markets (Crooks et al.

2018). Despite the recent uptick in interest in regional blue carbon distributions, however, understanding of the ecological and geological processes that govern the formation and preservation of long-term carbon stocks is still in its infancy.

In this paper we focus on belowground carbon stocks in mangroves. Mangroves store more carbon than most other forests (Donato et al. 2011) and tend to have the largest stocks among blue carbon ecosystems (Pendleton et al. 2012). These forests have been recognized for decades as ecosystem service hotspots (Costanza et al. 1997), providing fisheries nursery habitat (Aburto-Oropeza et al. 2008), timber, run-off purification, and protection from erosion and storm events (Ewel et al. 1998, Walters et al. 2008). As blue carbon sequestration and storage are now recognized as vital services provided by coastal vegetated ecosystems, the valuation of mangroves has taken on a new dimension of global relevance. Like other blue carbon ecosystems, mangroves are highly productive, with rates of net primary productivity of 13.6±4.5 $MgC_{org}/(ha \times year)$ (indicates mean ± standard error throughout unless otherwise stated; Bouillon et al. 2008). Terrestrial tropical forests can also achieve high rates of carbon uptake, however (Dixon et al. 1994); what sets mangroves apart is not their rapid productivity but the relatively high burial efficiency of their organic matter production (Duarte and Cebrián 1996), leading to the slow vertical accumulation of peat often meters deep and millennia old. The difference between relatively rapid upland tropical forest biomass turnover and long-term preservation in mangroves is mainly made possible by the physical conditions distinct to mangrove soils. Frequent flooding hinders the diffusion into the soil of oxygen, quickly consumed by microbial remineralization of organic matter (Kristensen et al. 2008). Nutrient demand by mangrove trees and by heterotrophic microbes remineralizing carbon-rich detritus, as well as flushing with often oligotrophic tropical seawater, also keeps nutrient availability low, with most nitrogen and phosphorus trapped in organic or minerally adsorbed forms (Alongi et al. 2004, Sánchez-Carrillo et al. 2009). This physical environment allows some fraction of detritus, especially of mangrove roots (McKee and Faulkner 2000), to be eventually deposited below the zone of active growth and potential bioturbation and remineralization into a peat layer that can remain essentially stable for millennia (McKee et al. 2007, Ezcurra et al. 2016). Determining the environmental controls on this process of forming long-lived peat from mangrove detritus can improve understanding of mangroves' blue carbon functioning.

A few studies have gathered mangrove datasets from around the world in order to build models that can predict regional variation in the pools of carbon in these ecosystems. As it is readily visible, both to a terrestrial observer and from satellites, and estimable using conventional forestry techniques, aboveground biomass has been the target of rapid and relatively comprehensive modeling effort. Hutchison et al. (2013) model global aboveground biomass as a function of local climate, particularly annual rainfall and temperature, using a dataset of measurements from 52 mangrove sites. Aboveground biomass is correlated with belowground biomass and with rates of primary productivity (Komiyama et al. 2008, Day et al. 1987), so modeled aboveground biomass may be a reasonable indicator of contemporaneous carbon sequestration. Similarly the concentration of organic carbon in mangrove soils is measured and modeled as an indicator of the magnitude of sequestration in these systems. Some researchers have hypothesized that the same climatic variables that covary with mangrove productivity and biomass also predict soil carbon concentrations. Jardine and Siikamäki (2014) predicted mangrove soil concentrations globally in a model driven mainly by annual rainfall and latitude. More local scale-models have shown similarly high predictive power using rainfall as a predictor of mangrove productivity or carbon stocks (López-Medellín and Ezcurra 2012, Hamilton and

Lovette 2015). Results such as these suggest the hypothesis that in wet, tropical areas where high annual rainfall boosts mangrove productivity and greater biomass, the soils are driven toward a higher concentration of carbon, presumably because the delivery of organic detritus is greater in proportion to inorganic sedimentation than in drier regions.

Beyond this simple, climate-driven model of mangrove productivity, some studies have recognized that patterns in local coastal geomorphology also drive variation in carbon cycling in mangrove systems. Rovai et al. (2018) showed that in mangroves around the world there are large differences in soil carbon concentrations across mangrove geomorphic settings, and that previous global models had underestimated these concentrations in some settings, such as karsts. Indeed, recent studies have begun to show a number of higher-level ecological correlates to blue carbon function. The impact of anthropogenic nutrient delivery to mangrove productivity and carbon sequestration has been investigated in several studies (Kristensen et al. 2008, Mcleod et al. 2011), with a range of results, suggesting a role for nutrient limitation status in controlling carbon cycling. Atwood et al. (2015) reviews evidence that blue carbon ecosystems with intact top predator populations increase biomass and sediment carbon content. Thus, mangrove blue carbon research has begun to delve more deeply into the full range of physical and ecological factors that may affect the accumulation of soil carbon.

The prevalent focus on modelling or measuring aboveground biomass (Hutchison et al. 2013), leaf litter production (Adame and Lovelock 2011), or surface soil concentrations (Jardine and Siikamaki 2014, Rovai et al. 2018) are attempts to characterize the current state of a mangrove ecosystem, its current productivity and soil carbon delivery, and the factors that drive them. The aspect of mangrove and other blue carbon ecosystem’s carbon cycling that is most relevant to climate change, however, is their long-term storage of carbon, not their instantaneous rates of uptake. For that reason, an indispensable element of understanding mangroves' capacity for climate change mitigation is the measurement and analysis of site history of accumulation from the time of wetland formation, over a period of years to millennia of peat formation, to the extant forest with its current rate of carbon production. Studies that capture the role of coastal geomorphic setting approach this perspective by recognizing that the way sites have physically evolved over time sets the conditions for trees today (Rovai et al. 2018, Twilley et al. 2018). But patterns of geological development and successional history at a site likely also affect the passage of organic matter from the actively cycling surface pool into long-term preservation in peat deposits, as well as the rates of decomposition of this organic matter after burial. For this reason, measuring the depth and age of peat deposits can reveal an important component of mangroves' carbon value (Kauffman et al. 2017, Kauffman et al. 2018).

Paleoecological studies, to a greater extent than those focused on carbon stocks and management, have captured the history and variation in mangrove peat deposits over the course of their formation. Because they form sequentially deposited layers of material rich in fossils and tracers of past environments over much of the Holocene, mangrove peats have been valuable objects of study for researchers interested in coastal dynamics (Thom 1967), sea-level rise reconstruction (Toscano and Macintyre 2003), and paleoenvironmental reconstruction (Seddon et al. 2011). Given their disciplinary focus, mangrove paleoecological studies have frequently not been concerned with the mechanisms and management of carbon fluxes and other processes at work today in these ecosystems, but their results and approach have promise for deepening the science of blue carbon. Over geologic time scales, core records indicate the evolution and spread of mangrove species across the world by their preservation of pollen microfossils (Ellison 2008). Over the more recent history of Holocene sea-level rise (SLR) and stabilization, they also contain information about the vertical accretion and landward succession of mangroves by the deposition of mangrove biomass-derived peats (Ellison 2008). Ellison (1993) measured a retreating mangrove peat deposit in Bermuda, showing the landward migration of peat over Holocene sea level rise and the overtopping of previous freshwater marsh peat with mangrove peat and estimating an average rate of peat accretion over the entire peat record of 0.8–1.0 mm/year. She attributes recent peat collapse in parts of this site to constrained peat accretion rates unable to keep up with modern rates of SLR. McKee et al. (2007) combined measurements of near-surface root deposition with analysis of deep peat cores at Twin Cays in Belize, showing that rates of peat accumulation can greatly exceed average deposition rates inferred from dating the bottoms of peat deposits. That study also demonstrated that fine root growth is the principle source of material in carbon-rich peat deposits, and that this growth is sensitive to the state of nutrient limitation of the trees. Ezcurra et al. (2016) measured the blue carbon stocks of mangroves on the Mexican Pacific in the context of their history over the last two millennia of SLR, observing that mangrove bays with steep coastal slopes have accomplished vertical mangrove accommodation of SRL via belowground peat accumulation, in contrast to the less vertically extensive deposits in laterally dynamic, shallowly-sloping coastal plains. In chapter 2 of this dissertation, I report peat cores in the Lower Gulf of California dating back > 5,000 years BP and demonstrates the importance of subterranean root growth to peat formation down to at least 50 cm, with implications on the interpretation of dated mangrove core records.

The study reported here compares belowground carbon stocks in mangrove forests in several areas of the Neotropics with similar communities of tree species but divergent climatic and geological conditions. We hypothesize that areas with greater annual rainfall possess higher soil carbon densities, supported by evidence of mangrove production limited by freshwater (Day et al. 1996) and nutrient (Feller et al. 2002) fluxes which are enhanced in riverine systems. Given the evidence for the ability of mangrove peat to accumulate in accommodation of relative SLR (relative to vertical land movements, RSLR) (McKee et al. 2007, Ezcurra et al. 2016), we also hypothesize that mangrove peat deposit depth is greater in areas where recent RSLR has been more rapid. Given the role of coastal geomorphology in setting the sensitivity of mangrove peat accumulation to RSLR (Ezcurra et al. 2016), we hypothesize that the effect of coastal slope on sediment depth is more positive in areas with higher rates of RSLR. These two quantities, sediment carbon density and total sediment depth, are likely shaped by different environmental drivers on different temporal scales, the former reflecting current productivity and sedimentation and the latter the entire history of wetland formation over millennia. They are also the two factors that together determine mangrove sediment carbon stock, and this study explicitly investigates them and their environmental correlates separately with the aim of building mechanistic understanding of the formation and preservation of mangrove peat deposits.

