Chapter 13
Causes and Consequences of Changes in Riparian Vegetation for Plant Litter Decomposition Throughout River Networks

John S. Kominoski, Samantha K. Chapman, Walter K. Dodds, Jennifer J. Follstad Shah, and John S. Richardson

Abstract Riparian ecosystems occupy land-water interfaces along upland-to-lowland and coastal gradients of river networks. Global changes in riparian vegetation alter the types and processing of organic matter at these interfaces and throughout river networks. Dominant pathways of structural changes in riparian vegetation are associated with (i) temperature increases and changes in precipitation and hydrology, (ii) range expansion/contraction of native and non-native species, (iii) altered land-use for agriculture/forest plantations and harvesting, and urban development, (iv) shifts in disturbance regimes, such as fire, disease, pest outbreaks, and storms, and (v) saltwater intrusion. Widespread changes in riparian vegetation alter above and below-ground carbon (C) stores and shift the relative proportion of algal and detrital basal resources in aquatic ecosystems. Global changes in riparian vegetation likely shift the sources and sinks of organic matter along river networks from upland headwaters to lowland rivers and coastal wetlands. Climate and global changes are expanding and contracting continental vegetation species ranges while sea-level rise and saltwater

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intrusion are transgressing coastal ecosystems landward. Understanding the general pathways and functional consequences of changes in riparian vegetation is vital to conserving ecosystem functions and services throughout continental river networks and coastal wetlands that are supported by organic matter processing.

13.1 Riparia & River Networks

Most aquatic ecosystems rely on allochthonous energy produced in riparian and terrestrial ecosystems (Cebrian & Lartigue, 2004). Riparian ecosystems contain unique species adapted to flooding, drought, erosion and deposition, which collectively result in riparian areas as being control points of biogeochemical cycling and organic matter processing (Bernhardt et al., 2017; McClain et al., 2003; Naiman et al., 2010; Sabo et al., 2005). Riparian and wetland vegetation drive the quantity, quality, and timing of organic matter in aquatic ecosystems (Batzer & Sharitz, 2014; Kominoski & Rosemond, 2012; Meyer et al., 1998), mediating the influence of surface waters on global carbon (C) budgets. Climate and land-use changes drive the transformation, export, and fate of organic matter from local habitats to entire river networks (Benda et al., 2004). However, the composition of riparian communities is in flux on a global scale, resulting in significant changes to aquatic ecosystem processes and services (González et al., 2017; Kominoski et al., 2013).

The river continuum (Vannote et al., 1980), serial discontinuity (Stanford & Ward, 2001; Ward & Stanford, 1983), and flood pulse concepts (Junk et al., 1989) provided conceptual frameworks that stimulated decades of research assessing the longitudinal and lateral connectivity of organic matter from small streams to large rivers to floodplains and wetlands. This research has demonstrated the importance of organic matter to energy and food web dynamics across spatial scales (e.g., Hall & Meyer 1998; Minshall et al., 1983; Thorp & Delong, 1994). Aquatic ecosystems are both connected and disconnected along hydrologic flow paths, influencing recipient and donor-controlled ecosystems through delivery of organic matter (Ball et al., 2010). Aquatic organisms amongst Earth's biomes have evolved over millennia to utilize organic matter inputs, whether delivered in seasonal pulses or supplied continuously over annual cycles (Benstead & Huryn, 2011; Yeung et al., 2019). This connection between organic matter input regimes and evolutionary adaptations likely has profound impacts on the quantity of energy and nutrients stored, transformed, or transported within river networks.

Despite the evolution of these frameworks towards understanding the river network, we know very little about the integration of organic matter processes over time and through multiple components of river networks, such as lakes, reservoirs, floodplains and wetlands. The role of inland aquatic ecosystems in processing terrestrial organic matter is critically large relative to the spatial extent that surface waters cover the globe (Battin et al., 2009). Wetlands, especially coastal wetlands, are foundational to the global storage of carbon, given that they retain and bury massive amounts of organic and inorganic matter relative to their land area (Chmura et al., 2003, McCleod et al., 2011). River networks actively fix, store, transform, and transport carbon (Cole et al., 2007), and stream litter decomposition processes integrate at network scales (Fig. 13.1). At local scales, riparian vegetation influences litter processing, organic carbon availability, and aquatic ecosystem services (Fig. 13.1). Further, threshold responses or unforeseen consequences caused by environmental

