Vascular-Plant Detritus Is a Globally Significant Contributor to Marine Carbon Fluxes and Sinks

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Abstract

More than two-thirds of global biomass consists of vascular plants. A portion of the detritus they generate is carried into the oceans from land and highly productive blue-carbon ecosystems—salt marshes, mangrove forests, and seagrass meadows. This large detrital input receives scant attention in current models of the global carbon cycle, though for blue-carbon ecosystems, increasingly well-constrained estimates of biomass, productivity, and carbon fluxes, reviewed in this article, are now available. We show that the fate of this detritus differs markedly from that of

strictly marine origin, because the former contains lignocellulose, an energy-rich polymer complex of cellulose, hemicelluloses, and lignin that is resistant to enzymatic breakdown. This complex can be depolymerized for nutritional purposes by specialized marine prokaryotes, fungi, protists, and invertebrates using enzymes such as glycoside hydrolases and lytic polysaccharide monooxygenases to release sugar monomers. The lignin component, however, is less readily depolymerized, and detritus therefore becomes lignin enriched, particularly in anoxic sediments, and forms a major carbon sink in blue-carbon ecosystems. Eventual lignin breakdown releases a wide variety of small molecules that may contribute significantly to the oceanic pool of recalcitrant dissolved organic carbon. Marine carbon fluxes and sinks dependent on lignocellulosic detritus are important ecosystem services that are vulnerable to human interventions. These services must be considered when protecting blue-carbon ecosystems and planning initiatives aimed at mitigating anthropogenic carbon emissions.

1. INTRODUCTION

Vascular plants constitute more than two-thirds of global biomass (Bar-On et al. 2018), predominantly on land but also in highly productive blue-carbon ecosystems—salt marshes, mangrove forests, and seagrass meadows. Detritus from vascular-plant detritus originates mainly from eudicots and conifers on land, commelinid monocots (particularly Poales) and eudicot herbs in salt marshes, eudicot trees and palms (commelinids) in mangroves, and alismatid monocots in seagrass meadows. Freshwater catchments gather, store, and transport this detritus, with a portion entering the sea, while salt marshes, mangroves, and seagrass meadows generate, store and exchange detritus with the coastal ocean. Dissolved organic carbon (DOC) is also exported from terrestrial and coastal ecosystems, with mangrove forests alone contributing 10% of coastal output of recalcitrant DOC from land (Dittmar et al. 2006). Water-borne transport of detritus and DOC originating from vascular plants is the means by which land-to-sea transfer of organic carbon occurs, driving production and carbon storage on continental shelves, which are disproportionately important in ocean carbon budgets (Bauer et al. 2013). However, the details of this transfer are generally overlooked in current models of the global carbon cycle, while the quantities involved are probably underestimated (Duarte 2017, Kirschbaum et al. 2019). The carbon storage capacities of salt marshes, mangrove forests, and seagrass meadows have led to them being termed blue-carbon ecosystems.

In the marine context, vascular-plant detritus is considered to be particulate organic carbon (POC), though detrital particles are generally larger than particles normally considered in models of marine carbon fluxes, such as whole tree trunks. Unlike all other forms of marine particulate organic matter, vascular-plant detritus is characterized by tough, woody tissues formed from lignocellulose—a complex of crystalline cellulose coated with branching hemicellulose and encrusting, amorphous lignin. This complex is rich in sugar monomers but is resistant (recalcitrant) to enzymatic degradation, so only a limited range of organisms have evolved the ability to achieve depolymerization (Cragg et al. 2015). Recalcitrance is rarely considered when marine detrital food chains are described but is a characteristic of vascular-plant detritus, which differentiates it from detritus originating from primary production in the water column. Consequently, there are distinct consortia of detritivores and saprobes that exploit vascular-plant detritus, particularly highly lignified detritus.

Above the reach of regular tidal inundation, soil bacteria, decay fungi, termites, and beetles degrade wood from terrestrial and mangrove sources. At a tidally determined boundary, marine organisms take over—wood-boring crustaceans, teredinid bivalves, ascomycetes, protists, and prokaryotes. Salt-marsh vegetation, mangrove leaves, and seagrasses are lignified to a lesser extent than wood, allowing a wider range of invertebrates to exploit detritus from these sources. Detritivores release undigested material into the pools of DOC and POC that are eventually mineralized by bacteria. POC enters the rhizosphere of blue-carbon ecosystems, while roots die in situ, contributing further to the accumulation of necromass, which accounts for the exceptional capacity of these ecosystems to sequester carbon (Macreadie et al. 2017, Robertson & Alongi 2016, Trevathan-Tackett et al. 2017a).

The blue-carbon concept has gained increasing traction with stakeholders, coastal-zone managers, and policy makers, whose thinking is informed (or should be) by the developing but incomplete understanding of the processes involved in carbon fluxes. This review sets out to evaluate the information required for modeling the role of vascular plant detritus in the coastal ocean and to highlight gaps in our understanding of the processes involved.

2. FLUXES AND SINKS OF LIGNOCELLULOSE-DERIVED CARBON

2.1. Terrestrial Runoff Inputs

Huge quantities of lignocellulose are stored in vascular land plants, which represent a large proportion of the estimated 450 Gt C of global plant biomass (Bar-On et al. 2018). Vascular-plant biomass that is not consumed by herbivores or harvested becomes detritus and, together with detritus-derived soil organic matter mobilized by erosion, may become subject to water-borne transport. Globally, approximately 0.5 Pg C is carried into estuaries each year, with half being DOC and half POC. An additional 0.23 Pg of DOC is transported in submarine groundwater discharge (Zhang & Mandal 2012). Data had previously suggested that terrestrial organic matter contributes a small fraction to marine DOC, but recent work has shown that photochemical alterations of terrestrial DOC in rivers and seawater transform refractory lignin into previously overlooked smaller hydrophilic components that accumulate in the ocean (Medeiros et al. 2016). In addition, delta and shelf sediments bury 30–35% of the terrestrial organic carbon delivered by rivers, which is less efficiently remineralized than ocean-derived organic carbon (Kandasamy & Nath 2016). Shelves are dynamic interfaces where terrestrial, estuarine, and marine organic carbon is recycled, buried, and respired (Bauer et al. 2013). Estimates of land-derived organic carbon are poorly constrained, partly because rare events are not well modeled. For example, large cyclone-induced floods are estimated to export 77–92% of POC eroded from a mountainous catchment (Hilton et al. 2008), while 40% of average annual riverine DOC export may derive from one tropical storm (Bauer et al. 2013). The tsunami that swept the eastern coast of Japan in 2011 redistributed colossal amounts of large woody debris (Carlton et al. 2017).

2.2. Fluxes and Sinks Into, Between, and Out of Vascular-Plant-Dominated Coastal Ecosystems

Mangroves can simultaneously import and export lignocellulose-derived carbon to adjacent ecosystems (Dittmar et al. 2006), sustaining coastal productivity (Lee 1995). Forest type affects the balance between import and export, partly through the agency of detritivores and saprobes (Adame & Lovelock 2011). Large woody detritus breaks down over years on the forest surface, while leaves are rapidly processed (see Section 7.2). The root architecture of mangroves such as *Rhizophora* reduces water flow rates and helps retain particulate organic matter. Crabs further transfer leaves (up to 80% of litterfall) into their burrows. These effects plus the high

belowground productivity and short life span of fine roots coupled with the long residence time of dead roots (Robertson & Alongi 2016) account for the remarkable carbon storage capacity of mangrove sediments (Donato et al. 2011). In global terms, geomorphological setting, hydrology, precipitation, and temperature affect litter export to the coastal ocean (Adame & Lovelock 2011). These are also key factors in determining the high but highly variable capacity of mangrove soils to store carbon (Twilley et al. 2018).

Odum (1968) established the outwelling theory, which was used to explain unusually high secondary production in coastal water adjacent to salt marshes. The main carbon transfer from marshes is DOC released from vegetation, detritus, and detrital POC (Hyndes et al. 2014). DOC is exported more than POC, as marsh height in the intertidal zone restricts export of POC, which, if exported, is buried in estuarine sediments, where it constitutes a significant fraction of detrital carbon (Hyndes et al. 2014).

Seagrass meadows are a highly productive sink and source for inorganic and organic carbon. Because they can slow down water, they trap significant amounts of POC (Gillis et al. 2014b), which is remineralized within the system (Duarte & Kraus-Jensen 2017). Carbon stocks accumulate within the sediment, especially in shallower seagrass beds, due to the refractory nature of some seagrass detritus, which can accumulate in thick layers called matte that may contain material hundreds or even thousands of years old (Kaal et al. 2016). In addition, seagrass meadows are a habitat for a great diversity of organisms, from shrimp, which bury leaf litter, to fish species, which export lignin-derived carbon (Duarte 2017). Seagrass derived POC can also be important as an export (representing 24% of the net primary production of seagrasses), which is directed by local hydrodynamics in the seascape (Bouillon & Connolly 2009).