Methods

Overview of Regional Sampling Areas

In field campaigns beginning in 2014 and concluding in 2017, we sampled mangrove sediments at 80 sites across four areas of the northern New World tropics and subtropics: the Baja Peninsula of Mexico, the Galapagos Islands of Ecuador, and the Caribbean and Pacific coasts of Panama (Figure 4-1). These sampling areas encompass a wide geographic, climatic, and geological range. The Galapagos Islands are situated on the equator, Panamanian areas in the center of the tropical zone between 7 and 10 °N, and the sites on the Baja Peninsula from just north of the Tropic of Cancer at 24 °N to 29 °N near the northern limit of mangroves on the west coast of North America. Climatic conditions varied from warm, semi-arid, and seasonal equatorial conditions in the Galapagos (Trueman and d'Ozuoville 2010) to the more consistent, warm, and rainy tropical conditions of Panama (Lovelock et al. 2005, McGowan et al. 2010) and the arid and highly variable subtropical conditions in the Baja Peninsula (Rebman and Roberts 2012). The geological settings of each region are distinct as well, with mangroves inhabiting rocky coasts formed from lava flows of varying age in the Galapagos, karst in Caribbean Panama, estuaries and sedimentary island formations in Pacific Panama, and protected, generally sandy bays among coastal hillsides in the Baja Peninsula. Rates of RSLR in recent decades vary among these sites as well, from 0.89 mm/yr in the Galapagos to 1.68 mm/yr in the Baja Peninsula (NOAA Center for Operational Oceanographic Products and Services 2018). The mangrove species of all four regions are essentially the same, however, with *Rhizophora mangle* forming the low intertidal fringe and occasionally occurring alone or in a mixed stand higher; *Laguncularia racemosa* in a mid-intertidal position, intermixed with *R. mangle*, or constituting a patchy fringe in some sandy or wave-exposed areas; and *Avicennia germinans* generally in the high intertidal. The only exception to the community similarity among sampling areas is the presence in Pacific Panama of *Pelliciera rhizophorae* in the mid- intertidal (Gross et al. 2014).

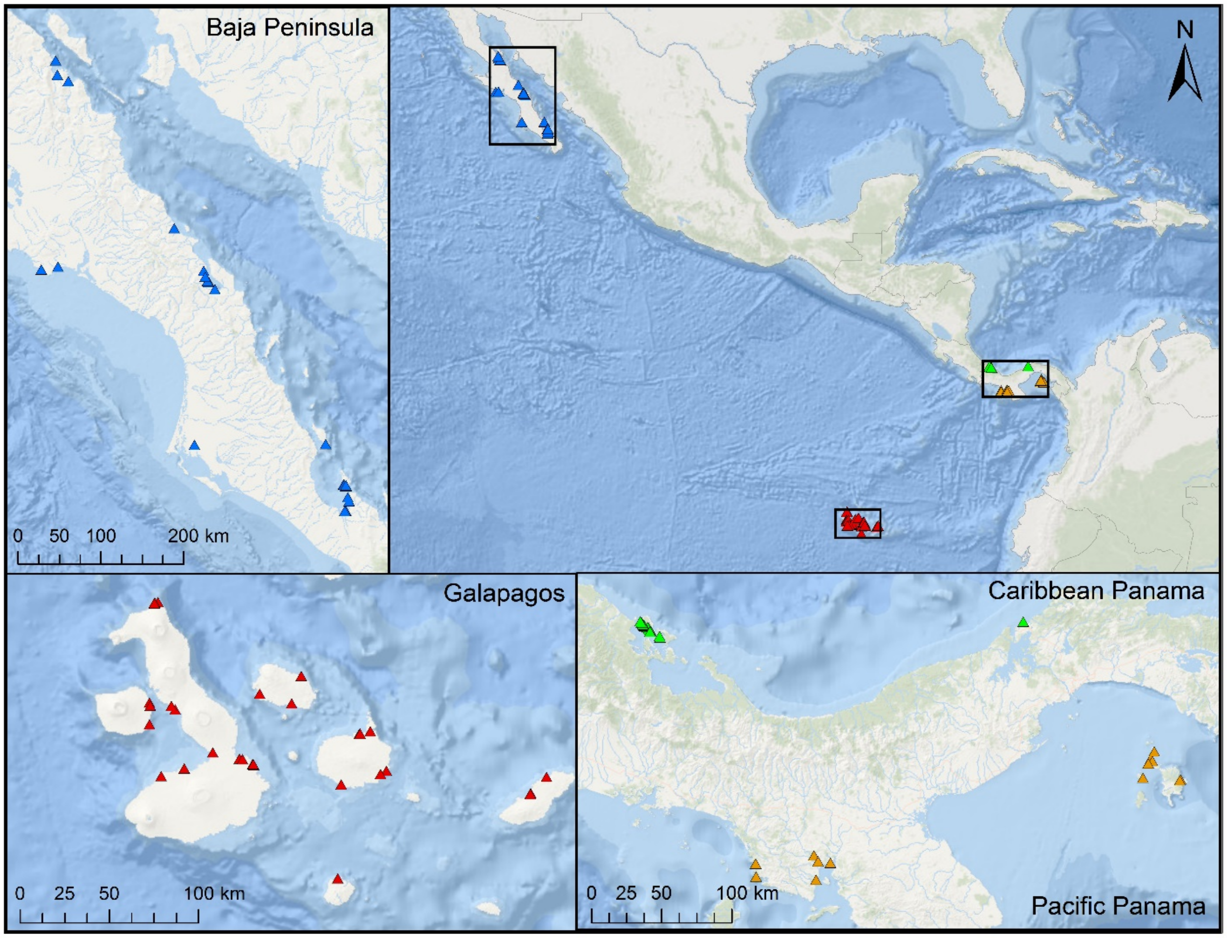

Figure 4-1: Map showing the 80 mangrove sites included in this study across four areas: the Galapagos Islands (29 sites), the Pacific coast of Panama (13 sites), the Caribbean coast of Panama (17 sites), and the Baja Peninsula (21 sites).

Sampling Areas

Galapagos Islands

The Galapagos are an archipelago of volcanic islands, with a distribution of sizes from Isabella's > 4,000 km^2 down to that of many small islets and rocks, and mangroves grow on all of the larger islands (Moity et al. 2019). The coasts of the Galapagos range from rocky shores composed of young volcanic rock to soils of moderate development (Costa et al. 2019). The typical daily air temperature range is 22–28 °C (mean of monthly means of daily minimum and maximum temperatures, throughout), and rainfall averages 578 mm/year, with strong seasonality (WMO 2019). Mean sea surface temperature is 24 °C, with considerable variation due to seasonal equatorial upwelling (Moity et al. 2019). Exposed to oceanic swell, these islands' mangroves are generally only found in bays or relatively protected indentations of the rocky coast. Arid conditions dominate the coastal zone in the Galapagos, with rainfall in the mountains reaching the sea only via groundwater flow (d'Ozouville et al. 2008). Average RSLR estimated from tide gauges from 1978 to 2007 is 0.89 mm/year (95% CI: ±3.83 mm/year; NOAA Center for Operational Oceanographic Products and Services 2018). Data from the mangrove coring conducted for this study are presented in Costa et al. (2019), the first investigation of mangrove sedimentary carbon in the Galapagos, along with a discussion of the interaction between locally variable coastal substrates and sediment carbon stocks in mangroves, likely mediated by groundwater hydrology.

We sampled 29 sites in total, covering all of the major mangrove forests in the archipelago, with the exception of those on the southeast coast of Isabella. The rocky coasts of these islands generally preclude the formation of well-developed basin forests inland of the fringe, so sampling was limited to the coastal fringe. As a result, most sites were adequately sampled with one core, though at five sites 2 or 3 cores were taken to cover local variation. Sampling was conducted in April 2015.