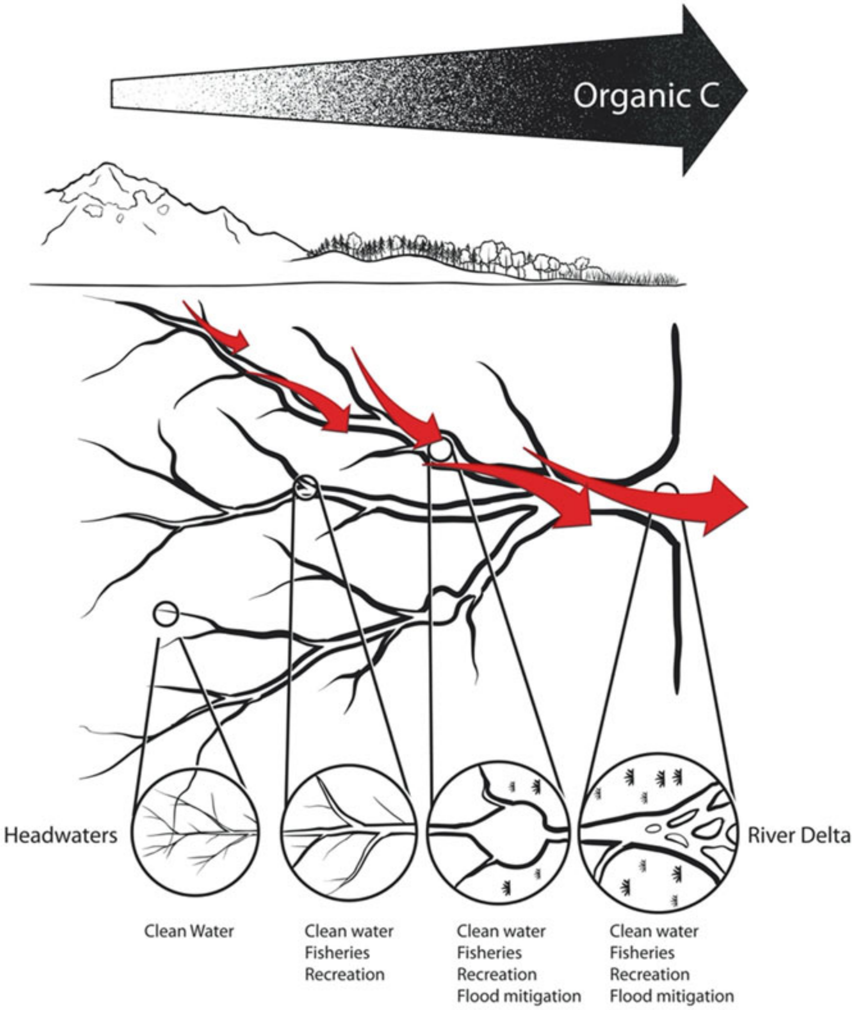

Fig. 13.1 Conceptual figure depicting a river network demonstrating how spatial heterogeneity in riparian and wetland ecosystems influences the distribution and processing of organic matter and ecosystem services. River networks integrate the sources, fluxes, and transformations of organic matter that vary along multiple flow paths from headwaters to the ocean that collectively influence ecosystem services. Copyright E. E. Nixon

change accumulating in separate sub-basins within larger river networks may occur downstream after convergence of multiple flow paths (e.g., Ward & Stanford, 1983).

Quantification of organic matter fate in river networks that includes interior and coastal wetlands is needed, as aquatic ecosystems receive and distribute organic matter from ecosystems to which they are coupled (Aufdenkampe et al., 2011). Carbon dynamics and ecosystem services at any given location in a river network depend on upstream processes that accumulate along hierarchical and conjoining flow paths (Benda et al., 2004; Fig. 13.1). Wetlands capture upland as well as marine inputs of organic matter, increasing retention. Understanding network-level sources, fates, and transformations of organic matter will aid in identifying the location and management of freshwater ecosystem services (Benda et al., 2004; Peters et al., 2008).

Here, we elucidate the major trends and pathways that result in shifting riparian plant assemblages, summarize the general patterns and effects of these shifts on organic matter dynamics in lotic ecosystems, and describe how organic matter processing is linked to key ecosystem services.

13.2 Global Changes in Riparian Vegetation: Streams, Rivers, & Coastal Wetlands

Shifts in riparian community composition are evident around the world, resulting from climate change, biotic homogenization and hybridization, land use change, altered disturbance regimes, and pollution (González et al., 2017; Kominoski et al., 2013). In some regions of the U.S., these shifts result in communities that are novel relative to historic communities (Macfarlane et al., 2017). These changes have myriad effects on the quantity, quality, and timing of organic matter inputs to surface waters. We explore each of the drivers of change in riparian assemblages and discuss how they influence allochthonous organic matter inputs, as well as the storage, transformation, and transport of organic matter within aquatic ecosystems.

13.2.1 Climate Change: Temperature, Precipitation, Hydrology, and CO_2 Concentrations

The biomes that freshwaters are embedded in have strong influences on riparian vegetation (Fig. 13.2; Dodds et al., 2015, 2019). When the amount of precipitation is less than the potential evapotranspiration, the riparian zone can shift from trees to grasses and shrubs. Intermittent habitats in extremely dry areas can have almost no woody riparian vegetation, through stream channels and wetlands are often wetter areas likely to support a greater plant biomass. In very cold areas (high altitude or latitude), the development of woody vegetation may be inhibited by climate severity