Globally, blue-carbon ecosystems have an organic carbon burial capacity comparable to that of terrestrial forests even though they occupy an area two orders of magnitude smaller (Lovelock et al. 2017, McLeod et al. 2011), but their degradation adds significantly to global CO_2 emissions (Pendleton et al. 2012) while reducing future capacity to mitigate emissions due to oxidation of sediment carbon stocks (Lovelock et al. 2017). Reducing land-use change is an important component of global strategies to curb CO_2 emissions.

2.3. Dissolved Organic Carbon in the Water Column

DOC derived from vascular plants contributes to the huge oceanic reservoir of DOC (662 Gt C), in which labile molecules dominate surface waters and recalcitrant molecules accumulate in deep

waters (Zigah et al. 2017). Lignin concentration varies across different oceans: The percentages of lignin phenols in dissolved organic matter decrease from the Arctic to the Atlantic to the Pacific, reflecting an increasing terrigenous dissolved organic matter diagenesis (Hernes & Benner 2006). The residence time of lignin phenols can vary from days (due to photooxidation to long-lived products) (Bauer et al. 2013) to centuries in deep waters in the North Pacific (Hernes & Benner 2006, Opsahl & Benner 1998). In the deep ocean, DOC utilization is limited by the diversity and dilute nature of the substrate (Arrieta et al. 2015), which limits the efficacy of enzymatic processes of bacterial surface-borne enzymes (Traving et al. 2015). The microbial carbon pump transfers organic carbon from labile to recalcitrant states through microbial transformation and production of DOC (Jiao et al. 2011). The microbial carbon pump may also act as a conveyer belt that transports and stores carbon in the deep oceans, where bacteria adapted to high-pressure environments may have a special capacity to degrade refractory DOC (Jiao et al. 2010). DOC is eventually recycled via various carbonate ions and dissolved CO_2.

2.4. An Overall Model of the Role of Lignocellulosic Carbon in the Marine Portion of the Global Carbon Budget

The inputs of lignocellulose-derived material into coastal oceans and shelves involve several routes as well as connecting fluxes between ecosystems (**Figure 1**). Seascape ecosystems such as salt marshes, mangrove forests, and seagrass meadows exchange lignin-derived material with each other and the coastal oceans (Gillis et al. 2014a, Hyndes et al. 2014). The coastal oceans and the shelf system are closely connected, and inputs from inland waters, rivers, and estuaries export carbon across the shelf to the coastal oceans.

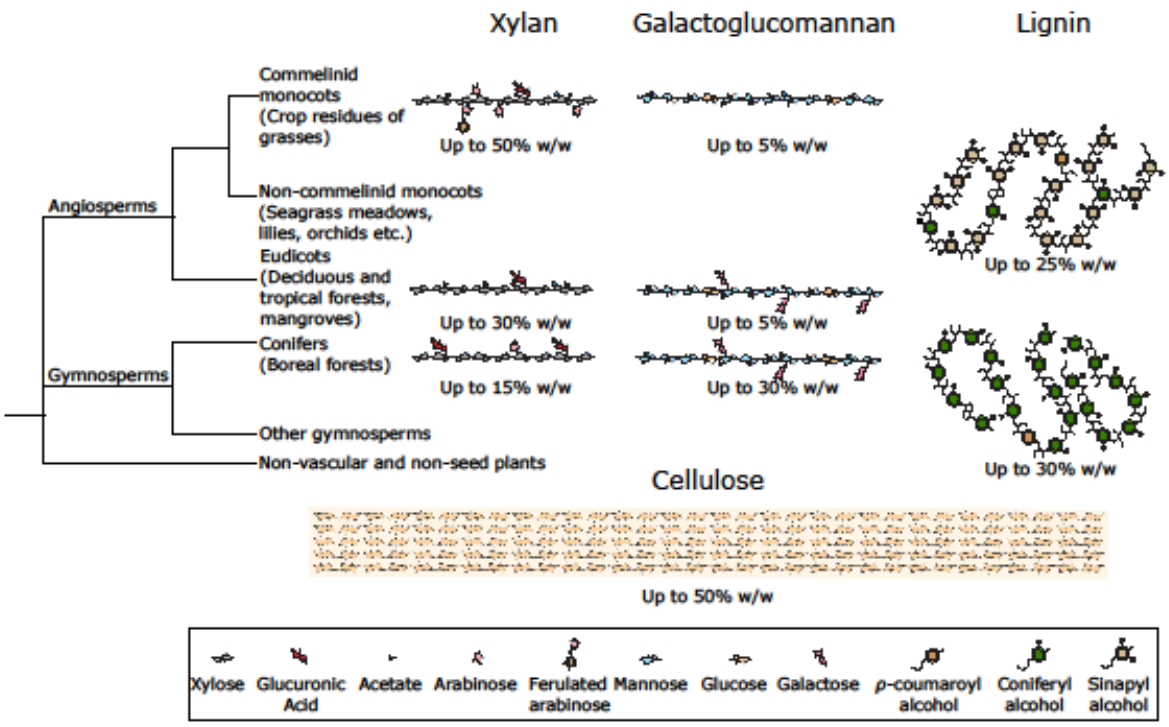

Figure 1 Simplified diagram of input from different vascular-plant reservoirs into shelf waters, shelf sediment, and the coastal oceans. The numbers represent fluxes of carbon (in Pg C y^{-1}) between different ecosystems and other reservoirs (*green*), with arrows indicating the direction of each flux. The short vertical arrows pointing into the blue-carbon ecosystems indicate carbon entering the sediment sink in those ecosystems. Abbreviations: DOC, dissolved organic carbon; OC, organic carbon; POC, particulate organic carbon; TC, total carbon.

Quantifying the exchange of lignocellulose-derived material among blue-carbon ecosystems, terrestrial reservoirs, and the coastal ocean on a global scale is a challenge. Stable isotopes have been used to determine the fate of organic carbon within organic matter; tracers such as lignin-derived phenols or ratios of POC to chlorophyll *a* should also be utilized (Bouillon et al. 2008, Gillis et al. 2014a). Ecosystems and the coastal ocean export and import material, creating difficulties in tracing DOC and POC sources. Assessment of export and accumulation rates is hampered by methodological difficulties and the extreme heterogeneity of the continental margins, which have hot spots in some places for the burial of carbon from vascular plants but in other places for the oxidation of POC (Bianchi et al. 2018). Even with the broad range of types of coastal environments in the studies reviewed by Bianchi et al. (2018), there is the challenge of extrapolating from local studies to accurate global models. Nonetheless, globally, the blue-

carbon ecosystems may export greater amounts of carbon than rivers (0.24–0.42 versus 0.03–0.4 Pg C y^{-1}), primarily because seagrass-bed ecosystems dominate total carbon export (0.2–0.4 Pg C y^{-1}). Furthermore, these ecosystems act as strong sinks for POC. Estuaries absorb and process the majority of carbon flowing into them for inland waters (0.9–1 Pg C y^{-1}). Inland waters export six times as much carbon to sediments as they do to estuaries (0.6 versus 0.1 Pg C y^{-1}) (**Figure 1**).

Blue-carbon ecosystems are important components of pathways leading to carbon sequestration but are particularly vulnerable to anthropogenic changes in coastal regions. Models of their role in carbon fluxes need to be better constrained by an improved understanding of the pathways followed by lignocellulosic breakdown products and by more comprehensive data sets of flux and sink measurements.

3. BIOMASS AND PRODUCTIVITY IN BLUE-CARBON ECOSYSTEMS

Vegetated coastal habitats are generally highly productive. Global estimates of net primary production range from 438 to 1,100 g C m^{-2} y^{-1} for salt marshes, from 394 to 1,000 g C m^{-2} y^{-1} for mangroves, and from 394 to 449 g C m^{-2} y^{-1} for seagrasses (Duarte 2017).

Salt marshes have a global distribution and are most abundant in mid-to-high latitudes on sheltered shores. The latest global estimate of salt-marsh areal cover is 55,000 km^2 (Mcowen et al. 2017), though this is likely to be a severe underestimate due to our poor knowledge of tropical salt-marsh distribution. Salt marshes have a low canopy formed by vascular plants, including grasses (commelinids), eudicot herbs, and low shrubs, with much of their biomass formed by rhizomes and roots. Dead material (necromass) may be retained on standing plants before mobile detritus is formed (Tripathee & Schafer 2015) (**Figure 2*a–c***), with tidal regime being a determining factor for necromass accumulation; in the high intertidal zone, the necromass may exceed biomass for most of the year (Montemayor et al. 2015).