Pacific Panama

The Pacific coast of Panama is divided by the Azuero Peninsula into two regions, the Gulf of Chiriqui to the west and the Gulf of Panama to the east. The geology of this coast features a mixture of sedimentary and igneous rocks uplifted during the formation of the Isthmus of Panama, resulting in dramatic coastal relief in some areas. In places where the open coast is predominantly rocky and steep as in much of the Gulf of Chiriqui area, mangroves are restricted to small river mouths or large estuaries, such as the Gulf of Montijo within the Gulf of Chiriqui (M. T. Costa, personal observation). The typical daily air temperature range is 20–34 °C, and average annual rainfall varies from 1907 to 2412 mm along the Pacific coast of Panama, with some seasonality (WMO 2019). (An average annual rainfall value of 2160 mm/year for the entire area was used in analysis.) Mean SST is 28 °C, but temperatures range from 18 to 31 °C, with large negative excursions due to upwelling in the winter dry season, especially in the Gulf of Panama (C. Randall, unpublished data). Average RSLR estimated from tide gauges from 1908 to 2016 is 1.45 mm/year (95% CI: ±0.22 mm/year; NOAA Center for Operational Oceanographic Products and Services 2018). This coastal area is set apart from the others in this study by its large tidal range, averaging 3.8 m (McGowan et al. 2010). Despite this and other unusual features of this region—including the addition of the species *Pelliciera rhizophorae,* specific to the Pacific Central American mangrove flora—the mangroves of the Pacific Coast of Panama have received very little published study (but see McGowan et al. 2010 and Gross et al. 2014).

In the Gulf of Chiriqui, mangroves were sampled in the large Gulf of Montijo and in several small river mouths to the west. In the Gulf of Panama, sampling sites were on the Pearl Islands, an archipelago about 40 km south of the mainland on which mangroves are widely distributed in most protected embayments (McGowan et al. 2010). In September 2017, we sampled 13 sites overall in Pacific Panama, taking one core 5 m landward from the fringe and, where possible another core 10 m farther landward, though the narrowness of the mangrove fringe on these steep coasts and issues with accessibility sometimes made a second core impossible.

Caribbean Panama

The Caribbean coast of Panama is characterized by conditions highly favorable for mangrove forest development, and as a result much of the coast is dominated by this ecosystem. Mangroves generally grow on peat or calcareous marl sediment overlying karst, with microtidal sea surface variation, typical of many Caribbean mangrove coasts (Lovelock et al. 2005). Typical daily air temperature range is 21–31 °C, and annual rainfall is 3458 mm, with a peak during the summer wet season but relatively wet conditions persisting all year (WMO 2019). SST averages 29 °C with relatively little seasonal variability (Kauffman and Thompson 2005). Average RSLR estimated from tide gauges from 1909 to 1980 is 1.41 mm/year (95% CI: ±0.22 mm/year; NOAA Center for Operational Oceanographic Products and Services 2018). Due to the presence of Smithsonian Tropical Research Institute (STRI) research stations at Bocas del Toro and Galeta and the widespread and well-developed distributions of mangroves, seagrass beds, and coral reefs on Panama's Caribbean coast, this area is one of the more well-studied in terms of tropical coastal ecosystems, including mangroves (Kauffman and Thompson 2005, Lovelock et al. 2005, Granek and Ruttenberg 2008, inter alia).

We sampled at 17 sites across Bocas del Toro and Solarte Islands and Galeta Point, at most sites taking a core 5 m landward from the fringe and additional cores at successive 10 m intervals landward given the greater extent of intertidal zonation in this well-developed mangrove area than in others in this study. Sampling was conducted in September 2015.

Baja Peninsula

The Baja Peninsula features a wide range of physical environments, but its coastal areas inhabited by mangroves are generally hot and arid. The daily air temperature range is 18–30 °C and the average annual rainfall 245 mm near the southern end of the mangroves' range on the peninsula around 24 °N, while at its northern end at 29 °N the average temperature range is 15–31 °C and the average annual rainfall 84 mm (WMO 2019). (An average annual rainfall value of 165 mm/year for the entire area was used in analysis.) Peak air temperatures frequently surpass 40 °C in summer, and fluxes of freshwater and associated nutrients are mainly available from groundwater flux (Urquidi-Gaume et al. 2016), especially limited on small islands in the Gulf of California. Average SST ranges from 18 °N on the Pacific coast and in the Central Gulf in winter to 31 °C in the Central Gulf in summer (Lavín et al. 2009). Average RSLR estimated from tide gauges from 1952 to 1984 is 1.62 mm/year (95% CI: ±1.48 mm/year; NOAA Center for Operational Oceanographic Products and Services 2018). Research on the geological history (Pedrín-Avilés et al. 1992), sedimentary carbon (Ezcurra et al. 2016, Costa et al. in prep), microbial ecology (Giani et al. 1996, Vazquez et al. 2000, Costa et al. in prep), and conservation (Páez-Osuna et al. 2003, Glenn et al. 2006, Holguin et al. 2006) of the mangroves of the area have been published.

We sampled at 21 sites spanning the entire latitudinal range of mangroves on both the Pacific and Gulf coasts of the peninsula. In 7 of these sites only one core was taken 5 m landward from the fringe, but in the rest there were well-developed enough forests to permit subsequent cores at 10 m intervals going landward from the fringe. Sampling was conducted in July and December 2015 and February 2017.

Field Methods

Within each sampling area, sites were selected in order to give the widest distribution of forests along the coast possible. In a local area, coring sites were chosen randomly by selecting a point along the mangrove fringe mapped out using satellite images before going into the field. In practice, these coring locations were only truly randomly selected in a subset of cases; more often than not the major limitations of the physical accessibility of sites in the forest and the time available at these remote sites significantly affected where cores were taken. Within each site, a core was taken 5 m landward from the mangrove fringe, and, when it was possible, another core 10 m farther in from that location, and so on another 10 m as long as it was possible to extend the transect into the intertidal. Many sites presented narrow fringes of mangrove without significant extent of (or access to) further forest landward. Most sites were accessed by small boat, and we located sites using a water-resistant handheld GPS device. Though we generally attempted to core at low tide, in locations where the sediment surface was inundated, the person operating the corer used snorkel gear guide the corer into the sediment while the corer operator, or second person above using an extension rod, drove it downward. In inundated locations, the snorkeler also held the core chamber closed while the corer was being extracted from the sediment.

We sampled mangrove sediments using a Russian peat corer (Aquatic Research Instruments), taking vertical, semi-cylindrical sections of sediment 5 cm in diameter and up to 50 cm in length. By adding extension rods, we then returned to the same hole to obtain successively deeper 50-cm sections of sediment. We repeated this process to rejection, when the core tip hit a hard substratum of rock or gravel. Each core section was photographed and subsampled with depth at least every 25 cm with depth and just above any apparent change in horizon (of clay, peat, sand, et c.). To ensure that each subsample was of a known volume of sediment , we used a knife and a measuring tape to obtain samples of measured vertical extent, at least 2 cm, though in some cases up to 5 cm when it was necessary to have enough material for a broader set of analyses than are presented in this paper. Each subsample was sealed in a labelled glass jar.

Laboratory Methods

We placed each sample in its opened jar in a drying oven at 60 °C until dry (≥ 24 hours). In cases where field circumstances prevented quick access to a drying oven, we kept the sample jars on ice until they could be dried. We weighed the dried samples to determine bulk density and then homogenized them using a mixer mill and mortar and pestle until they passed through a 500-μm sieve. To remove $CaCO_3$, the samples were HCl-fumigated following the method of Ramnarine et al. (2013) before analysis, so that the only carbon remaining was organic. For the samples from the Galapagos, very few sites contained $CaCO_3$ in the sediment, so most samples were not acidified before analysis (see Costa et al. 2019).

From each sample, 6-9 mg were precisely weighed into a tin envelope and analyzed by CG-MS (Carlo Erba NA 1500 elemental analyzer), which measures the mass percentage of carbon. Because $CaCO_3$ was removed from or not present in the samples, this value is the mass percentage of organic carbon (%C hereafter). For the 179 samples from Caribbean Panama, %C was instead estimated by loss on ignition (LOI) at 550 °C. We then analyzed a subset of 20 samples, chosen to cover evenly the range of LOI values, to analyze by GC-MS in order to construct a calibration curve for the conversion of LOI to %C.

From some cores, individual pieces of mangrove root tissue were picked out of the dried samples for radiocarbon analysis at the KCCAMS radiocarbon facility at UC Irvine following standard procedures.

Data Analysis

The measured bulk density of the sample multiplied by its %C gives the mass of organic carbon per unit volume, or carbon density (in gC_{org}/cm^3). The carbon stock of each coring location was estimated by averaging the carbon density of subsamples downcore within a sediment horizon and then integrating the carbon content of each horizon over the measured depth interval of that horizon, giving carbon stock (in gC_{org}/cm^2). The carbon stock of each horizon was then summed, giving the carbon stock of the entire sediment column (the values presented in this paper are converted by multiplying by 100 from gC_{org}/cm^2 to MgC_{org}/ha). Carbon stock is thus essentially the product of carbon density and sediment depth.

Average carbon density for a core is the average of the carbon densities in the samples with depth in each core, weighted by the vertical extent of the sediment horizon from which the sample came. Average carbon density for a site with multiple cores is the simple average of those cores' average carbon density values. Similarly, the average sediment depth reported for a site in which multiple cores were taken is the average of the depths of those cores, and the carbon stock reported for a site is the average of those cores' carbon stocks.