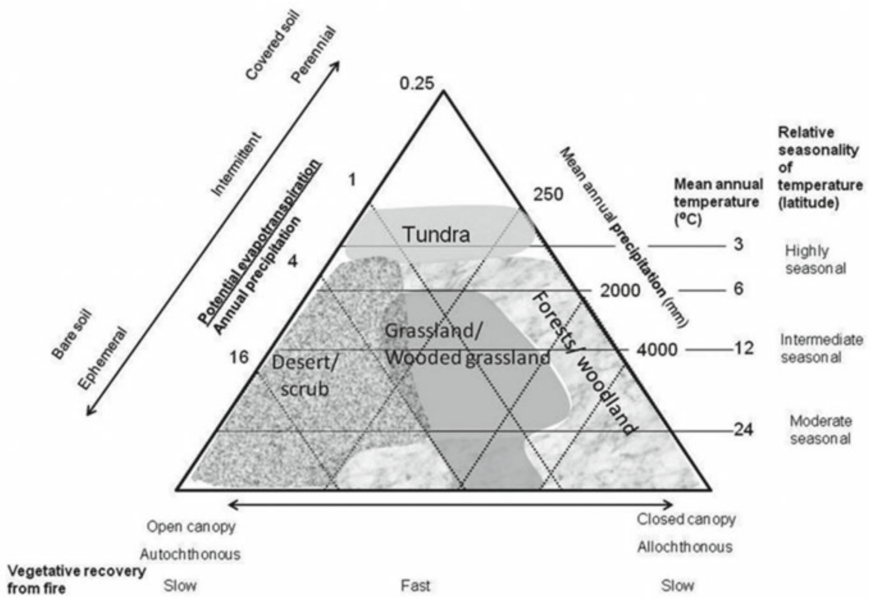

Fig. 13.2 Climate zones, vegetation types, and relationship to stream characteristics (modified from Holdridge [1947]). Image from Dodds et al. (2015)

allowing only low-stature vegetation in riparian zones. Woody vegetation can have indirect influences on decomposition as well. In restoring Australian rivers to mitigate temperature increases, a 10% increase in riparian cover leads to a 1 degree Centigrade lowering of temperature (Davies, 2010).

Within areas where precipitation is, at least seasonally, unable to meet demands for plant growth, the effects on riparian vegetation may be strong. Climate change will increase climate variability, and intense dry periods could alter riparian community composition. For example, climate change and lower fire frequency and intensity may be responsible for riparian woody expansion into tallgrass prairie streams (Veach et al., 2015) and this expansion has substantial influence on stream food webs and community composition (Riley & Dodds, 2012; Vandermyde & Whiles, 2015; Veach et al., 2015), water chemistry, and whole-stream metabolic rates (Larson et al., 2018). In similarly dry Mediterranean habitats, climate change is expected to inhibit early successional riparian communities slowing regeneration of these communities in response to disturbances such as floods (Rivaes et al., 2013).

Increased temperatures associated with climate change will alter Arctic and high altitude riparian vegetation. For example, alterations in ice breakup and scour will change riparian communities (Prowse et al., 2006). Warmer temperatures will allow higher stature and greater biomass of riparian vegetation to move to higher latitudes and altitudes. In the Boreal zone, increased temperature is predicted to allow invasive species to take hold, and lead to shifts in community structure as well as narrowing of riparian zones (Nilsson et al., 2013). In tundra habitats, this invasive vegetation could be trees.

Climate change leads to hydrologic alterations, and many studies link shifts in riparian communities with altered flooding and drying of flowing waters (Datry et al., 2018). In semi-arid to arid western North America, combined effects of elevated temperatures, altered precipitation regimes, and river regulation are expected to reduce the abundance of dominant, native, early-successional tree species (e.g., cottonwoods and willows) and favor herbaceous species, non-native drought-tolerant species (e.g., cheatgrass and tamarisk), and late-successional, woody shade-tolerant species (Perry et al., 2012; Reynolds & Shafroth, 2017). Some of these changes are associated with shifts in seeding phenology that result in asynchrony between seed release and snowmelt runoff or monsoonal precipitation, shifts in flood intensity and frequency, and higher plant water demand (Perry et al., 2012, 2020). Changes in the frequencies of large floods are also important in other regions (Hoffman & Rhode, 2011). For example, global climate models predict up to 27% change in riparian vegetation area in the Lake Michigan region (Primack, 2000).

Between 1965 and 2009, woody riparian vegetation in the Grand Canyon of the Colorado river increased in response to less flooding associated with river regulation. Experimental floods during the later portion of the time did not slow the movement of riparian vegetation to colonize and stabilize sand bars (Sankey et al., 2015). Increased flooding (flood augmentation) in Rocky Mountains (upper Arkansas River basin) decreased riparian wetland vegetation cover by 10% (Dominick & O’Neill, 1998). The North Platte River narrowed and more dense riparian tree cover developed in response to decreased spring flooding, however the upper Missouri River did not demonstrate similar responses (Johnson, 1998).

13.2.2 Native and Non-native Plant Species Changes

Shifts in native and non-native riparian plant species can have predictable effects on aquatic ecosystem structure and function (Kominoski et al., 2013). Invasive riparian plant species such as salt cedar (*Tamarix* spp.) Russian olive (*Elaeagnus angustifolia*), Japanese knotweed (*Fallopia japonica*) and others may displace native species and alter leaf litter quality and ecosystem functions in inland streams and rivers worldwide (e.g., Kominoski et al., 2013; Lecerf & Chauvet, 2008) (Fig. 13.3). The phylogeny of riparian plant species strongly influences leaf litter decomposition in adjacent aquatic ecosystems (LeRoy et al., 2020). A number of studies have shown that differences in litter quality are linked to genotypes of individual trees, resulting in variable rates of decomposition rates in streams (Marks, 2019). LeRoy et al. (2006) showed that different genotypes of poplar and their hybrids had very different decomposition rates in streams, and a similar result was seen in experimental ponds (Crutsinger et al., 2014). Jackrel and Wooton (2014) demonstrated using an experiment of reciprocal transplants of leaves that communities of detritivores showed adaptations to leaf litter derived from the local genotypes of red alder. Phylogeny