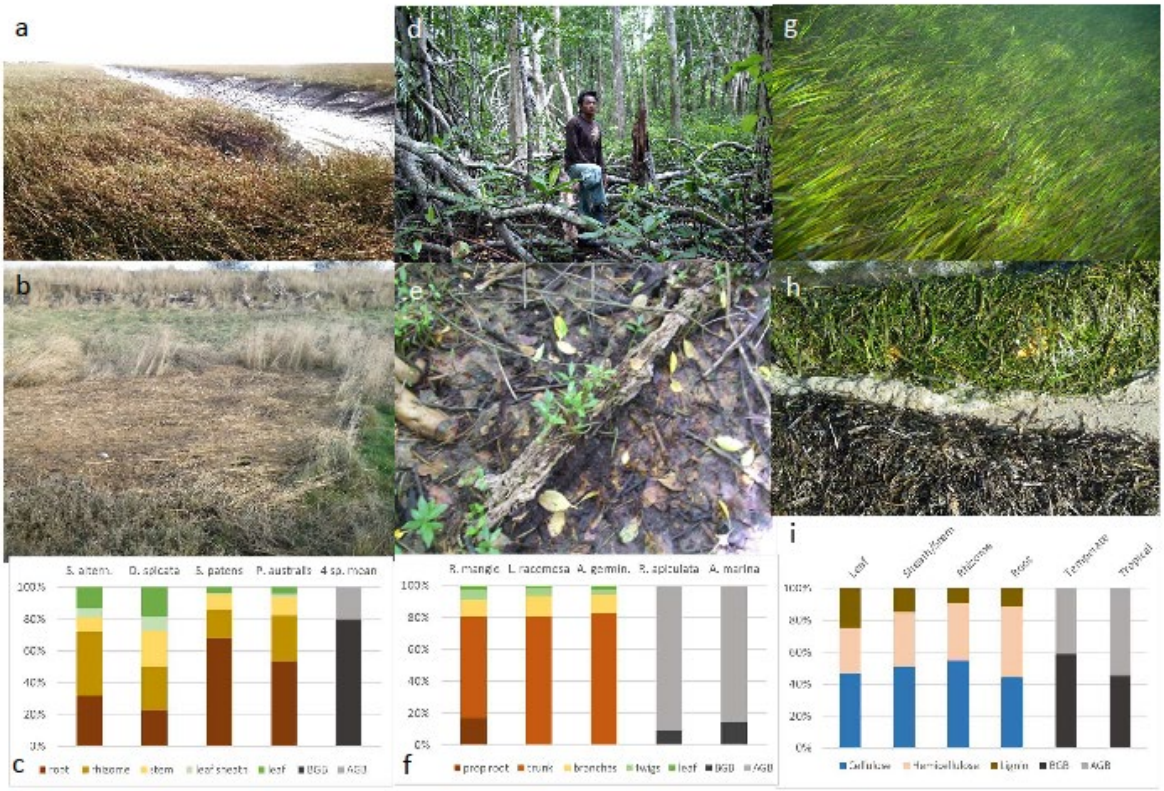

Figure 2 Biomass, necromass, and biomass partitioning in blue-carbon ecosystems: salt marshes (*left*, panels *a–c*), mangroves (*center*, panels *d–f*), and seagrass meadows (*right*, panels *g–i*). (*a*) *Spartina anglica*–dominated salt marsh and creek at Welwick near Hull, United Kingdom. Photo courtesy of Daniel Leadbeater. (*b*) Phytodetritus in the Welwick salt marsh. Photo courtesy of Daniel Leadbeater. (*c*) Biomass partitioning in four salt-marsh plants (*Spartina alterniflora*, *Distichlis spicata*, *Spartina patens*, and *Phragmites australis*) and their above- and belowground biomass proportions in the Hudson–Raritan estuary ecosystem, New Jersey, USA. Data are from Tripathee & Schafer (2015). (*d*) A *Rhizophora*-dominated mangrove forest in Wakatobi, Indonesia. (*e*) Detritus and woody debris in the Wakatobi forest. (*f*) Biomass partitioning in three mangrove species (*Rhizophora mangle*, *Lumnitzera racemosa*, and *Avicennia germinans*) from the Dominican Republic, along with the aboveground and live belowground biomass proportions of *Rhizophora apiculata* in Malaysia and Thailand and *Avicennia marina* in Australia. Data are from Alongi (2014). (*g*) *Posidonia oceanica* meadow in the Ligurian Sea. Photo courtesy of Marco Bertolino. (*h*) Fresh and weathered *Zostera* wrack on a beach of Stradbroke Island, Queensland, Australia. Photo courtesy of Peter I. Macreadie. (*i*) Relative proportions of lignocellulose components in the tissues of a range of seagrasses, along with the above- and belowground biomass proportions of temperate and tropical seagrasses. Data are from Trevathan-Tackett et al. (2017a).

Mangrove forests occur along tropical, subtropical, and warm temperate coastlines, intergrading into salt marshes at higher latitudes. The most recent estimates suggest that mangroves covered a global area of 137,600 km^2 in 2010 (Bunting et al. 2018), though a

different methodology and criteria for characterizing mangrove areas yielded a much smaller estimate of 81,500 km^2 in 2014 (Hamilton & Casey 2016). However, mangroves are threatened by conversion for aquaculture, agriculture, and urban development. Rates of loss have decreased from an estimated high of 1–3% per year in the second half of the twentieth century to 0.2–0.7% in the last decade (Feller et al. 2017). Nonetheless, this loss still has an important impact on large-scale carbon cycling; studies have estimated that mangrove deforestation causes the emission of 0.007–0.03 Pg CO_2 y^{-1} (Atwood et al. 2017, Hamilton & Friess 2018). Much of this carbon would be emitted to the atmosphere, though a substantial proportion would leave deforested systems in particulate or dissolved form. At their latitudinal limits, mangrove forests consist of shrubs, but in the humid tropics, the canopy is much higher (**Figure 2*d***) and may reach more than 60 m (Simard et al. 2019). Leaves and twigs form a small portion of the total biomass but turn over at a much higher rate than the more woody portions of the tree. Necromass consists of leaves, branches, and standing plus fallen main stems (**Figure 2*d*,*e***). Quantities of large woody debris retained in relatively undisturbed forests are near the upper end of the range for forested wetlands (Allen et al. 2000).

Mangroves are highly productive systems and play an important role in coastal carbon fluxes. They generally store three to five times as much carbon per unit area as tropical rain forests, with substantial aboveground biomass but more root biomass and necromass in their anoxic sediments (Donato et al. 2011). Mangroves tend to have a ratio of aboveground to belowground biomass carbon of 2:1–3:1, allocating more biomass to roots than other forest types, though the total stock and percentage of allocation differ by species, climate, and geomorphic setting (Komiyama et al. 2008). Studies that distinguished between living and dead roots show that live belowground biomass is a smaller proportion of the total biomass (**Figure 2*f***). However, the turnover of root biomass is rapid, and mangrove-forest sediments generally contain a large amount of fine root necromass (Robertson & Alongi 2016). Soil nutrient status also affects rhizosphere biomass (Cormier et al. 2015), and sampling methodology has a large effect on estimates of belowground biomass (Adame et al. 2017).

Biomass partitioning also changes with age; allometry indicates that young *Rhizophora apiculata* trees allocate 20% of their biomass to belowground roots and 15–20% to their trunks, while older trees allocate only 5% to their belowground roots and 60–70% to their trunks (Ong et al. 2004). More biomass is also allocated to woody tissues as trees age (Cintron & Schaeffer

Novelli 1984). Canopy height markedly affects biomass and is globally variable. While 50% of the world's mangroves are shorter than 13.2 m, maximum canopy heights exceed 62 m in West Africa and South America (Simard et al. 2019). Biomass allocation to different aboveground and belowground pools has implications for the quantity of debris produced and the types of tissues available for degradation.

Seagrass meadows have a low flexible canopy and a substantial proportion of their biomass invested in belowground biomass—that is, root and rhizome tissue (**Figure 2*g*,*i***). They produce huge amounts of mobile leaf detritus, which may, after storms, include nonsenescent leaves (**Figure 2*h***). Seagrasses are the only organisms that produce lignocellulose subtidally. As they evolved from lineages of coastal or freshwater aquatic plants, seagrasses lost most of their structural components to cope with buoyancy and wave action (Klap et al. 2000). Although seagrasses have less lignocellulose than salt-marsh or mangrove plants, the lignocellulose plays an important function in the physical protection of young tissue, water and solute transport, anchorage (Kuo 1978, Kuo & Cambridge 1978), and as a source of fiber for marine herbivores (de los Santos et al. 2012, Siegal-Willott et al. 2010). A recent review has shown that seagrass lignocellulose is also a key source of organic carbon within the detrital pool (Trevathan-Tackett et al. 2017a). Notably, sheaths and stems have a high lignocellulose content (on average ~60% by dry weight) and likely represent an unaccounted-for pool that could contribute to carbon stocks. On average, seagrass leaves, rhizomes, and roots contain approximately 40% lignocellulose by dry weight, but this can be highly variable depending on climate and tissue (Trevathan-Tackett et al. 2017a). On average, the global stock of living seagrass biomass of 7.2 Mg of dry weight per hectare suggests that 87–174 Tg of lignocellulose by dry weight is produced by seagrasses globally (based on 40% by dry weight and 300,000–600,000 km^2 of seagrass meadows habitat) (Fourqurean et al. 2012, Trevathan-Tackett et al. 2017a). Since up to 17% of biomass production by dry weight enters the local detrital pool (Cebrián et al. 1997) or can be exported into the deep ocean (Duarte & Kraus-Jensen 2017), seagrass lignocellulose carbon has an important impact on carbon cycling and sequestration in coastal vegetated ecosystems.