The hypothesized effect of coastal geomorphology on mangrove carbon stocks was investigated by estimating coastal slope using a digital elevation model (USGS et al. 2014). Coastal slope was estimated as: $(40\text{ m} - E)/D$, where E equals the DEM elevation at the coring location, and D = the horizontal distance between the coring location and the nearest point on the 40 m elevation contour. This rise-over-run metric is a dimensionless ratio. Contours of 40 m elevation were created from the DEM in ArcGIS Desktop 10.5 using the "contour" tool. Elevation at each coring site was extracted from the DEM at each site's GPS location using the

"Extract Values to Points" tool. The horizontal distance between each coring site and the nearest point on the 40 m contour was calculated using the "Near" and "XY to line" tools. The resulting distances were then projected into each the sites' respective UTM zones to calculate horizontal length in meters.

Radiocarbon estimates of the fraction of modern carbon in each sample are corrected for isotopic fractionation using $\delta^{13}C$ measurements at the Keck AMS facility and calibrated using the OxCal tools to estimate the predicted calendar age ranges (Ramsey 2008), given 95% confidence intervals (CI). Ages and accumulation rates are reported as the mean ± 95% CI.

Statistical comparisons were conducted using the R software (R Core Team 2016). Differences in carbon density, sediment depth, and carbon stock by area and with annual rainfall, RSLR, and coastal slope were tested using fixed-effect ANOVA. The response variables of carbon density, sediment depth, and carbon stock were $\log_{10}(x + 1)$-transformed to reduce error in ANOVA due to non-normal distribution.

Results

Average belowground carbon stock, as well as its constituent factors carbon density and sediment depth, varied across the areas studied (Table 4-1). The distribution of carbon stocks for each area was right-skewed and non-normally distributed (Shapiro-Wilk test; Galapagos: $W = 0.88$, $p = 0.004$; P. Panama: $W = 0.75$, $p = 0.002$; C. Panama: $W = 0.77$, $p < 0.001$; Baja: $W = 0.83$, $p = 0.002$), and the distributions were heteroscedastic (Levene test, $F = 3.7$, $p = 0.016$). For that reason, carbon stock values were $\log_{10}(x + 1)$-transformed for the purpose of comparing among areas, rendering them normally distributed (except for the Galapagos: Shapiro-Wilk test, $W = 0.93$, $p = 0.059$; but other areas: P. Panama: $W = 0.91$, C. Panama: $W = 0.98$, Baja: $W =$

0.97; $p > 0.1$ for each), and homoscedastic (Levene test, $F = 1.6$, $p > 0.1$). Using the log-transformed data, there is a significant difference in mean carbon stocks across areas (ANOVA, $F = 3.4$, $p = 0.021$; Figure 4-2). The carbon stock from Caribbean Panama is greater than those from the Baja Peninsula (Tukey test, $p = 0.024$) and the Galapagos ($p = 0.031$; for all other comparisons, $p > 0.1$).

Table 4-1: Average sediment carbon density and depth values and total belowground carbon stocks in the four areas studied. Values reported are mean ± standard error.

Area	**Carbon Density (gC_{org}/cm^3)**	**Sediment Depth (cm)**	**Carbon Stock (MgC_{org}/ha)**
Galapagos	0.044±0.003	50±7	213±34
Pacific Panama	0.020±0.001	145±42	347±107
Caribbean Panama	0.025±0.001	97±21	486±116
Baja Peninsula	0.025±0.002	83±10	157±25

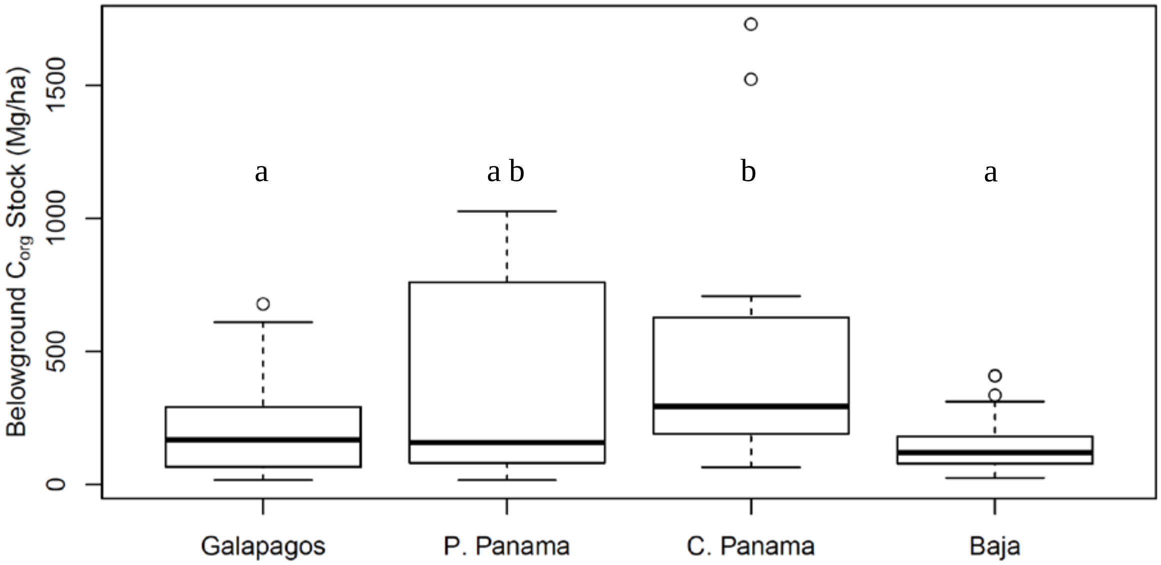

Figure 4-2: Belowground organic carbon stock across the areas sampled is plotted. Boxes mark the median and 1st and 3rd quartiles, and whiskers include all points within 1.5 × the interquartile range. Letters indicate statistically significant *post hoc* comparisons of log-transformed means.

The distributions of carbon densities for some of the areas were right-skewed and not normally distributed (Shapiro-Wilk test; Galapagos: $W = 0.89$, $p = 0.007$; Baja: $W = 0.90$, $p = 0.033$; but P. Panama: $W = 0.90$, $p = 0.143$; C. Panama: $W = 0.98$, $p = 0.954$), and the distributions were heteroscedastic (Levene test, $F = 6.1$, $p < 0.001$). For that reason, carbon density values were $\log_{10}(x + 1)$-transformed for the purpose of comparing among areas. Using the log-transformed data, there is a significant difference in mean carbon density across areas (ANOVA, $F = 25$, $p < 0.001$; Figure 4-3). The carbon density from the Galapagos is higher than those of the other areas (Tukey test, $p < 0.001$ for all comparisons with Galapagos, $p > 0.1$ for all other comparisons).

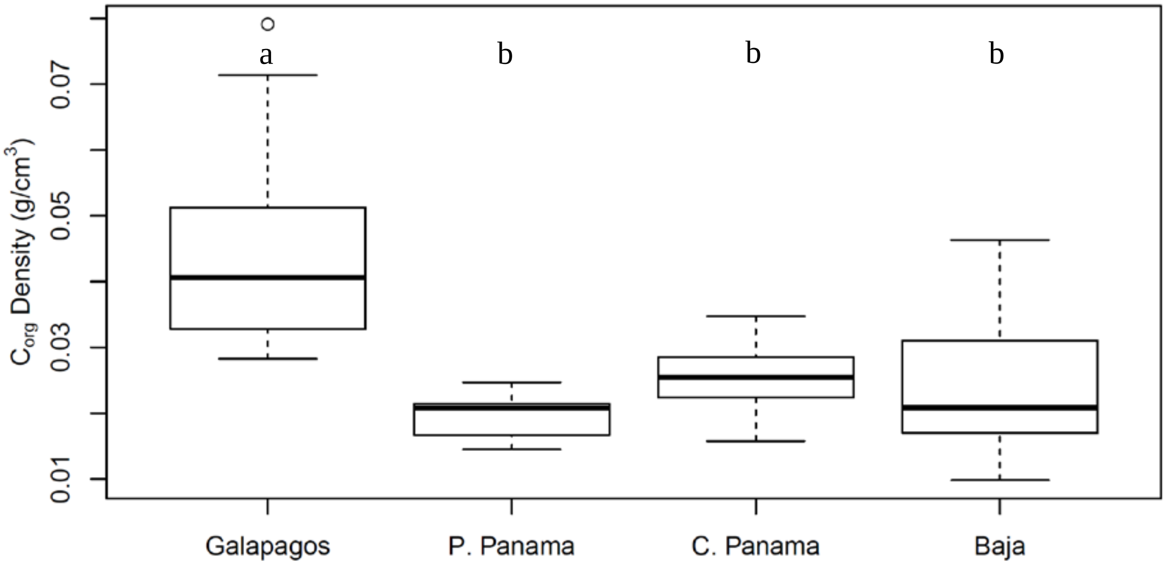

Figure 4-3: Sediment carbon density across the areas sampled is plotted. Boxes mark the median and 1st and 3rd quartiles, and whiskers include all points within 1.5 × the interquartile range. Letters indicate statistically significant *post hoc* comparisons of log-transformed means.