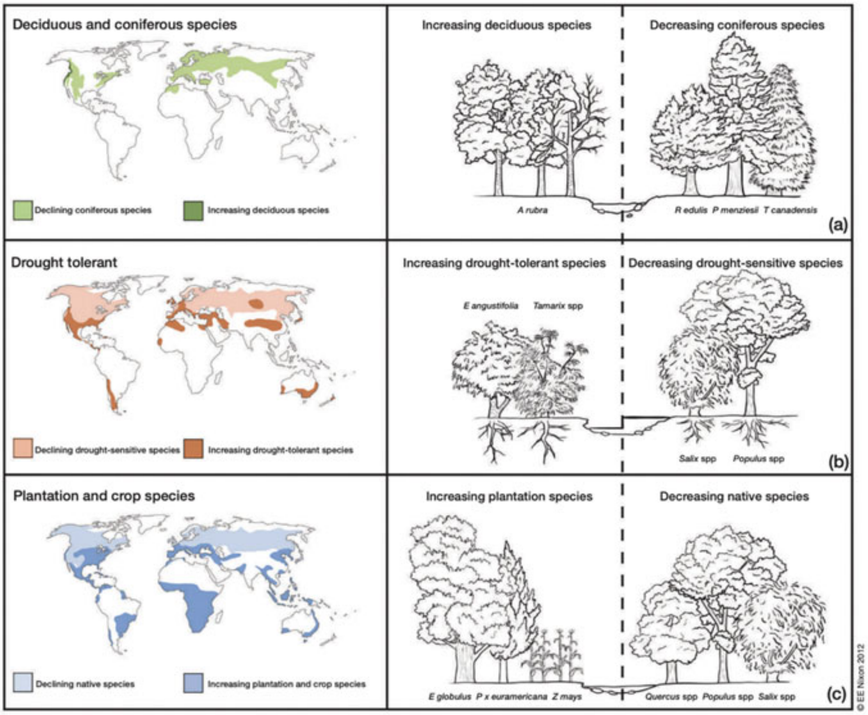

Fig. 13.3 Three global examples of broad-scale changes in riparian plant species composition: **a** shifts in coniferous and deciduous tree species, **b** increases in drought-tolerant species, and **c** global distribution of plantation and crop species. Distribution of increasing and decreasing tree species for each of the three examples are shown separately on each map. **a** *Pinus and Tsuga* species are declining throughout the Northern Hemisphere. These species are being replaced by deciduous species, such as *Alnus* species in North America. **b** *Populus* and *Salix* species are declining throughout the Northern Hemisphere, whereas drought-tolerant specious such as *Tamarix* specious (native to Eurasia) and *Elaeagnus angustifolia* (native from the Middle East to central Asia) are gaining in North America, Europe, South America, Asia, and North Africa. *Acer negundo (*native to North America) is increasing in Europe, and Salix (native to Europe) is invading Australia and New Zealand. **c** *Populus* and *Salix* species are declining throughout the Northern Hemisphere, with the exception of *Populus* hybrids grown in plantations in North America and Europe. Native riparian vegetation throughout North America, Europe, Asia, Australia, and South America are declining as land is used for plantation and crop species, such as *Eucalyptus* species and *Zea mays,* which are being planted globally. Illustrations of increasing and decreasing species emphasize how shifts in plant species composition have structural and functional consequences for riparian and aquatic ecosystems. Image from Kominoski et al. (2013)

also plays a role with regards to the rate at which litter mixtures decay in streams and rivers. Boyero et al. (2016) found that lower phylogenetic distance amongst leaf species decaying together in 24 streams along a latitudinal gradient promoted greater rates of mass loss in temperate biomes but slower rates of mass loss in the tropics.

In coastal wetlands, mangroves are invading marsh-dominated ecosystems globally, in one of the most dramatic plant range shifts occurring today (Perry & Mendelssohn, 2009; Saintilan et al., 2014). The expansion of mangroves into higher latitudes on a global scale is driven by various factors including sediment increases, sea level rise, and a declining frequency of severe freeze events, which is one of the four major drivers of structural change described in this chapter (Cavanaugh et al., 2014; Osland et al., 2013). Though air temperatures often drive mangrove expansion (Osland et al., 2013), finer-scale changes in mangrove extent respond to many secondary environmental factors such as erosion, land subsidence and accretion (Giri & Long, 2014). Thus, some mangrove expansion may be due to re-emergence from previous populations. As described above, woody plant invasion into herbaceous-dominated upland ecosystems alters belowground processes such as root productivity, organic matter decomposition (and its quality) and microbial carbon cycling (Knapp et al., 2008; Rundel et al., 2014). Similar changes in coastal wetlands could have dramatic consequences not only for biogeochemical cycling, but for the viability of the ecosystem as a whole, as organic matter buildup in coastal wetlands also maintains surface elevation (Krauss et al., 2014).

The declining frequency of freeze-related disturbances in Florida, U.S.A. has resulted in increased mangrove extent, and Doughty et al. (2015) found that mangrove coverage increased by 69% in just 7 years at a site in Eastern Florida. Similarly, a northeastern site in Florida saw a doubling of mangrove cover from 1986 to current day (Cavanaugh et al., 2014).