4. CHARACTERISTICS OF LIGNOCELLULOSIC BIOMASS AND DETRITUS

Detritus often forms after a process of senescence, when parts detach from the living plant and when the plant dies. Fresh terrestrial-plant detritus, detritus degraded by terrestrial processes, humus from eroded soil, and dissolved breakdown products from detritus are delivered to coastal waters via estuaries and direct groundwater runoff. The detritus, mainly from eudicots and conifers, may be small particles, plant components, and even whole trees. Blue-carbon ecosystems also generate vascular-plant detritus. Subsequent detrital processing, in which the chemical nature and particle size of the detritus change, is described in Section 6.

4.1. Salt-Marsh Biomass and Detritus

The vast majority of data on the lignocellulose content of salt-marsh plants come from one species, *Spartina alterniflora*, which has a general lignin content of 12–14% (Hodson et al. 1984, Valiela et al. 1984), and the structural lignin content increases with age (from 63% to 70% lignocellulose). Stems have the highest aboveground lignocellulose content, though some belowground components seem to have similar levels (Hodson et al. 1984). There are indications that woody-shrub salt-marsh species have a higher recalcitrant lignocellulose content than the grass forms (Klap et al. 1999, Trevathan-Tackett et al. 2015).

Chemical composition of salt-marsh detritus, particularly lignin and nitrogen content, is a major regulator of decay rates (Opsahl & Benner 1995, Valiela et al. 1984, Wilson et al. 1986a). Chemical plant defenses and tougher tissues reduce feeding by invertebrates, while increased nitrogen uptake often increases plant productivity. Detritus with more nitrogen and less fibrous content is more effectively transformed into animal tissue and is preferred by detritivores (Montemayor et al. 2011). Salt-marsh plants from lower latitudes are less palatable to arthropod herbivores than their high-latitude relatives, perhaps due to their greater toughness and lower nitrogen content (Pennings et al. 2007). Large salt-marsh herbivores, such as geese, are influenced by low phenolic concentrations and the ability to pull the plants from the sediment but not nutritional quality (Sieg & Kubanek 2013).

4.2. Mangrove Biomass and Detritus

The leaves of many mangrove species have a high (>20%) concentration of condensed tannins (Kandil et al. 2004). Producing these tannins imposes a high metabolic cost on the plant but serves to deter herbivory and control fungal colonization. Tannin levels decrease with

senescence, which is adaptive, enabling recycling of useful molecules while reducing their antifungal constraint on nutrient recycling. The veins of the leaf contain lignified cells, while the cell walls of the rest of the leaf are less recalcitrant, containing cellulose, pectin, hemicelluloses, and proteins. Many mangrove species have leaves with a well-developed extracellular cuticular membrane at their aerial surfaces. This membrane is rich in cutin, an amorphous polyester formed of hydroxylated C16 and C18 fatty, wax, and cutan acids (Opsahl & Benner 1995). The triterpenols in the leaf cuticle, including the stable mangrove marker taraxerol, carry a molecular fingerprint into the detritus and adjacent sediments (Koch et al. 2011). Live mangroves resist colonization of woody tissues by producing tannins in response to damage (Hendy & Cragg 2017) and passively protecting extractives contained in heartwood (Borges et al. 2008).

4.3. Seagrass Biomass and Detritus

Seagrass carbohydrate content is dominated by labile carbohydrates and hemicelluloses (Trevathan-Tackett et al. 2017a). The dominant storage carbohydrate is sucrose (stored primarily in rhizomes), which forms more than 90% of the total labile carbohydrate pool. Temperate seagrasses may have more labile storage carbohydrates than tropical seagrasses (Trevathan-Tackett et al. 2017a). The lignin proportion is lower in seagrass lignocellulose (**Figure 2*i***) than it is in woody tissues, but roots and rhizomes of seagrasses contain more lignin than leaves do, contributing to recalcitrance (Klap et al. 2000). Also, high concentrations of *p*-hydrobenzoic acid are produced in leaf sheaths, roots, and outer parts of rhizomes and are retained in the more recalcitrant portions of the plants.

Structural traits (tissue toughness) combined with chemical traits (low nutritional quality) reduce seagrass palatability to grazers (Sieg & Kubanek 2013). Phenolics also reduce plant palatability and microbial settlement or growth. Seagrass chemical defenses employed when plants are alive also prevent the breakdown of dead tissues, because shredding by detritivores facilitates subsequent microbial degradation of tissue, but lingering chemical defenses delay the entrance of plant matter into the microbial loop (Sieg & Kubanek 2013). Decomposing seagrass leaves and rhizomes lose carbon faster than they lose nitrogen, but they are a net source of nitrogen to the ecosystem. However, during decomposition, the C:N ratios of seagrass leaves generally do not change significantly, because they are nitrogen rich. Furthermore, seagrass detritus with low C:N ratios has sufficient food quality to decompose rapidly (Fourqurean & Schrlau 2003, Holmer & Olsen 2002).

5. LIGNOCELLULOSE: COMPONENTS, RECALCITRANCE, AND ENZYMATIC DEGRADATION

Lignocellulose in secondary cell walls makes up the majority of plant biomass. It is composed mainly of the polysaccharides cellulose, xylan, and galactoglucomannan combined with polyphenolic lignin (**Figure 3**). The wide range of chemical bonds in these polymers and the cross-linkages between them generate a complex that is recalcitrant to enzymatic breakdown. Here, we consider the lignocellulose composition of angiosperm (flowering) and gymnosperm (mostly conifer) plants, which are the predominant source of lignocellulosic detritus.

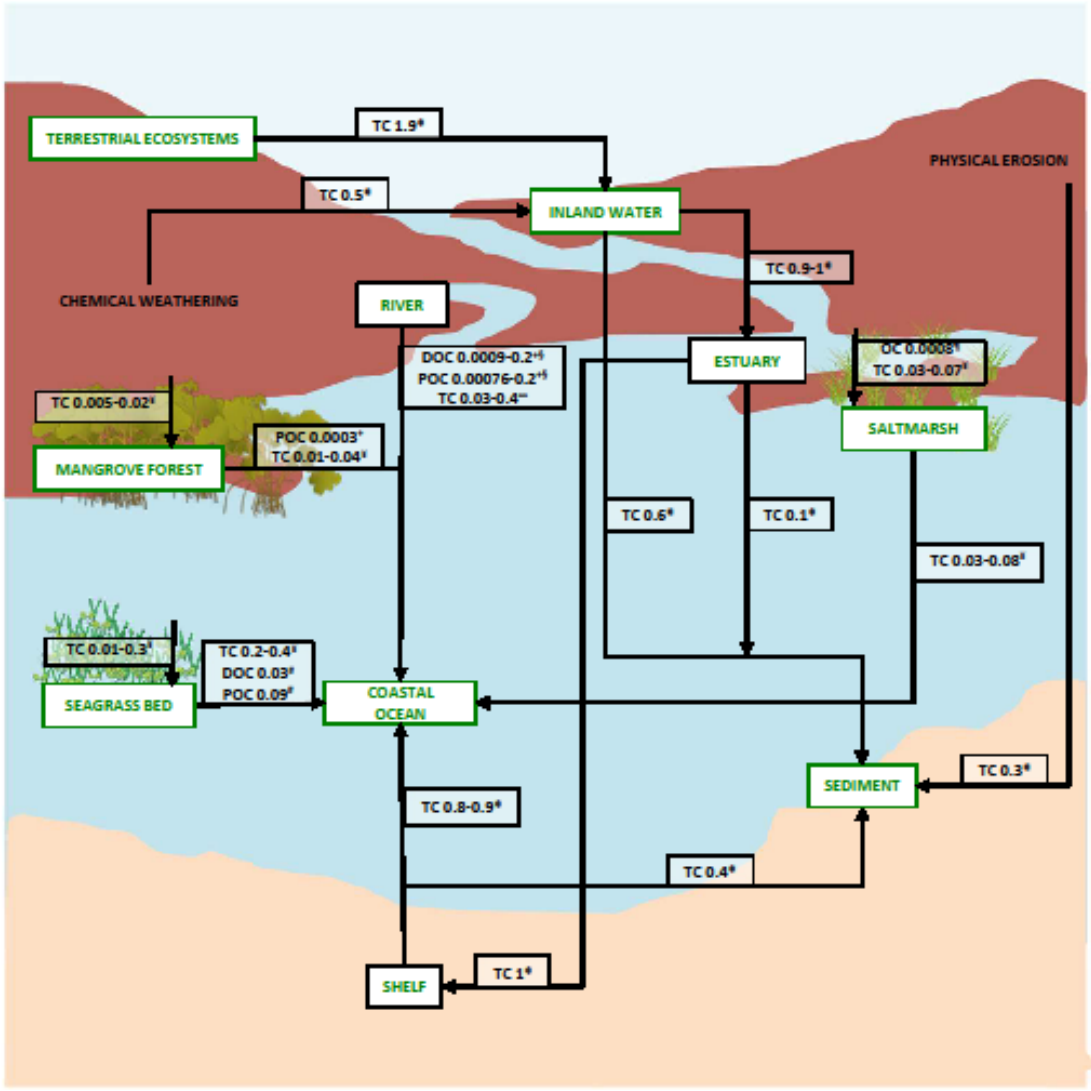

Figure 3 Diversity across the vascular-plant phylogenetic tree of the major components of lignocellulose. The structure of cellulose microfibrils is shared across the tree. The figure shows