The distribution of sediment depths for each area was right-skewed and not normally distributed (Shapiro-Wilk test; Galapagos: $W = 0.88$, $p = 0.003$; P. Panama: $W = 0.78$, $p = 0.004$;

C. Panama: $W = 0.77$, $p < 0.001$; Baja: $W = 0.92$, $p = 0.087$), and the distributions were heteroscedastic (Levene test, $F = 4.1$, $p = 0.009$). For that reason, sediment depth values were $\log_{10}(x + 1)$-transformed for the purpose of comparing among areas, rendering them normally distributed (Shapiro-Wilk test; Galapagos: $W = 0.94$, P. Panama: $W = 0.93$, C. Panama: $W = 0.96$, Baja: $W = 0.97$; $p > 0.1$ for each), and homoscedastic (Levene test, $F = 1.9$, $p > 0.1$). Using the log-transformed data, there is a significant difference in mean sediment depth across areas (ANOVA, $F = 4.1$, $p = 0.009$; Figure 4-4). The sediment depth from Galapagos is lower than those of the other areas (Tukey test; Galapagos–P. Panama: $p = 0.040$, Galapagos–C. Panama: $p = 0.062$, Galapagos–Baja: $p = 0.036$, all other comparisons: $p > 0.1$).

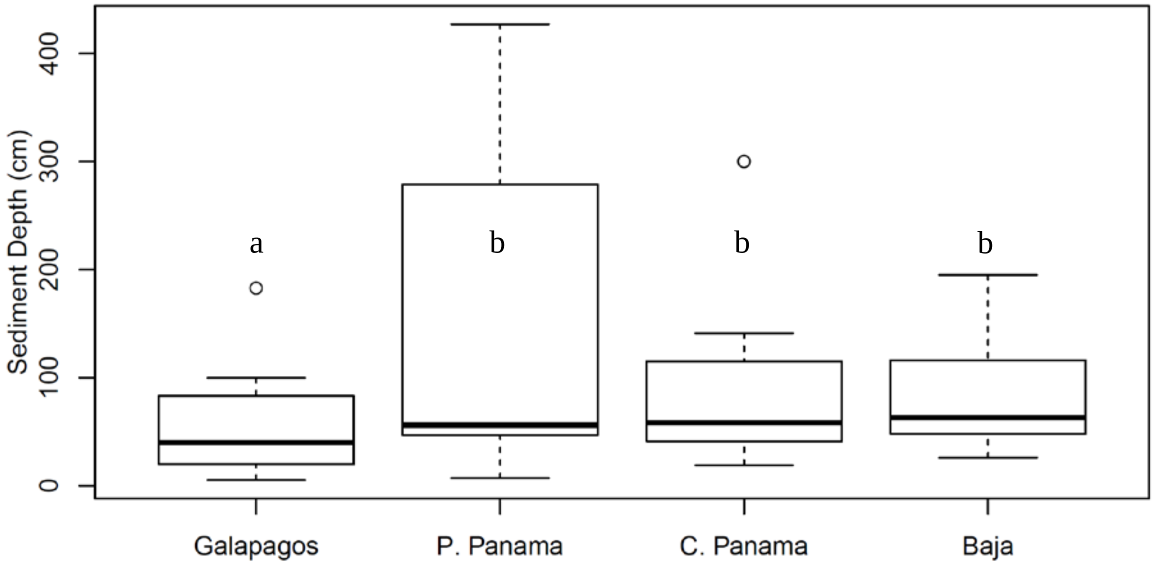

Figure 4-4: Sediment depth across the areas sampled is plotted. Boxes mark the median and 1st and 3rd quartiles, and whiskers include all points within 1.5 × the interquartile range. Letters indicate statistically significant *post hoc* comparisons of log-transformed means.

We hypothesized that sediment carbon density increases with an area's annual rainfall. Using the log-transformed carbon density data, the null hypothesis of no linear relationship with rainfall was rejected, but contrary to our hypothesis, the log-linear relationship is negative rather than positive (linear regression, slope = $-1.50\pm0.49\times10^{-6}$ $\log_{10}(\text{g/cm}^3)/(\text{mm/yr})$, intercept = $1.53\pm0.09\times10^{-2}$ $\log_{10}(\text{g/cm}^3)$, $t = -3.1$, $R^2 = 0.11$, $p = 0.003$; Figure 4-5). We also hypothesized that sediment depth increases with an area's recent rate of RSLR. Using the log-transformed depth data, the null hypothesis of no linear relationship with RSLR was rejected, and the log-linear relationship is positive as hypothesized (linear regression, slope = 0.469 ± 0.138 $\log_{10}(\text{cm})/(\text{mm/year})$, intercept = 1.16 ± 0.18 $\log_{10}(\text{cm})$, $t = 3.4$, $R^2 = 0.13$, $p = 0.001$; Figure 4-6). In addition, to test the hypothesis that sediment depth increases with coastal slope under high rates of RSLR, we tested a linear regression model of log-transformed sediment depth in which the coastal slope factor is nested within the RSLR factor. This model again showed that RSLR is a positive predictor of sediment depth (linear regression, slope = 0.610 ± 0.160 $\log_{10}(\text{cm})/(\text{mm/year})$, intercept = 1.04 ± 0.19 $\log_{10}(\text{cm})$, $t = 3.8$, multiple $R^2 = 0.16$, $p < 0.001$), and it yielded a weaker, negative interaction term between RSLR and coastal slope (slope = -0.559 ± 0.327 $\log_{10}(\text{cm})$, $t = -1.7$, $p = 0.091$). This negative interaction indicates that the effect of coastal slope on sediment depth becomes *less* positive with increasing RSLR, the opposite of what was hypothesized.

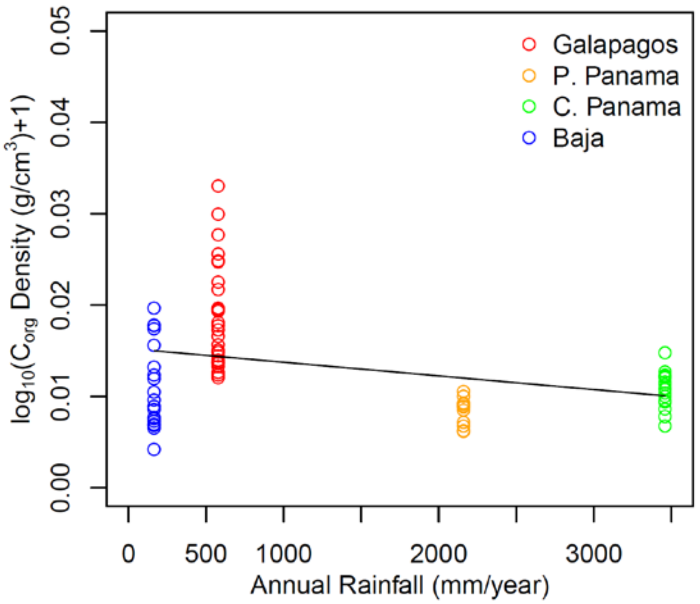

Figure 4-5: Mean, log-transformed sediment carbon density across areas plotted against annual rainfall. The line plotted is a linear regression model of log-transformed carbon density against annual rainfall (linear regression, slope = -1.50±0.49×10^{-6} $\log_{10}$(g/cm^3)/(mm/yr), intercept = 1.53±0.09×10^{-2} $\log_{10}$(g/cm^3), t = -3.1, R^2 = 0.11, p = 0.003).

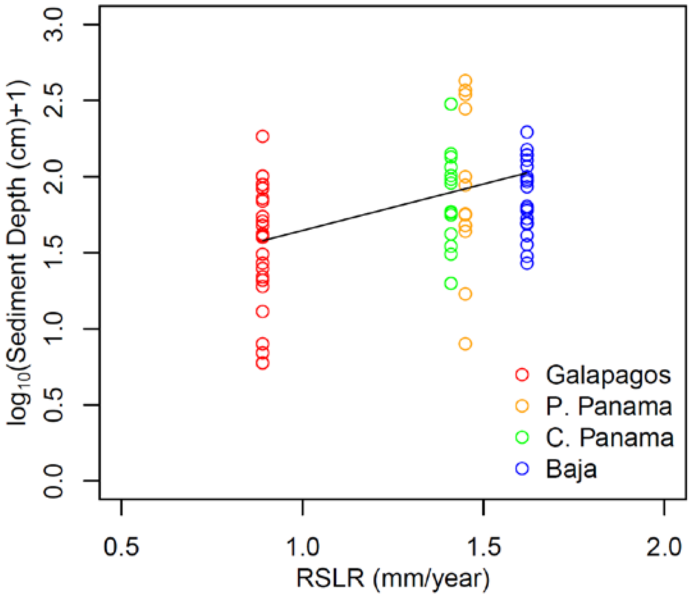

Figure 4-6: Mean, log-transformed sediment depth across areas plotted against recent RSLR rate. The line plotted is the relationship between log-transformed sediment carbon density and annual rainfall in a linear regression model of log-transformed sediment depth with RSLR as a factor and coastal slope nested within RSLR as a second factor (linear regression, slope = 0.610±0.160 $\log_{10}$(cm)/(mm/year), intercept = 1.04±0.19 $\log_{10}$(cm), $t = 3.8$, multiple $R^2 = 0.16$, $p < 0.001$).