13.2.3 Agriculture and Forest Harvesting

Shifts in the composition of riparian contributions of leaf litter can result from natural disturbances, human disturbances, and long-term changes in land use. These events often create space for fast-growing, disturbance-dependent trees, some of which have undefended and high-quality leaf litter, such as red alder (*Alnus rubra*) and yellow poplar (*Liriodendron tulipifera*). These species depend on primary succession to establish, but are often unable to persist at a site without further disturbance, so over a time span of 60 to 80 years these trees are replaced by later successional species. Some similar successional changes can occur due to forest harvesting (e.g., Kominoski et al., 2011). The types of leaf litter inputs from riparian vegetation has a profound impact on the resulting stream community, particularly the composition of the detritivores trophic level (Kominoski et al., 2013).

In many parts of the world, there has been extensive planting of non-native species as forest crop trees. Some of the trees most commonly planted outside of their native ranges are eucalypts (*Eucalyptus globulus* and *E. nitens*) and radiata pine (*Pinus radiata*) (Ferreira et al., 2019; García et al., 2012). Ferreira et al. (2019) demonstrated that decomposition rates of same leaf species in streams flowing through *Eucalyptus* plantations are on average 23% lower than for streams in native forests, mostly due to reduction in macroinvertebrate densities. In that study, the magnitude of the inhibition of decomposition varied geographically, with greater effect sizes in more temperate regions, attributed to the greater influence of macroinvertebrates in subtropical regions (Ferreira et al., 2019). In addition to *Eucalyptus* plantations for fiber, other trees, such as palm oil and rubber trees are planted close to streamsides. In Malaysia, there were very small differences in macroinvertebrate assemblages on leaf packs draining palm oil forests versus native forest (Chellaiah & Yule, 2018).

Many tree species planted for fiber production in riparian habitats have leaf litter of low quality. In particular, conifers (pines, firs, etc.) and eucalypts are considered as low-quality due to being well defended physically and chemically against breakdown, having low N:C, and possibly chemical defenses (Graça & Cressa, 2010). Pine plantations in the UK have been a common target for afforestation, however, pine litter decomposes less than 20% as quickly as birch leaves, despite similar detritivore assemblages, and suggests planting pines or other conifers alongside streams could lead to reductions in stream productivity (Collen et al., 2004). In other parts of the world, North American trees such as Douglas-fir and Sitka spruce have been planted, often right up to streamside (e.g., Gee & Smith, 1997), although the impacts of these plantings on instream decomposition are not clear. Kominoski et al. (2011) showed that leaf litter decomposition rates were lower in streams flowing through conifer forests than streams with a larger component of angiosperms, primarily red alder). The overall productivity and yield of particulate detritus from catchments in Alaska with a high component of alder in riparian areas were much higher than streams draining mostly conifer stands (Wipfli & Musselwhite, 2004). These forestry related shifts in streamside species composition and consequent inputs will affect decomposition rates, either through types of inputs or catchment characteristics.

Forest harvesting, and other land-use, can impact instream decomposition rates. In some studies forest harvest has resulted in decreased rates of decomposition (e.g., Kreutzweiser et al., 2008; Lecerf & Richardson, 2010), whereas other studies have documented increased rates from forestry (Benfield et al., 2001, McKie & Malmqvist, 2009). In each of these studies there was little evidence for why decomposition rates changed, particularly in opposite directions in different regions. These impacts of forestry on decomposition rates occur whether or not riparian buffers are retained during harvesting, and the mechanisms for these changes remains an open research question.

Agricultural crops may be grown right up to stream edges in some jurisdictions. This would certainly alter leaf litter composition, and probably reduce input rates. An additional consideration is that in some parts of the world, crop plants have been genetically modified, and their leaf litter may include anti-herbivory chemicals. In much of the USA corn has been so-modified to include *Bacillus thuringiensis* (Bt) genes to reduce insect damage. The leaf litter from this corn has been shown to slow the growth rate of a detritivorous caddisfly larva, *Lepidostoma liba*, although there were no other large-scale effects on stream communities from such studies (Chambers et al., 2010). Conversion of forest to pasture has several effects on instream processes, including the particular types of leaf litter inputs. In three streams in Ecuador, the contrast between reaches in forest and pasture showed lower decomposition rates of a standardized leaf litter in pasture reaches, largely attributed to the absence of a single species of shredding caddisfly larvae from pasture streams (Encalada et al., 2010). Young et al. (1994) found rates of leaf litter decomposition were higher in streams draining more intensively managed pastures, which they attributed to higher nutrient yield, particularly Nitrogen, from pastures.