part of a microfibril with five sheets of hydrogen-bonded cellulose chains stacked on top of each other in a paracrystalline array. The xylan and galactoglucomannan structures of commelinid monocots, eudicots, and conifers are shown. The majority of plant biomass is derived from these sources. The structure of noncommelinid monocot and nonconifer gymnosperm hemicelluloses are not shown due to their additional complexity and their low contribution to global biomass. Portions of the three-dimensional lignin polymer structures of angiosperms and gymnosperms are shown in a simplified two-dimensional form.

5.1. Components of the Lignocellulose Complex

Cellulose forms approximately 30–50% of lignocellulose by weight. It is composed of glucan chains formed from glucose units that are β-1,4 linked (Jarvis 2018) in glucan chains that can form flat ribbons. The chains hydrogen bond to neighboring chains to form sheets that, through hydrophobic interactions, stack on top of each other to form the semicrystalline cellulose microfibril. Because of this structure, microfibrils have hydrophobic faces (where inter- and intrachain hydrogen bonding is satisfied) and hydrophilic faces (where hydroxyl groups on carbons 2 and 3 are available for hydrogen bonding to water or to other polysaccharides). There are typically 18 chains in a microfibril, but many more in certain tissues or species.

Secondary cell walls contain 30–50% hemicellulose by weight (Scheller & Ulvskov 2010). Hemicellulose refers to noncellulosic polysaccharides with a β-1,4-linked backbone. Unlike cellulosic glucan chains, hemicellulose chains have single sugar units or acetyl groups attached directly to backbone units at frequent intervals. In secondary cell walls, the most common hemicelluloses are xylan and galactoglucomannan (proportions varying phylogenetically; see **Figure 3**), with minor amounts of mixed linkage glucan and xyloglucan. Xylan with a 5-carbon-sugar xylose backbone is found in all lignocelluloses. Xylans can bind as a flat ribbon to the hydrophilic face of cellulose microfibrils (Simmons et al. 2016). From 30% to 60% of the xylose units are branched due to substitutions on the hydroxyl groups, which vary phylogenetically and affect interactions with cellulose and lignin (Terrett & Dupree 2019). In angiosperms, xylose units can be acetylated at carbon 2 and/or 3, and glucuronic acid can be attached at carbon 2 and arabinose at carbon 2 or 3. While all angiosperm xylans have acetyl and glucuronosyl branches, monocots are the only angiosperms with abundant arabinose branches. The arabinose branches of monocots, such as seagrasses, can be more complex and have ferulic acid esterified to them, permitting cross-linking of xylan chains; xylan and lignin can be similarly linked together. Gymnosperms have unacetylated xylan (Busse-Wicher et al. 2016), which is branched with glucuronic acid and arabinose. Galactoglucomannan constitutes up to 30% of the cell wall by

weight in gymnosperms (Scheller & Ulvskov 2010) but just 1–5% in angiosperms (Goubet et al. 2009). The backbone is approximately 80% mannose and 20% glucose, both of which are 6-carbon sugars. The mannose units can be acetylated on carbon 2 and 3. Approximately 1 in 10 mannosyl residues are α-1,6 galactosylated (Hannuksela & Hervé du Penhoat 2004).

Sulfated polysaccharides occur in marine angiosperms—arabinogalactans in mangroves and galactans in seagrasses (Aquino et al. 2005). Sulfation seems to be a response to the osmotic stress of the marine environment, as seagrasses produce sulfated galactans only in seawater, and the sulfation degree correlates with the osmolality of the seawater (Aquino et al. 2011). Pectins are a component of nonlignocellulosic primary cell walls (Atmodjo et al. 2013), which have galacturonic acid in their backbone. They are highly soluble and accessible to enzymatic digestion, and thus are probably digested early in detrital breakdown.

Lignin forms up to 30% by weight of lignocellulose. It is cross-linked to hemicellulose and may interact with cellulose, but the details are poorly understood (Kang et al. 2019, Terrett & Dupree 2019). It is a heterogeneous phenolic polymer synthesized from monolignols that differ by the number of methyl ethers on the phenyl ring [the *p*-hydroxyphenyl (H), guaiacyl (G), and syringyl (S) units have 0, 1, and 2 methyl ethers, respectively) (Mottiar et al. 2016). During lignin synthesis, the monolignols are radicalized and then undergo combinatorial coupling, yielding several types of linkages to form amorphous polymers of a range of sizes, up to 100,000 Da (Crestini et al. 2011). Angiosperms produce lignins composed of G and S units with a small amount of H units, while gymnosperms produce G units with a small amount of H units (Mottiar et al. 2016). An exceptionally high proportion of G and S units within seagrass that generates particularly recalcitrant detritus are *p*-hydroxybenzoylated (Kaal et al. 2018).

5.2. Recalcitrance of the Lignocellulose Complex to Enzyme Activity

The breakdown of vascular-plant detritus is constrained by recalcitrance to enzymatic deconstruction, which arises from multiple features of lignocellulose, such as the degree of cellulose crystallinity, the content of lignin, cross-linking between the polymers, and the presence of specific substitutions of hemicelluloses.

Pores less than 10 nm across in the densely packed polysaccharides and lignin render much of lignocellulose impenetrable to enzymes (Meng & Ragauskas 2014). In eudicots, glucuronosyl substitutions on xylans are crucial for recalcitrance, as demonstrated in mutant plants that lack this substitution (Lyczakowski et al. 2017). Links between lignin and hemicellulose may

contribute to recalcitrance: An ester link between lignin and glucuronic acid has been proposed, and an ether bond between lignin and glucomannan has been demonstrated (Terrett & Dupree 2019). The recalcitrance of the lignocellulose of monocots is decreased by a reduction in the feruloylation of xylan arabinosyl substitutions (de Souza et al. 2019). The ferulic acid component of these substitutions cross-links both to other xylans and to lignin (Scheller & Ulvskov 2010). Galactoglucomannan is thought to bind to cellulose and may contribute to recalcitrance in detritus derived from gymnosperms.

Lignin content promotes the recalcitrance of the cell wall, partly by affecting pore size (Mottiar et al. 2016) but also because glycoside hydrolase (GH) enzymes may be diverted from cellulose or celluloses by binding nonspecifically to lignin (Yarbrough et al. 2015). Mutants with reduced lignin content are more digestible with enzymes (Van Acker et al. 2013). The composition of lignin is also important for recalcitrance. Mutants with high-H lignin or lignins with a large amount of aldehydes have strongly reduced recalcitrance (Bonawitz et al. 2014).

5.3. Enzymatic Deconstruction of Lignocellulose

Lignocellulose is broken down by a wide array of hydrolytic and oxidative enzymes. These carbohydrate-active enzymes are categorized into GH, carbohydrate esterase, and auxiliary activity families in the Carbohydrate-Active Enzymes (CAZy) database (Abbott et al. 2018). Because each enzyme is specific for a narrow range of chemical bonds, organisms are limited in the degradation of lignocellulose by their repertoire of enzymes or those available within microbial consortia. Our understanding of enzyme activity is based on studies of enzymes from terrestrial organisms, though adaptations to the marine environment, such as high activity at high salt levels and an acid surface to the enzyme, have been reported in marine cellobiohydrolases (Kern et al. 2013).

Hydrolytic enzymes break the glycosidic bonds in polysaccharides. Each type of sugar linkage can require a different GH, necessitating many hundreds of enzymes for complete breakdown of the entire plant cell wall. Moreover, despite the structural simplicity of some polysaccharides, the required hydrolytic machinery can be much more complex. Although cellulose contains only β-1,4 bonds between glucose units, there are at least three GH families with different activities involved in the synergistic depolymerization of cellulose. Endoglucanases (e.g., GH9 and GH45) hydrolyze the glucan chains into shorter fragments, producing polysaccharide ends that allow cellobiohydrolase (e.g., GH7) enzymes to hydrolyze

the glucan chains into cellobiose. The cellobiose units are hydrolyzed to glucose by β-glucosidases (e.g., GH1). When the lignocellulose complex is depolymerized, the number of GH enzymes involved becomes much larger. Esterases remove acetyl and feruloyl links to hemicelluloses.