Radiocarbon dates were obtained from the bottoms of one core each from 11 sites. For each of those sites, these dates provide estimates of the time before present when mangrove colonization occurred. By dividing the depth from which the sample was taken by that age, the average accumulation rate of sediment at that site was estimated, assuming constant accumulation over time and no vertical compaction over time. Estimated accumulation rates varied significantly across sites, even within sampling areas (Table 4-2). At one site no accumulation rate was inferred as the bottom of the 137 cm deep core was of modern radiocarbon age. Across the other sites accumulation rate ranged from 0.44±0.01 to 2.75±0.12 mm/year.

Table 4-2: Reported here are the radiocarbon age of a sample near the core bottom, the depth of that sample, the inferred accumulation rate, the depth-weighted average sediment carbon density, and the total belowground carbon stock for 11 sites.

Area	**Site Name**	**Latitude (°N)**	**Longitude (°E)**	**Age (years BP)[a]**	**Core Depth (cm)[b]**	**Accumulation Rate (mm/year)[a]**	**C_{org} Density (gC_{org}/cm^3)[c]**	**Belowground C Stock (MgC_{org}/ha)[d]**
Pacific Panama	Golfo de Montijo	7.855364	-81.098322	1541±68	424.5	2.75±0.12	0.024	1027
	Isla del Rey	8.388987	-78.850368	1485±107	96.5	0.70±0.05	0.022	222
Baja Peninsula	El Mérito	24.300967	-110.32678	5263±124	282.5	0.54±0.01	0.030	905
	San Gabriel	24.432316	-110.34722	740±15	56.5	0.76±0.02	0.018	106
	San José B	24.869417	-110.57533	4186±110	182.5	0.44±0.01	0.035	644
	San José A	24.880417	-110.56678	1835±54	116.5	0.63±0.02	0.020	234
	Bahia Magdalena	25.234729	-112.08037	1301±51	127	0.98±0.04	0.030	390
	Santa Barbara	26.698539	-111.87582	571±20	73	1.28±0.45	0.018	137
	Punta Abreojos	26.775105	-113.65858	Modern	137	N.A.	0.010	138
	San Lucas	27.223676	-112.21264	296±76	47.5	1.60±0.44	0.013	65
	Las Ánimas	28.820237	-113.36529	738±17	194	2.63±0.06	0.017	336

[a] Values are reported as the mean and 95% CI.

[b] The depth reported is the midpoint of the depth interval of the sample used for radiocarbon analysis, and is thus slightly higher in the core than the total sediment depth.

[c] Average carbon density for a core is the average of the carbon densities in the samples with depth in each core, weighted by the vertical extent of the sediment horizon from which the sample came.

[d] Total belowground carbon stock is the product of the depth-weighted average carbon density and the total sediment depth of the core.

Discussion

Sediment Carbon Density

Though variation in sediment carbon density is the focus of much blue carbon research, we observed relatively well-constrained densities across sites and areas, with only the Galapagos standing out as possessing significantly greater densities. The significantly greater sediment carbon density in the cores from the Galapagos than other areas is a surprising result given the harshness of the islands' environment for mangrove forest development. Though their equatorial position might suggest the presence of more favorable mangrove habitat, the archipelago features arid conditions near the coast, the complete absence of surface flow of freshwater and sediment from inland, and bare and often wave-exposed rocky shores (Simkin 1984). These inhospitable characteristics of the islands, and presumably their general remoteness, are likely the reasons why the Galapagos have been mostly ignored in the larger mangrove literature (but see Costa et al. 2019 and Moity et al. 2019). Though the lack of riverine flows may partly explain the very patchy distribution of mangroves, with subterranean freshwater flows likely shaping distributions (Costa et al. 2019), this peculiar feature of the islands may help explain the unusually high carbon density in their mangrove sediments. In those specific coastal environments in the Galapagos where, due to physical protection from waves and a potential supply of groundwater, mangroves are able to grow and to develop peat deposits, this organic deposition happens in a setting with no source of inorganic sediment. Well-protected rocky coves with narrow and silled mouths shield mangrove environments from wave energy as well as marine-sourced sediment, and the lack of rivers precludes a source of terrestrial sediment. There are sandy coastal bays on some of the islands that are afforded enough protection from wave energy to be home to mangroves, and the sediment organic matter of these sites is much more diluted with inorganic sediment, resulting in the large variance in carbon densities seen in the Galapagos (Figure 4-3). Similarly, the mangroves of the Baja Peninsula show a large range of carbon densities because these sites range from sandy lagoons with large influxes of marine inorganic sediment to more protected locations, often high in the intertidal, with deep layers of carbon-rich peat, sometimes overlain by surface deposition of fine, clay sediment.

We hypothesized that variation in sediment carbon density across regions would be explained by annual rainfall as a result of climate-driven trends in mangrove productivity (Hutchison et al. 2013, Jardine and Siikamäki 2014). Though a significant log-linear relationship was uncovered, it was of the opposite sign to what was expected (Figure 4-5). Carbon density in mangrove soils decreases across the geographic areas studied with increasing annual rainfall. This result is especially compelling given the fact that the annual rainfall values for the areas included in this study range from some of the driest conditions in which mangroves live (Baja Peninsula, 89–245 mm/year) to highly rainy conditions (Caribbean Panama, 3458 mm/year). Though unequal variance across groups may raise doubts about the exact interpretation of the log-linear model, the data make clear that the expected positive relationship between carbon density and rainfall does not hold true across these geographic areas.

Sediment Depth and Accumulation

Sediment depth varied by two orders of magnitude across sites. A comparison of the sites' log-transformed average sediment depth values across areas shows that the Galapagos' mangroves have significantly shallower sediments than the others. The active volcanism of the Galapagos results in relatively young coasts, actively reforming, leaving less time for sediment accumulation. In addition, the lack of inorganic sedimentation that helps drive up the carbon density in the sediments of these forests also reduces the total volume of sediment available to accumulate. The Pacific Panama sites show an enormous range of sediment depth values, as the mangrove environments here form on both relatively open, steep coasts, with little sediment, and estuaries that receive large quantities of inorganic sediment from tropical rivers. The large variance in sediment depth in this area results in no statistically significant *post hoc* comparison with the Baja Peninsula or Caribbean Panama. The magnitude of that very variance, however, demonstrates the large role that sediment depth has in setting mangrove sediment carbon conditions across sites (Figure 4-4).

Despite the large variation observed across sites, there is a positive relationship across areas between mean sediment depth and the recent rate of RSLR. A linear regression of log-transformed sediment depth against an estimate of each area's RSLR yields a significant positive relationship (Figure 4-6). This result supports the hypothesis that in areas that have experienced significant RSLR, extant mangroves should possess deeper peat deposits, which had allowed them to accommodate that sea-level rise. Several sites from the Baja Peninsula included in this study and examined in more detail in Ezcurra et al. (2016) and Costa et al. (in prep.) typify this phenomenon. However, the negative interaction between RSLR and coastal slope in a linear model of sediment depth implies that the relationship between sediment depth and coastal slope becomes less positive under higher rates of RSLR, contrary to what was hypothesized. This result may be explained by the fact that sites, such as many on the Baja Peninsula, where coastal slope and recent RSLR rates are relatively high are not usually very favorable environments for mangrove forest formation. These conditions may tend to make mangrove forests locally ephemeral, resulting in shallower peat deposits in any given location. Perhaps only a small subset mangrove sites possess characteristics that allow for vertical peat accumulation on steep coastal slopes to accommodate RSLR. Research at several sites in Bahia de La Paz suggests that a surface layer of fine clay sediment, rather than an inorganic fraction dominated by sand, is associated with extensive, old peat deposits (Ezcurra et al. 2016, Costa et al. in prep). To elucidate these patterns, further research is needed on the interaction of coastal geomorphology, sedimentation, sea level, and mangrove ecology.

Regional estimates of the sea-level rise impacts experienced by mangrove forests in the past are useful for forming predictions of how peat formation and other coastal processes respond to environmental change, especially in light of currently accelerating sea-level rise. However, it is unclear to what extent the estimates of RSLR in this study based on individual tide gauges in recent decades are representative of long-term rates experienced by mangroves across these areas (NOAA Center for Operational Oceanographic Products and Services 2018). Especially in the geologically active Galapagos and, to a lesser extent, Baja Peninsula, RSLR rates over the last few millennia may likely vary across the 100s of km within these areas due to fault movements affecting some sites and not others. Local displacement by > 1 m of the intertidal by geological activity has been observed historically in the Galapagos (Simkin 1984). As a result, caution is advised in interpreting sea-level rise history of a particular site based on generalizations made across large areas.