13.2.4 Urbanization

The urban stream syndrome represents the suite of alterations to stream ecosystems that accompany urbanization (e.g., Booth et al., 2016; Paul & Meyer, 2001). These include increased peaks in flows, increased nutrients and contaminants, warmer peak temperatures and rapid shifts, channel simplification, altered riparian vegetation, etc. All of these aspects can influence litter decomposition rates (Young et al., 2008). Litter decomposition rates are often different in urban streams from those in comparable forested sites, due to a host of potential influences. For example, in urban streams in Puerto Rico, decomposition rates were only 30% or lower than rates in forested streams, attributed to loss of consumer species in urban streams (Classen-Rodriguez et al., 2019). Similarly, breakdown rates in urban streams in Brazil were about half that of rates in forested streams, considered to be due to shifts in decomposer assemblages, especially loss of detritivorous invertebrates (Martins et al., 2015). Decomposition of litter in a stream in Malaysia was nearly twice as rapid in urban reaches than in forested sections, presumably due to nutrient enrichment (Yule et al., 2015). Breakdown rates in streams in Maine were higher in more urbanized catchments, and was attributed to elevated concentrations of nutrients along the rural to urban gradient (Huryn et al., 2002). Rates of breakdown were almost four times higher in urban streams in the Southeast USA compared to forest streams (Paul et al., 2006). The influence of urbanization is large, but the direction and magnitude are highly variable, and depends on the suite of processes altered in any given urban setting.

13.3 Impacts of Altered Litter Decomposition Throughout River Networks

13.3.1 Land-Use Change Impacts

Organic matter source and bioavailability are closely linked to human land use activities. Global reductions in terrestrial C are attributed to increasing human co-option of terrestrial gross primary production (Running, 2012). For example, wetland drainage and riparian land clearing remove terrestrial organic matter storage, and widespread replacement of native vegetation with agricultural crops for direct and indirect human consumption reduce carbon availability for ecosystem functions and services (Allan, 2004; Running, 2012). Projected increases in cultivated land area coupled with increased nutrient mobilization (MEA, 2005) will reduce the amount of terrestrial organic matter loading (Running, 2012) and increase in situ aquatic organic matter production, which is more bioavailable. This shift towards more readily available organic matter will influence secondary production and energy flow paths within aquatic food webs from headwaters to downstream lakes and rivers (Griffiths et al., 2009). The distribution of dissolved organic carbon in the Ipswich River, Massachusetts demonstrates how organic matter processes throughout a river network potentially contribute to nutrient regulating and water supply ecosystem services (Stewart et al., 2011). In agricultural regions, the interaction of increased nutrient inputs, reduced terrestrial carbon inputs, and reduced light limitation explain why most carbon export from the Mississippi River Basin is due to aquatic primary production (Shih et al., 2010).

13.3.2 Climate Change and Eutrophication Impacts

Global changes in soil and water temperatures, hydrologic variability, and nutrient availability will increase rates of ecosystem metabolism and alter organic matter export (Acuña & Tockner, 2010). Elevated temperature increases rates of leaf litter decomposition in streams and rivers (Follstad Shah et al., 2017). The magnitude of this increase is similar, whether decay is mediated by microbes alone or due to the combined effects of microbes and detritivores (Follstad Shah et al., 2017). However, this thermal response of detritivores may not scale to the level of river networks, as decomposition rates at this scale depend on the availability of terrestrial organic matter inputs. For example, some of the land use changes (described above) reduce inputs of terrestrial organic matter inputs to streams and rivers. In addition, net primary production may be diminished in water-stressed riparian plant communities, despite elevated CO_2 concentrations that promote higher rates of photosynthesis and growth and greater water use efficiency (Perry et al., 2013). These studies imply that changes to riparian community organic matter production can modulate predicted effects of climate change at the scale of river networks. Reservoirs alter upstream-downstream organic matter linkages via increased storage of organic matter within reservoirs (Vörösmarty et al., 2003) and enhanced loss of carbon as CO_2 and methane (CH_4) emissions (Kominoski & Rosemond, 2012; Tranvik et al., 2009). Streams with lower terrestrial organic matter inputs and lower standing stocks of benthic organic matter, as well as downstream reaches of river networks that have lower quality organic matter, are likely to remove less nutrients (Barnes et al., 2012; Taylor & Townsend 2010), potentially contributing to denitrification efficiency loss (Mulholland et al., 2008). Reductions in standing stocks of organic matter could result in lower secondary production of food webs that support downstream fisheries (Cross et al., 2006).

Elevated temperature and moderate eutrophication are shifting streams and rivers towards greater heterotrophy, resulting in more emissions of CO_2. Whole-stream metabolism studies along natural thermal gradients show that ecosystem respiration increases in response to rising temperature to a greater extent than gross primary production, resulting in declines in net ecosystem production (Demars et al., 2011). Moderate nutrient enrichment stimulates organic matter decomposition rates in streams and rivers (Woodward et al., 2012) and at the network scale results in reduced terrestrial C residence time (Rosemond et al., 2015). In temperate biomes, terrestrial C losses can exceed instream C production resulting in greater net heterotrophy (Rosemond et al., 2015). Again, however, this pattern is dependent on terrestrial C supply concomitant with heterotrophic demand for C in eutrophic systems.

Model simulations show that flow regime alterations have a greater effect on organic C dynamics within river networks than altered thermal regimes, but this effect is most pronounced in headwater streams relative to mainstem rivers (Acuña & Tockner, 2010). More floods and longer droughts are predicted to reduce the amount of organic C processed within the river network due to reduced rates of respiration and increased C export (Acuña & Tockner, 2010). Some of the increased export of C in Mediterranean systems may also be due to drought-induced phenological shifts in leaf litter senescence, followed by winter flood events (Acuña et al., 2007).