Oxidative enzymes act on both lignin and polysaccharides. Hemocyanin acting as a phenol oxidase has been shown to enhance GH activity in wood boring isopods (Besser et al. 2018). Lytic polysaccharide monooxygenases bind polysaccharides and produce radicals to oxidize backbone glycosidic bonds (Walton & Davies 2016). They boost the activity of GH enzymes by producing chain breaks, thereby increasing the binding sites for GHs (Harris et al. 2010). Lytic polysaccharide monooxygenases are activated by electron donor systems, including phenols generated by lignin depolymerization (Kracher et al. 2016). Lignin is depolymerized by laccase, peroxidase, and manganese-dependent peroxidase enzymes from white rot fungi and certain bacteria (Martinez et al. 2004). Brown rot fungi employ chelator-mediated Fenton chemistry to reduce iron and generate reactive oxygen species that degrade cellulose and hemicellulose oxidatively, breaking bonds within the lignin polymer and causing nanostructural changes that may reduce recalcitrance (Goodell et al. 2017).

6. ORGANISMS THAT EXPLOIT LIGNOCELLULOSIC DETRITUS IN COASTAL ECOSYSTEMS

The ability to exploit lignified substrates is widely but sparsely distributed across the tree of life; the vast majority of microorganisms and animals cannot effectively extract the energy from this recalcitrant substrate (Cragg et al. 2015). Nonlignocellulose specialists may be able to exploit plant tissues with low lignin levels. Herbivores digest live lignocellulosic plant tissues using enzymatic processes similar to those of detritivores.

6.1. Bacteria and Archaea

The role of bacteria and archaea in plant detritus degradation becomes increasingly important as particle size decreases and as the particles become enriched with particularly recalcitrant remnants of lignin. However, due to problems with culturability, the organisms responsible have often evaded isolation and identification. Nonetheless, genomic analysis indicates that the majority of genes associated with lignocellulose degradation in the CAZy database are of bacterial origin, and metagenomes indicate that laccases and other essential pathways are

widespread in bacteria (Tian et al. 2014). Although less is known about archaeal degradation mechanisms, recent studies indicate that they too play an active role in lignin degradation (Rinta-Kanto et al. 2016).

Degradation of organic matter of terrestrial origin, particularly in aquatic systems, is highly dependent on prokaryotic breakdown mechanisms. In aquatic habitats, the location of degradation is critical to its efficiency, as nutrient and oxygen availability and the accessibility of the organic matter will affect rates of degradation (Marin-Spiotta et al. 2014). Using novel in situ lignin-associated beads in tropical soils, DeAngelis et al. (2011) detected the enrichment of key lignin-degrading bacterial phyla, including Acidobacteria, Chloroflexi, Firmicutes, and Verrucomicrobia. Novel culturing approaches in combination with next-generation sequencing techniques are yielding a much better understanding of the prokaryotic community involved in lignin degradation. For example, Woo & Hazen (2018) recently determined that bacteria, rather than white rot fungi, are the major decomposers of lignin under marine conditions. Rapidly developing sequencing technologies will enable a better understanding of the organisms and enzymes involved in in situ degradation of lignocellulose in sediments and in the water column.

6.2. Protists

Unlike detritus degradation on land, marine degradation involves a significant (though poorly understood) contribution from single-celled eukaryotes, particularly from oomycetes and thraustochytrids. These are heterokonts within the kingdom Chromista, with oomycetes being classified as Pseudofungi and thraustochytrids as Labyrinthulea (Cavalier-Smith 2018). Thraustochytrids have been found in the water column from the coasts to the deep sea, correlating with elevated POC (including terrigenous phytodetritus) (Kimura et al. 2001) and in sediments rich in refractory organics (Bongiorni et al. 2005), and probably exploit relatively large (micrometer-sized) particles (Kimura et al. 2001). Oomycetes and labyrinthulids act as pathogens of seagrasses (in't Veld et al. 2019, Trevathan-Tackett et al. 2018), but some are saprotrophs. Both oomycetes and thraustochytrids are early colonizers of senescent mangrove leaves due to their chemotactic zoospores, which respond to chemical cues from the leaves (Raghukumar et al. 1995). Thalli of thraustochytrids grow on the surfaces of particles, and elements of their ectoplasmic net can penetrate the particles, enabling assimilation and anchorage. Filamentous oomycetes such as *Halophytophthora* can live within particulate detritus. A range of enzymatic capabilities have been detected in cultures of isolates of

thraustochytrids, but low levels of carbohydrate-active enzymes have been found (Bongiorni et al. 2005). Genomic studies show that plant-pathogenic oomycetes have a wide range of carbohydrate-active enzymes (Brouwer et al. 2014), but similar studies of saprotrophic forms have yet to be reported.

6.3. Fungi

Terrestrial basidiomycete fungi flourish above the high-tide mark in mangrove forests, while ascomycetes are the dominant marine fungi on lignocellulosic substrates from intertidal down to abyssal depths. The diversity of marine fungi based on morphological and culturing data (Jones et al. 2015) represents a fraction of the total marine fungal diversity that is now being revealed (but has not yet been characterized) by sequencing of environmental samples (Richards et al. 2012). Marine fungi flourish wherever lignocellulosic biomass or detritus occurs, which includes not only salt marshes, mangrove forests, and seagrass meadows (where filamentous growth forms predominate) but also the plankton and in anoxic sediments (where yeast-like cells predominate). The Dothideomycetes are a speciose taxon of ascomycetes found on salt-marsh plants, the mangrove palm (*Nypa*), mangrove wood, and seagrasses (Suetrong et al. 2009). Rich fungal communities that may play a role in the decomposition of organic matter occur in anoxic mangrove sediments, but fungal growth under anaerobic conditions is poorly understood (Arfi et al. 2012). Saprotrophic planktonic fungi are postulated to attach to and degrade particulate organic matter (Taylor & Cunliffe 2016). Wood in the open ocean favors the growth of Halosphaeriales, which have ascospores adapted for flotation, while in the intertidal zone Loculoascomycetes, which eject spores during low tide, are common on wood (Hyde et al. 1998).

Saprotrophic filamentous fungi secrete enzymes onto the substrate, releasing monomers that can be absorbed by the fungus. Fungal degradative activity on wood is categorized by enzymatic capabilities and effects on the wood cells (Daniel 2014). In white rot, lignin, hemicellulose, and cellulose are depolymerized by a battery of enzymes: GHs, carbohydrate esterases, oxidoreductases, and lytic polysaccharide monooxygenases (Floudas et al. 2012). In brown rot, cellulose and hemicelluloses are degraded by GHs, assisted by a chelator-mediated Fenton mechanism that generates reactive oxygen species (Goodell et al. 2017). In soft rot, cellulose, hemicellulose, and sometimes lignin are degraded by hyphae tunneling in the cell wall (Bucher et al. 2004). Basidiomycota cause brown and white rot in supratidal conditions. Ascomycota

cause soft rot and dominate in waterlogged and in some cases anoxic conditions, though some cause white rot (Dittmar & Lara 2001).

6.4. Mollusca

The bivalve families Teredinidae and Xylophagaidae are the most important consumers of wood and woody-plant materials in marine environments, with the former dominating at depths above approximately 100–200 m and the latter dominating below (Turner 1966, Voight 2015). The two families have a worldwide distribution, together encompassing tropical to Arctic latitudes, brackish to marine salinities, and intertidal to abyssal depths (Turner 1966, Voight 2015). The shells of both families bear fine teeth used to burrow in wood, producing micrometer-scale particles that are subsequently ingested and digested (Distel & Roberts 1997, O'Connor et al. 2014). Both families harbor endosymbiotic bacteria within specialized cells of the gills (Distel & Roberts 1997, Popham & Dixon 1973). In the Teredinidae (commonly called shipworms), these bacteria produce enzymes that aid wood digestion by the host, and at least one teredinid species produces endogenous nucleus-encoded lignocellulose-degrading enzymes as well (Sabbadin et al. 2018). The symbionts also fix nitrogen, and the resulting compounds are taken up by the host shipworm (Lechene et al. 2007), thus helping the host to overcome the unfavorable C:N ratio in its wood diet.

Teredinidae and Xylophagaidae are sister taxa, and the gill endosymbionts harbored by both families are closely related, indicating a single evolutionary origin and likely a common core of ancestral properties for their unique form of symbiotic xylotrophy (Distel et al. 2011). However, despite their common origins, both hosts and symbionts have undergone significant diversification. Indeed, Teredinidae is considered to be among the most morphologically diverse of the mollusk families (Turner 1966), spanning two orders of magnitude in adult size (<1 mm to >1 m) and displaying an extraordinary diversity in anatomy, habitat selection, reproductive modes, and digestive strategies. While phytoplankton may contribute to the diet, most teredinid species feed primarily on wood. Many taxa are exclusively specialized for a distinct and narrowly defined subset of lignocellulosic substrates, such as mangrove roots, seagrass rhizomes, or floating palm fruits, while others are generalists that may inhabit a broad range of floating or deposited wood types. An exception is *Kuphus polythalamius*, which burrows in lignocellulose-rich marine sediments and harbors sulfur-oxidizing chemoautotrophic endosymbionts rather than cellulolytic bacteria in its gills. The reduced sulfur compounds consumed by these symbionts

may be produced by sulfate-reducing bacteria growing on decaying wood. Thus, *Kuphus* has adopted an alternative feeding strategy that allows indirect use of the energy contained in plant materials (Altamia et al. 2019).