In order to address local-scale variation in mangrove sediment accumulation, we estimated accumulation rates at 11 sites by measuring the radiocarbon age of organic matter from near the base of the sediment core (Table 4-2). These data demonstrate widely variable accumulation rates. Among the sites from the Baja Peninsula, the inferred accumulation rates of 0.76±0.02 at San Gabriel and 0.63±0.02 are similar to the rate of 0.70±0.07 mm/year estimated for other mangrove peats in the region by Ezcurra et al. (2016). The rates inferred at El Mérito of 0.54±0.01 and at San José B of 0.44±0.01 are significantly lower. Furthermore, chapter 2 of this dissertation demonstrates that at El Mérito a lower rate of peat accumulation is obtained using peat dates from throughout the peat deposit than using just the core bottom age. In contrast, the rates at Bahia Magdalena, Santa Barbara, San Lucas, and Las Ánimas, ranging from 0.98±0.04 to 2.63±0.06, significantly exceed that from Ezcurra et al. (2016). The modern age of organic matter all the way down to 137 cm at Punta Abreojos may imply fast enough sedimentation that accumulation rate is not easily captured by radiocarbon dating. This interpretation is supported by the low sediment carbon density of 0.010 gC_{org}/cm^3 at the site, implying significant dilution of organic matter with inorganic sediment. The highest accumulation rate inferred in the study, 2.75±0.12 mm/years, was measured at Pacific Panama's Golfo de Montijo, site of the deepest sediment core in this study (427 cm), with an only moderately old bottom date of 1541±68 years BP. This site, in a large estuary that receives the sediment of several large rivers, is typical of a scenario in which sedimentation is strongly decoupled from sea-level rise trends. Rather, coastal settings in which terrestrial or marine sedimentation are more limited are more appropriate for the use of mangrove peats for investigations of past interaction between sea-level trends and mangrove ecosystem. Once a RSLR-accommodation-linked rate of peat accumulation has been established for a region, deviations from that rate can be used as indicators of average sedimentation dynamics for a site over recent millennia. For instance, the low rates of inferred accumulation at El Mérito and San José B in this study are indicative of these sites' position higher in the intertidal (see Costa et al. in prep.), where elevation dynamics respond less strongly to rising sea level than in the low intertidal (McKee et al. 2007). Higher accumulation rates observed elsewhere indicate sedimentation in excess of that needed for sea-level accommodation, associated with rapid sediment redistribution in dynamic coastal lagoon systems (Thom 1967) or general intertidal progradation (Woodroffe et al. 1985).

Total Belowground Carbon Stock

Total belowground carbon stocks varied by a factor of 100 in this study, from 17 MgC_{org}/ha at a site in the Galapagos with sediment only 7 cm deep to 1730 MgC_{org}/ha at a site in Caribbean Panama whose sediment reached 300 cm deep. The very large range in sediment depths both within and across regions drives the variation in carbon stocks calculated (Table 4-1). With the exception of the Galapagos, with a mean carbon density less than double those of the other areas, sediment carbon density was similar across areas. Sediment depth varied widely, however, playing a larger role in determining carbon stock patterns. For instance, though the Galapagos has the highest carbon density of the areas included in the study, its carbon stock values are among the lowest. Costa et al. (2019) demonstrated that inter-site variation in sediment depth dominates the spatial distribution of carbon stocks within the Galapagos, and the results of this study support the broader relevance of this hypothesis. The coefficient of variation (standard deviation / mean) of sediment carbon density is less than that of sediment depth, both across all sites in the study and within each area (Table 4-3). As total belowground carbon stock equals depth-integrated sediment carbon density (i.e., the product of the vertical-extent-weighted average of carbon density and the depth of the sediment column), the greater variation in sediment depth than carbon density means that sediment depth explains most of the variation in total carbon stock.

Table 4-3: The coefficient of variation (CV, equal to standard deviation / mean) of depth-averaged sediment organic carbon density (g/cm^3) and sediment depth (cm) across sites in the four areas studied, and across all sites.

Study Area	**CV of Sediment Carbon Density**	**CV of Sediment Depth**
Galapagos	0.31	0.80
Pacific Panama	0.17	1.1
Caribbean Panama	0.19	0.88
Baja Peninsula	0.42	0.56
All Sites	*0.45*	*1.0*

The Role of Sediment Depth for Blue Carbon

The results of this study highlight the importance of sediment depth in shaping belowground carbon stock in mangroves. Though interesting patterns in sediment carbon density were observed, the large variation in carbon stock values obtained are due mainly to variation in sediment depth. Thus, to characterize mangrove sedimentary carbon stocks accurately, both sediment depth and carbon density with depth must be measured. In many sites, the bulk of the carbon stock is missed by only measuring the top 50 or 100 cm of sediment. Though protocols state the importance of measuring mangrove sediment at depths beyond 1 meter (Kauffman and Donato 2012), it is common for field studies not to consider sediment deeper than 1 meter (Alongi et al. 2004) and for major syntheses of blue carbon data to assume 1 meter of sediment depth and to attempt to model sediment carbon stock as a function of carbon density (Pendleton et al. 2012, Holmquist et al. 2018). Working within the assumption of one meter of sediment in blue carbon ecosystems is justified as being conservative, or necessary for comparison across studies and regions. We argue, however, that ignoring the major source of variation in carbon stock and focusing on the more constrained range of values of carbon density will not bring research efforts any closer to understanding patterns and processes in mangrove carbon in the real world. Ironically, measurements of sediment depth, as they are gathered completely in the field, are easier to obtain in most situations than measurements of carbon density, which require additional laboratory equipment and analysis. The repeatability, narrower range of values, and perceived rigor of laboratory-based estimates of sediment carbon density may have made them attractive to academic researchers producing the first wave of blue carbon publications over the last decade. Recognition of the dominant role of sediment depth in shaping carbon stocks, however, will make it possible to leverage field measurements as much as possible for the characterization of mangrove ecosystems. Especially given the distribution of mangroves mainly in developing countries (Giri et al. 2011), where access to specialized laboratory equipment is likely to be limited, taking this approach can help meet the challenge of increasing sampling of mangrove sediments globally.

It has been hypothesized that carbon deeper than one meter is sufficiently buried such that it is invulnerable to human disturbance and thus can be ignored by research with a management focus. Even if it is asserted that only the top meter of sediment is relevant for study, much variation in sediment depth occurs within the top meter. The average sediment depth of 43% of the sites in this study is < 50 cm, and that of 76% < 100 cm. For this reason, assuming a constant meter of sediment and modelling carbon density within that constraint misses important variation in depth and thus actual depth-integrated carbon stock. In any case, the assumption that carbon from deeper than 1 m is decoupled from human impacts on the surface is imprudent. The loss of primarily surface carbon from cleared mangroves has been observed, but processes of carbon loss resulting from clearing are ambiguously understood and take place over many years after disturbance (Granek and Ruttenberg 2008). Moreover, losses of carbon due to mangrove clearing from much deeper than 1 meter have been documented (Kauffman et al. 2016). Thus, assuming that carbon deeper than 1 meter in mangrove sediments is no longer affected by surface ecological changes fails to apply the precautionary principle to our management of these systems given our uncertain understanding of the fate of buried carbon under environmental change. Further application of a paleoecological approach will stimulate progress in blue carbon research, as the study of responses of these ecosystems to past environmental fluctuations allows for better predictions of their behavior under anthropogenic global change (Ellison 1993, McKee et al. 2007, Seddon et al. 2011). The variation even within relatively local areas in accumulation rates inferred in this study indicates that more cores and paleo-reconstructions are justified to characterize past sedimentation and mangrove ecosystem development processes. Important objectives of future paleoecological research of relevance to blue carbon include measuring the contribution of specific mangrove taxa across intertidal zonation to the bulk carbon composition of the sediment column and tracking the fate of buried mangrove peat after the overlying forest subsides to RSLR.

As mangrove leaves are abundantly produced and shed, forming leaf litter on the forest floor, a flurry of studies has accumulated in the last ten years that estimate mangrove carbon productivity, sequestration, and storage in near-surface sediments. And just as only a very small fraction of surface production in mangroves reaches down into the long-term sediment pool, relatively few blue carbon studies have penetrated the ecological and geological processes that drive the formation and longevity of deep, old mangrove carbon pools. Future work should explore, rather than eschew, the variation in mangrove sediment depth from the local to regional scales and incorporate it into models of carbon distribution. Understanding where blue carbon is distributed, however, will only be useful for managing these ecosystems' carbon fluxes if it is combined with knowledge of how those carbon distributions respond to natural and anthropogenic interventions. This mechanistic understanding of mangrove carbon fluxes should be sought both from examination of past changes in these systems through paleo-reconstruction and through long-term, integrative ecosystem monitoring of mangroves as they undergo diverse human impact, conservation, and restoration trajectories into the future.