Climate change further poses unprecedented effects on coastal regions by causing saltwater intrusion into vulnerable ecosystems through accelerating rates of sea-level rise, changes in the hydrologic cycle and temperature regime, and potentially the increasing strength and frequency of storms (Farfan et al., 2014; Herbert et al., 2015, Nicholls & Cazenave, 2010; Osland et al., 2016). Direct effects of climate change on coastal ecosystems can result in loss of wetland area and ecosystem function if and when rates of sea-level rise exceed the natural capacity of foundation species in wetlands to adapt (Charles et al., 2019; Saha et al., 2011; Wilson et al., 2018). Low-lying coastal ecosystems are periodically influenced by storms and continuously influenced by sea-level rise and saltwater intrusion (Dessu et al., 2018; Herbert et al., 2015; Osland et al., 2016). Our collective understanding is that saltwater intrusion generally decreases C storage and increases nutrient export in coastal wetlands (Ardón et al., 2013, 2016; Charles et al., 2019; Herbert et al., 2015, 2018; Neubauer, 2013; Wilson et al., 2018).

13.3.3 Impacts of Altered Hydrologic Connectivity

Ecosystems are becoming increasingly more or less connected through globalization, fragmentation, and climate change. Connectivity—the flow of organisms, water, materials, and ecological processes across landscapes (Taylor et al., 1993)—can be used to understand how to better manage and restore threatened and declining ecosystems (Haddad et al., 2015; Kominoski et al., 2019; Pringle, 2001). The extent and health of coastal ecosystems are declining worldwide (Dahl & Stedman, 2013; Nicholls et al., 2007), so understanding how changes in hydrologic connectivity influence the structure and function of these threatened ecosystems is paramount (Sheaves, 2009). Storage and accumulation rates of carbon and nutrients in coastal wetlands are sensitive to underlying topographic gradients that influence hydrologic connectivity to these sources, as well as temporal changes in connectivity that can be both directional (e.g., sea-level rise) and episodic (e.g., hurricanes, droughts, floods). Therefore, hydrologic connectivity can influence biogeochemical processes, including net primary productivity and organic matter mineralization (Bouillon et al., 2008; Castañeda-Moya et al., 2013; Koch et al., 2012; Noe et al., 2001).

Changes in hydrology associated with urbanization and river regulation influence the sources and fates of organic matter in river networks. Urbanization increases impervious cover, reducing infiltration rates and increasing the tendency of flash floods as well as increasing organic matter via septic and sewage inputs (Paul & Meyer, 2001; Walsh et al., 2005). Therefore, urban watersheds are likely to have less continuous sources of soil carbon due to reduced infiltration rates, but potentially more C point sources associated with engineered open spaces (Aitkenhead-Peterson et al., 2009) or instream production and wastewater inputs (Newcomer et al., 2012). Urban watersheds may also exhibit increased retention and burial of C in reservoirs (Vörösmarty et al., 2003). All of these factors ultimately alter the quantity and bioavailability of organic matter in urbanized waterways. River regulation alters the hydrologic regimes, but also the distribution of lotic and lentic surface waters in river networks. Acuña and Tockner (2010) showed that the majority of organic C inputs to river networks is processed within reservoirs, which altered C dynamics in river reaches below impoundments. Reservoirs alter upstream-downstream organic matter linkages via increased storage of organic matter within reservoirs (Vörösmarty et al., 2003) and enhanced loss of carbon as CO_2 and methane (CH_4) emissions (Kominoski & Rosemond 2012; Tranvik et al., 2009).

13.3.4 Impacts on Ecosystem Services

Detrital organic matter is a critical supporting component of many ecosystem functions, and the production, storage, transformation, and transport of organic matter are spatially and temporally dynamic throughout watersheds and river networks (Fig. 13.1; Hall & Meyer 1998; Minshall et al., 1983; Thorp & Delong, 1994). The ability for science to link biophysical processes of litter, to societal values of ecosystem services requires a mechanistic understanding of how these functions and services are related and linked spatially and temporally (Bennett et al., 2009; Daily et al., 2009; Rosemond et al., 2015). A critical knowledge gap is understanding how these ecosystem services are driven by network-level organic matter dynamics, which is required given dynamic and heterogeneous changes in transport, sources, and processing of litter from various locations throughout river networks. The relative importance of organic matter sources changes longitudinally within river networks (Vannote et al., 1980). The relative support of the basal resources supporting aquatic food webs from particulate and dissolved terrestrial and aquatic sources is highly variable throughout river networks and estuaries (Cawley et al., 2014; Sobczak et al., 2002). Worldwide construction of dams for hydropower generation increases the accumulation and burial of organic matter (Downing et al., 2008) that can lead to sources of CO_2 and methane (Kominoski & Rosemond, 2012; St Louis et al., 2000; Tranvik et al., 2009). The cycling of nitrogen and phosphorus are closely linked to the availability of detrital carbon (Kominoski et al., 2018; Rosemond et al., 2015; Seitzinger et al., 2006; Taylor & Townsend, 2010) and thus the amount of nutrients retained on land rather than exported downstream where eutrophication and hypoxia of coastal waters has caused collapse of estuaries (NRC, 2000; Rabalais et al., 2002). Organic matter primarily contributes to regulating and supporting ecosystem services via its control of ecosystem function through microbial food webs and biogeochemical processes that are foundational to many—if not all—aquatic ecosystem services.