6.5. Crustacea

The ability to exploit vascular-plant detritus and to overcome the recalcitrance of lignocellulose is found in a range of crustaceans. The dominant leaf detritivores in mangrove ecosystems are crabs—sesarmids in the Indo-Pacific and the ocypodid *Ucides* on the coasts of the Americas (Kristensen et al. 2017). Several detritivorous sesarmid crabs produce an endogenous enzyme capable of splitting cellulose chains (Bui & Lee 2015). Isopods of the family Limnoriidae tunnel superficially into cellulosic substrates. Some are borers of the bases of seagrass leaves, and some burrow into macroalgae, but most are wood borers. Limnoriids occur in mangroves where the waters are not too brackish and in seagrass meadows. *Limnoria* has a gut that is devoid of a resident microbiota, so its ability to digest crystalline cellulose in lignocellulose is due entirely to the activities of the proteins it secretes in its hepatopancreas (King et al. 2010), whereas the isopod *Idotea* has a gut microbiota that varies with diet (seagrass or macroalgae) (Mattila et al. 2014). Principal among these enzymes are ones belonging to the CAZy families GH7 (cellobiohydrolases), GH9 (endoglucanases), and GH5 (enzymes that carry out various activities, including hemicellulose cleavage) (King et al. 2010). Some sphaeromatids burrow into descending, unattached *Rhizophora* prop root tips and shafts, but they use the burrow for suspension feeding (Si et al. 2002) and protection from predators. They burrow into live roots, causing local dieback in the roots but also causing increased root branching.

6.6. Insects

Herbivorous and detritivorous insects operate in the supratidal portions of mangrove trees and rarely extend their activities into the intertidal zone. The diversity of insect leaf consumers has been best described from mangroves of Singapore (Murphy 1990). Cerambycid beetle larvae consume the cambium, phloem, and outer xylem of *Rhizophora* stems (Feller 2002) and cause characteristic bark scars on trunks of dead *Excoecaria* (Cragg & Hendy 2010). Arboreal termites, such as the higher termite *Nasutitermes*, build carton nests above the reach of tides with foraging tunnels extending along stems and branches (Vane et al. 2013). They consume xylem, which is

digested with a battery of endogenous and microbial enzymes provided by bacterial and protist endosymbionts, enabling them to digest xylans as well as cellulose (Tokuda et al. 2018).

7. LIGNOCELLULOSE DEGRADATION ACROSS BIOMES

Lignocellulosic detritus breakdown is achieved by a combination of microbial action and detritivore activity that vary in rate and sequence according to the nature of the substrate and the environment in which the breakdown takes place. Decomposition by microbes of less lignified detritus is typically modeled in three phases (Berg & McClagherty 2008). First, the leaching phase consists of a passive loss of soluble compounds that are often rapidly consumed by the resident microbes. Next, detritus undergoes active breakdown by microbes that produce lignocellulose-specific enzymes (Sinsabaugh et al. 2002). The last phase is characterized by slow to no mass loss, because either the remaining detritus is inaccessible to consumers or the enzymes are not available. The ratio of surface area to volume is a critical measure of the proportion of the particle that is accessible to surface-inhabiting microorganisms: The smaller the particle is, the greater the role of microorganisms in deconstruction (Arnosti et al. 2018). Large woody debris is riddled by tunneling animals, which facilitates subsequent microbial deconstruction. This review does not explore the final microbial mineralization phase of marine lignocellulose degradation.

7.1. Salt Marshes

The lignin content of litter from different species of salt-marsh plants varies considerably, but rapid increases during the first weeks of exposure are followed by stabilization (Klap et al. 1999). Although lignin contributes only 7% to degraded salt-marsh detritus, its breakdown products can represent 30% of the carbon in lignocellulose-derived DOC (Vernberg 1993). When salt-marsh detritus begins to decay, DOC accounts for 50–60% of total degradation products of the lignin fraction of lignocellulose; however, 20–30% of the polysaccharide portions of lignocellulose accumulate as DOC during decomposition. In general, C:N patterns for salt marshes are characterized by increasing values during the leaching stages of decomposition, and the C:N ratio then steadily decreases (Klap et al. 2000). During the initial decomposition of salt-marsh detritus, there is a net loss of nitrogen, as a phase of nitrogen immobilization begins that is tightly coupled with rates of microbial degradation of tissues (Benner et al. 1991). During

the late refractory phase of the decomposition process, the relative content of lignin in the detritus increases due to the formation of recalcitrant lignin and nitrogen-rich complexes, thus making further degradation limited. However, given the variation between plant tissues of lignocellulose content and the expected range of across-species lignocellulose content, further research on salt-marsh organic matter recalcitrance and on the influence of lignocellulose content on decomposition (Stagg et al. 2018) would provide a higher-resolution picture of salt-marsh organic carbon decomposition and sequestration.

Temperature and nutrient availability affect salt-marsh litter decomposition (Valiela et al. 1984), but redox chemistry is also a crucial abiotic factor driving salt-marsh biodegradation. Oxygen availability is less important for decomposition during the leaching phase, but during the microbial remineralization and refractory phases, anaerobic conditions can reduce the rate of long-term salt-marsh degradation threefold (Valiela et al. 1984). However, sediment microbial communities can remineralize lignin under both aerobic and anaerobic conditions (Benner et al. 1984), testing the paradigm that anoxic conditions limit sediment carbon remineralization. Furthermore, there is increasing evidence that the preferential degradation of nonaromatic compounds (Benner et al. 1991, Wilson et al. 1986b), the microbial community present, and the microbes' enzymatic capabilities (see Section 5.3) are key factors in lignocellulose biodegradation in coastal marine environments. Fungi and prokaryotic microbes are key to salt-marsh lignocellulose degradation, and their activities are regulated by oxygen availability. Ascomycete fungi are particularly important colonizers of senescing plant material and fresh litter (Calado et al. 2015, Lyons et al. 2010, Newell et al. 1996), causing decay of the soft rot type in *Spartina* (see Section 5.3) (Newell et al. 1996). There is also evidence for cometabolism between fungi and bacteria belonging to ascomycete and alphaproteobacteria groups, respectively.

Lignocellulose can be further degraded in the sediments, driven by bacteria, including those from the taxa Desulfosarcina, Spirochaeta, and Kangiella (Darjany et al. 2014). Interestingly, sediment bacteria can also promote the preservation of carbon by forming refractory nitrogen-enriched complexes via enzymatic processes that promote humification (Tremblay & Benner 2006; Wilson et al. 1986a,b). It is also important to note that biodegradation can be assisted by invertebrates (Arambalza et al. 2014, Creach et al. 1997, Treplin et al. 2013) but also inhibited

through grazing practices that reduce the enzymatic activities of the sediment microbes (Mueller et al. 2017).

7.2. Mangrove Forests

Mangrove biomass biodegradation is governed by tides, sediment redox conditions, tree architecture, and tree age. Herbivores and pathogens crop biomass above the high-tide mark, and detritus drops to the forest floor. Sapling detritus consists of senescent leaves, propagules, and twigs. In maturing trees, lower branches are shaded out and shed, while within the intertidal zone, above-sediment roots, particularly prop roots, are subject to a degree of turnover. Overmature trees lose large branches and portions of their canopy, eventually collapsing, and there have been few attempts to quantify the input of large tree components. Litter-processing regimes differ markedly between microtidal Caribbean forests with limited circulation and the tide-dominated delta complexes of the Indo-Pacific. Lightning strikes, storms, erosion, and tsunamis transfer pulses of biomass to the forest floor, with effects that are now being modeled (Vogt et al. 2014). Managed forests are usually harvested before maturity, thus limiting the amount of large woody debris within the forest.

Herbivores, detritivores, saprobes, and pathogens consume or weaken aerial parts of mangroves, though chemicals in leaves, bark, and heartwood provide protection. *Sonneratia* leaves, which are less protected, dominate the diet of proboscis monkeys (Matsuda et al. 2017). Stem miners can cause dieback of up to 50% of *Rhizophora* canopy in Caribbean forests (Feller 2002), while insect herbivores can consume up to 20% of leaf area in *Avicennia* forests (Feller et al. 2017). Arboreal termites nest above the reach of tides and form galleries by consuming woody tissues. The fecal material forming their nests is highly enriched with lignin-derived refractory compounds, indicating cellulose and hemicellulose digestion. On falling to the forest floor, the nests contribute to the refractory carbon pool in the sediment (Vane et al. 2013). Teredinids can riddle live mangrove roots but rarely compromise tree stability (Hendy & Cragg 2017).