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CHAPTER 5

Conclusions and future directions

The research presented in this dissertation measures belowground mangrove carbon stocks across three spatial scales: with depth in the sediment, on varying coastal landscapes, and across the northern New World tropics and subtropics. The information presented here provides insight into the processes that form and preserve peat deposits in mangrove sediments and the factors that shape the distribution of these carbon stores across a range of environments. In chapter 2 we showed that carbon density does not decline with depth and age even in 5,000-year-old peat deposits, though there is a slight loss of nitrogen. Microbial cycling of nitrogen derived from peat material gradually discriminates in favor of the heavier isotope, causing a positive correlation between $\delta^{15}N$ and peat age. For the first time, sediment microbial community composition was assessed across depth profiles in deep peat deposits, with community composition with sediment type and depth and the diversity of microbial taxa decreasing with peat age. In chapter 3, the first study of mangrove blue carbon in the Galapagos islands, we demonstrated the over an order of magnitude variation across sites along the coasts of this rocky archipelago. Site carbon stock was predicted neither by lava *versus* soil substrate along the coast nor by the direction toward which sites were exposed to open water and thus wave energy. However, variance of carbon stocks was greater among lava sites than sites with more developed soils, suggesting greater spatial heterogeneity of conditions favorable to mangrove biomass production and retention on geologically younger coasts. Chapter 4 brought together cores from 80 sites from the Galapagos, the Pacific and Caribbean coasts of Panama, and the Baja Peninsula to conduct a regional comparison of the drivers of mangrove sediment carbon density and depth. Carbon density variation did not conform to the predicted positive relationship with annual rainfall supported by the literature, with the semi-arid Galapagos having the highest average densities. Sediment depth increased with RSLR, as hypothesized, but the relationship between sediment depth and coastal slope became less positive with increasing RSLR, contrary to our hypothesis. Carbon accumulation rates are inferred using core radiocarbon dating at 11 sites, yielding vertical accretion rates ranging from slightly lower to considerably greater than late Holocene SLR.

The deep coring and high resolution radiocarbon sampling with depth in the study of sites in Baja California Sur presented in chapter 2 illustrate a pattern of peat production that has important implications for the measurement of these sediments for blue carbon accounting. We observed that actively forming peat deposits at San José feature a layer of organic sediment of modern age from the surface down to 45 cm at one site and to 85 cm at another. This pattern indicates that active root growth contributes new carbon to a zone as deep as 85 cm, with vertical mixing of sediment in this range likely caused by invertebrate burrowing near the surface and root growth farther down. Beneath this zone, peat age increases with depth, indicating the beginning of actual long-term carbon deposition. This division of the sediment column into an active root growth zone and a peat deposit zone has important implications for the measurement of blue carbon sequestration and storage. For instance, estimating a carbon sequestration rate by measuring carbon density from the surface downward and applying an accretion rate based on ^{137}Cs or ^{210}Pb decay, which capture sedimentation but not belowground root turnover, can lead to inaccurate results. With the understanding that root detritus is the main contributor of long-stored carbon, the place that accretion measurements should begin is at the bottom of the active root zone. From this point downward, radiocarbon and other radioisotope estimates should both yield similar accumulation rates with depth, as at this depth no root growth or bioturbation can interfere with the vertical sediment record. The carbon density of this aging material with depth divided by that deep accumulation rate would allow the estimation of the accumulation of peat carbon over time.

In addition to providing information to improve blue carbon assessment protocols, the distinction between root growth and peat formation zones in mangrove sediments sheds light on the ecosystem process that allows mangroves to function as long-term net carbon sinks. In chapter 1, I introduced the apparent contradiction between the model of asymptotic biomass accumulation over the course of ecosystem development presented by Odum and the long-term roughly linear net influx of carbon into blue carbon ecosystems (1969). A resolution to this dilemma can be formulated if the interface between the active root growth zone and the deeper peat deposit is recognized as one of the boundaries of the mangrove system. Fluxes of all kinds are commonplace across ecosystem boundaries (Polis et al. 1997), and their delineation is inevitably somewhat arbitrary. Still, the distinction made in this case is based in biological reality in that the roots of living mangrove trees do not, by definition, reach into the peat accumulation zone; burrowing invertebrates are generally inconspicuous, if not completely absent, beyond the top 10 cm of mangrove sediment (personal observation); and, as shown from the molecular results in chapter 2, there is a distinctive community of microbes associated with deep peat. If this belowground boundary of mangrove ecosystems is included in a theoretical carbon budget, then these forests can retain constant biomass at maturity. The net positive carbon imbalance is in fact exported through the bottom of the system. The underlying peat deposit ecosystem, through the import of detritus, increases its total carbon stock over time, not by increasing the density of biomass as in a developing forest, but by expanding its volume upward. The boundary between mangrove and peat ecosystems moves upward over geologic time, as mangrove elevation increases due to deep and surface accretion processes linked by negative feedbacks with sea level (McKee et al. 2007). Thus, peat deposits underlying coastal wetlands expand linearly with sea level. Of course, the ecological and geomorphic feedbacks that maintain this linear relationship likely only function under moderate rates of RSLR. Research aiming to estimate critical RSLR rates beyond which mangroves cannot accommodate has not approached consensus, though the coming decades will likely bring rates significantly faster than any experienced since the early Holocene, the time period during which all known mangrove peats have been formed (Cahoon and Lynch 1997, Twilley et al. 1998, Mckee et al. 2007). Thus, mangrove peats and their status as long-term net carbon sinks appears to have depended on Holocene sea-level rise. To know whether they can survive Anthropocene sea-level rise, further research on the ecological, oceanographic, and geological processes that govern the passage of carbon from the root zones of mangrove forests into underlying deposits is necessary.

In addition to conducting in-depth investigations of the belowground processes driving peat formation, there is considerable value in further measurements of the variation in the spatial distributions of these deposits. The results of chapters 3 and 4 demonstrate the wide-ranging variation in carbon stocks, shaped largely by variation in the vertical extents of peat deposits, that exists across local and regional scales. The field is however currently limited by the availability of tools for efficiently sampling with enough spatial coverage to describe the hidden world of mangrove sediments in detail. Coring mangrove sediments is time-consuming and laborious and requires trekking through flooded, muddy, and often impenetrable thickets of trees at remote sites. Analysis of hundreds of sediment samples distributed with depth across many cores is even more time consuming. Intensive coring across a mangrove landscape is also destructive to the sediment and to the plants trampled and damaged while transiting between sampling sites. As a result, attaining sufficient spatial resolution to characterize mangrove sedimentary landscapes would be aided by the availability of more tools than sediment coring. Ground-penetrating radar or transient electromagnetic resistivity systems (d'Ozouville et al. 2008), particularly versions that have been adapted to mangrove environments and designed to be remotely operated, combined with the collection of a limited number of ground truth cores at each site, would revolutionize belowground observations in these ecosystems.

To model the distribution of mangrove carbon on yet larger scales, other research questions must be addressed. This study examined the relatively species-poor mangroves of the New World. It remains to be seen whether mangrove species zonation or diversity affect carbon stock distributions across bioregions. Though some evidence suggests that mangrove sediment biogeochemical processes are related more to edaphic conditions than to local tree species (Alongi et al. 1993), other work suggests a role in peat formation of some taxa that is disproportionate to their aboveground abundance (Ezcurra et al. 2016). In addition to species effects, more work on the role of local coastal geomorphological variables in setting sediment carbon density will provide valuable information (Twilley et al. 2018). As chapter 4 of this dissertation demonstrates, extending this research to consider variation in sediment depth explicitly can bring the field much further toward mechanistically-driven and realistic models of carbon stock distributions globally.

Despite systematic ecological study extending back more than a century (Bowman 1917), many basic scientific questions remain to be addressed in mangrove ecosystems, especially in the belowground worlds beneath them. The objectives of the blue carbon field extend beyond basic science, however, given the urgent need to utilize this science to protect and to restore coastal carbon sequestration and storage capacity. Ecosystem data can be compiled and converted into ecosystem service valuations that provide explicit economic justification for the argument in favor of sustainable ecosystem management over destructive exploitation (Costanza et al. 1997). For example, the results of the Galapagos blue carbon study presented in chapter 3 were also used in another publication in which colleagues and I included carbon storage, fisheries provision, and eco-tourism in a combined ecosystem service estimate for the archipelago's mangroves (Tanner et al. 2019). For this information to be used, however, publication is just the beginning. Effort must be put into addressing results of carbon research to stakeholders, such as local land owners and managers, and translating them into forms that they can share and use on the ground (Costa et al. 2015). Targeted information campaigns can be directed toward the goal of including blue carbon considerations into broader sustainability policy objectives. And education at all levels of society can create awareness of and demand for the management of coastal environments to maximize their ecosystem service value. These activities are well beyond the mindset and skillset obtained from conventional scientific training, requiring natural scientists who want to advance the goals of sustainability and conservation to work with teams of social scientists, dataset managers, communications specialists, educators, and policy experts. Rather than a dilution of scientific effort, these interactions can stimulate productive inquiry by directing research questions toward areas of practical need, which are likely the same areas that have yet to be adequately addressed by science.

While providing pointed motivation, the enormity of the challenges faced by mangroves and other natural ecosystems worldwide (Valiela et al. 2001), can impart an impression of futility on research efforts aimed at science-based, sustainable management. Ecological anxiety can be balanced by the recognition, unavoidable when spending time in the field, that natural places yet hold far more mysteries than have ever been explained by even the most careful study. This work has shown the value of direct observations of the invisible world below mangrove forests, revealing landscapes of peat variation that vary spatially and incorporate the vertical dimension of time over the course of ecosystem development. This perspective allows us both to probe the histories of these dynamic coastal environments and to apply understanding of these systems to their sustainable management into the future.

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