In coastal wetlands, mangrove encroachment can increase ecosystem C storage (Doughty et al., 2015; Kelleway et al., 2016), but the magnitude of these C storage differences depends on environmental setting (Yando et al., 2016). The majority of mangrove carbon storage increases are often due to aboveground biomass (Charles et al., 2020; Doughty et al., 2015) but some studies show that soil carbon can also increase either over longer time scales (Kelleway et al., 2016) or in some cases rapidly (Simpson et al., 2019). Using experimental mangrove removals, Guo et al. (2017) found that mangrove cover was positive related to soil organic carbon content. Increases in soil carbon storage when mangroves invade into marshes are likely driven by an increase in root growth (Fig. 13.4; Coldren et al., 2019). Although organic matter decomposition is an important driver of the blue carbon storage in wetlands and of surface elevation, less is known about how decomposition changes when mangroves encroach into salt marshes (but see Charles et al., 2020). Decomposition rates in coastal wetlands depends in part on litter quality, but also are controlled by the oxygen availability in oils, as anoxic conditions limit enzyme reactions that control organic matter breakdown (Chapman et al., 2019). It's possible that mangrove encroachment into salt marshes could alter both the litter quality and the oxygen availability. Perry and Mendelssohn (2009) found no difference in decomposition rates in plots where mangroves had encroached into the marsh as compared to those still dominated by the salt marsh grass *Spartina alterniflora*. However, Charles et al. (2020) found that mangrove litter decomposed much more slowly than the dominant salt marsh plant *Batis martima* in coastal Texas sites where mangroves are encroaching. Taken together, these findings suggest that changes in organic matter decomposition with mangrove encroachment may depend on the species composition of the salt marsh.

The ability of aquatic ecosystems to support ecosystem services for society depends on the timing, quantity, and source of organic matter inputs. Global environmental changes (e.g., climate, land-use, and hydrology) influence the quantity, source, and processing rates of organic matter (Kominoski & Rosemond 2012; Tank et al., 2010), which challenge our ability to maintain and sustain aquatic ecosystem services (Fig. 13.1 and examples above). The magnitude and speed of these global changes lends urgency to better quantify organic matter dynamics that support aquatic ecosystem services at network scales. The variability in organic matter sources and transformations across different aquatic ecosystems (streams, lakes, wetlands) will result in retention, production and transport dynamics that vary over space and time.

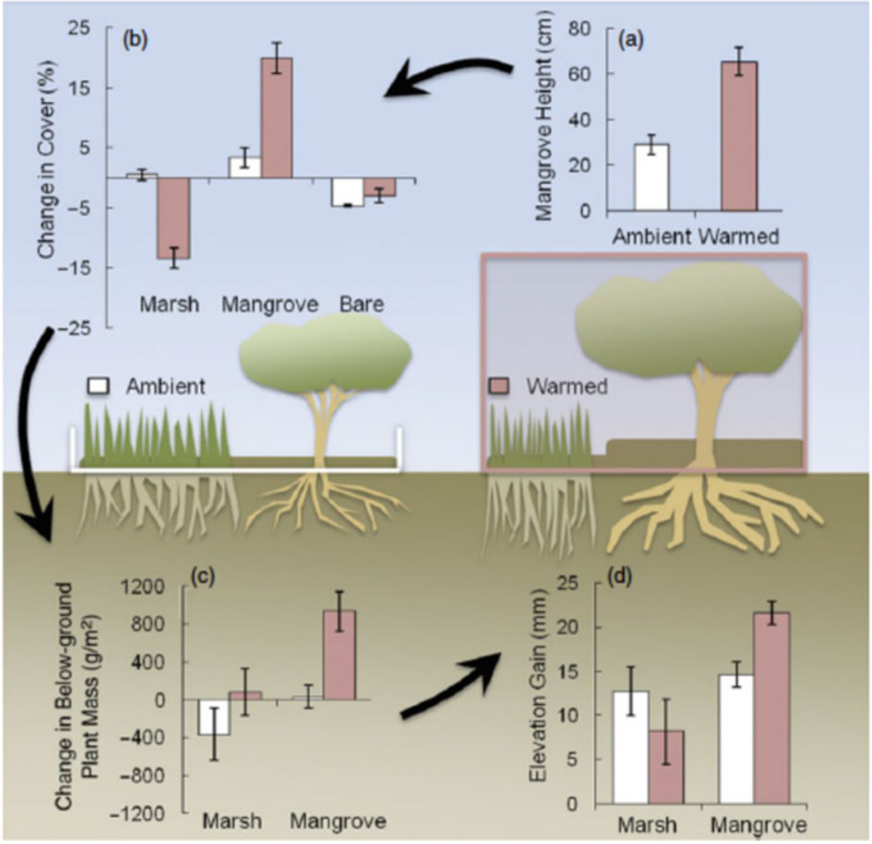

Fig. 13.4 Response of mangroves and salt marshes to warming conditions: **a** mangrove height (cm), where chronic warming accelerates vertical growth, **b** percent change in cover, where areal expansions of mangrove shade out salt marsh plants, **c** change in below-ground plant mass (g/m^2), where increased root productivity and areal coverage of individual mangroves result in greater below-ground growth, and **d** change in elevation (mm), which is largely determined by changes in below-ground biomass. Warming treatments included ambient (control) and warming chamber. Data are means ± SE. Image from Coldron et al. (2019)

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