Leaf litter follows three main degradation paths—tidal export, crab detritivory, and microbial processing—with the predominant path determined by tidal regime (Robertson & Daniel 1989b). Crabs capture fallen leaves at low tide and often store them in their burrows, processing up to 80% of available leaf litter (Nordhaus et al. 2011). Their fecal matter transfers lignin-enriched matter into the sediment or water column, where its contribution to carbon fluxes can be traced

using leaf-species-specific chemical signatures (Bakkar et al. 2017). In Southeast Asia, crabs have significant gastropod competitors for detrital resources (Raw et al. 2017). In the absence of detritivore intervention, newly fallen mangrove leaves are rapidly colonized by oomycetes, thraustochytrids, and ascomycetes, followed by bacteria (Raghukumar et al. 1995). Leachable compounds are rapidly broken down, followed by polysaccharides, leaving a lignin-enriched residue after approximately a year. The C:N ratio shifts from 45:1–47:1 in green *Rhizophora* leaves to 58:1–76:1 in leaf litter (Scharler et al. 2015), but during decomposition, C:N ratios decrease due to colonization by bacteria, which incorporate nitrogen from seawater or sediment in order to metabolize material with a high C:N ratio (Fourqurean & Schrlau 2003, Holmer & Olsen 2002).

Large fallen wood is less mobile due to the density of most mangrove timbers and the tendency of long pieces to become snagged in the aboveground root complex. Where inundation is sufficiently protracted and frequent, such wood is rapidly colonized by teredinids, which can ingest up to 70% of the volume (I.W. Hendy, personal communication) while releasing lignin-enriched feces (Sabbadin et al. 2018). Such waterlogged, riddled wood has a vastly increased surface area for surface-penetrating decay by ascomycete fungi and bacteria. Robertson & Daniel (1989a) estimated that the carbon flux due to the breakdown of woody detritus in a mature mangrove forest in tropical Australia was somewhat lower than fluxes due to leaf-consuming crabs, though the wood-derived flux from young forests was naturally much smaller. In very-high-canopied forests (Simard et al. 2019), wood-derived fluxes probably exceed those from leaves. The mechanisms of degradation of belowground detrital particles and roots are challenging to investigate, with wide variations in decay coefficients, partly explained by redox conditions (Robertson & Alongi 2016) that vary with the coastal environmental settings in which mangroves grow (Twilley et al. 2018).

7.3. Seagrass Meadows

Biodegradation of seagrass biomass can be performed by megaherbivores (manatees, dugongs, and sea turtles), birds, fish, and invertebrates (Nienhuis & Groenendijk 1986, Shipway et al. 2016, Thayer et al. 1984, Valentine & Heck 1999), as well as microorganisms. The leaf biomass targeted by most grazers has a high cellulose content compared with other marine food sources, and digestion is aided by gut bacteria (Clementz et al. 2007, Eigeland et al. 2012). The remaining portion of seagrass biomass that is not exported or consumed by grazers enters the detrital cycle.

Decomposition of seagrass leaf, sheath/stem, rhizome, and root detritus is generally caused by microorganisms, though studies detailing the microbial remineralization of belowground structures are less comprehensive than those for leaf biomass (Trevathan-Tackett 2019).

Seagrass decomposition increases at higher temperatures but, like the decomposition of other blue-carbon detritus, is inhibited in anoxic conditions (Trevathan-Tackett et al. 2017b). Most of what is known about seagrass decomposition comes from studies that have focused on the short-term aerobic decomposition of seagrass leaves, particularly the change in elemental chemistry within the first year of decay. The major research gaps that remain include (*a*) the dynamics of rhizome, root, and sheath/stem decomposition, considering that these tissue types contain the highest lignocellulose content (see Section 4.3); (*b*) the influence of anoxic conditions on recalcitrant carbon decay (Trevathan-Tackett et al. 2017b); and (*c*) the activities and capacity of the microorganisms to degrade seagrass lignocellulose. We know that seagrass-associated eukaryotic communities (i.e., fungi and heterotrophic protists) are important in the biodegradation of seagrass tissues (Sathe & Raghukumar 1991, Supaphon et al. 2013). Additionally, bacterial communities, including anaerobic taxa, show successional shifts that are linked to the substrate degradation as well as lignocellulolytic enzyme production (Liu et al. 2017, Trevathan-Tackett et al. 2017b). With the developing technology and affordability of next-generation sequencing, biomarker techniques, and microscopy, the field of seagrass microbial ecology is expected to grow exponentially in the coming years (Fahimipour et al. 2017, Seymour et al. 2018).

7.4. Sunken Wood Falls

Wood fall from shipwrecks (Björdal 2012) and other anthropogenic and natural sources to large depths provide an important source of carbon and energy in a unique aquatic environment for lignocellulose degradation. Decomposition is slow, taking more than a decade in the case of large pieces of wood, which provides the opportunity for complex communities of dependent organisms to develop (Distel et al. 2000). Considerable progress has been made in understanding the prokaryotes associated with eukaryotic hosts in these systems (Dubilier et al. 2008), but few studies have examined the free-living microbes involved. Laboratory-based studies and in situ analysis of deep-water wood fall have demonstrated relationships among microbial diversity, substrate type, and temporal and spatial factors (Kalenitchenko et al. 2015). Much remains to be understood about these complex deep sea systems, though studies have shown that bacteria alone

are responsible for the production of hydrogen sulfide without bivalve hosts (Kalenitchenko et al. 2018). Wood falls support chemosynthetic biota (Bienhold et al. 2013), which vary temporally and spatially (Ristova et al. 2017). Microbial communities around wood falls are structured by xylophagaid boring activity and exploit the fecal matter that they generate (Fagervold et al. 2014).

7.5. Continental Margin

Continental margin sediments are critically important in the carbon cycle and are a key location of the decomposition and degradation of lignocellulosic materials. Bacteria comprise the majority of biomass and chemical activity in these sediments (Nealson 1997). Microbes are capable of anaerobically degrading lignin and aromatic breakdown products (Fuchs et al. 2011), as evidenced by changes in lignin chemistry (Dittmar & Lara 2001). Furthermore, our understanding of these complex environments is very limited. A recent study found that a member of an archaeal phylum is capable of anaerobic lignin degradation (Yu et al. 2018), and because this phylum is one of the most abundant on Earth, this finding could have major implications for our understanding of aquatic lignocellulose degradation. No doubt global climate change would affect degradation rates, as seagrass decomposition in sediments increases in elevated temperatures (Trevathan-Tackett et al. 2017b).

8. POLICY IMPLICATIONS OF MARINE LIGNOCELLULOSE BIODEGRADATION

Climate change has made global carbon dynamics an important international policy issue, and vegetated coastal ecosystems are expected to make an important contribution to climate mitigation attempts. Coastal ecosystem carbon stocks have therefore been discussed by the United Nations Framework Convention on Climate Change at the Conference of the Parties, including the recent Paris Agreement. However, the incorporation of blue-carbon ecosystems into global carbon models is constrained by poor knowledge of key processes relevant to terrigenous and coastal carbon cycling (Kirschbaum et al. 2019) (see Section 2).

While we lack policy-relevant knowledge relating to carbon export and recalcitrance (linked to marine lignocellulose), we do have a strong knowledge of carbon stocks. We have quantitative estimates of wetland carbon stocks at policy-relevant scales (i.e., national and global) and estimates of annual emissions using a stock change approach (Atwood et al. 2017, Hamilton &

Friess 2018), as required by the United National Framework Convention on Climate Change. The stock change approach represents the loss of carbon that has been sequestered over decades to centuries, including from lignocellulose sources. The stock change approach is also the basis for conservation interventions such as payments for ecosystem services. One example of this for mangroves is the REDD+ initiative, which aims to reduce emissions from deforestation and degradation, by paying stakeholders to avoid deforestation and associated carbon emissions (Locatelli et al. 2014). However, financially incentivizing the protection of forests and their carbon through REDD+ is still limited in mangrove ecosystems because it often cannot include soil carbon, owing to the variation of soil carbon across depth and space, leading to difficulties in soil carbon accounting. Thus, the major carbon pool of blue-carbon ecosystems, including the pool that benefits most from lignocellulose deconstruction and the accumulation of more accessible forms of carbon, cannot currently be included in many conservation initiatives based on payments for ecosystem services.

A focus on carbon stocks misses important temporal variability that could be captured by a stronger incorporation of fluxes, including emissions to the atmosphere from degraded wetland areas that continue long after the initial land-use conversion and carbon stock loss (Cameron et al. 2019, Lovelock et al. 2017). Such fluxes also include those from surface water, pore water, and groundwater that may transport dissolved and particulate organic matter that contains lignocellulose and its derivatives. Fluxes would be expected to change under deforestation and degradation (Sippo et al. 2016), though the exact magnitude and direction of dynamics are not well understood.

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