Beyond the mangroves: a global synthesis of tidal forested wetland types, drivers and future information needs

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Abstract

There is increasing awareness of the global diversity of tidal forested wetlands (TFWs) and their significance in the provision of ecosystem services. These ecosystems, including mangrove forests, tidal freshwater forested wetlands, supratidal forests and transitional forests together span tropical to temperate climatic zones and occur across diverse geomorphic, inundation and salinity regimes. We utilise twelve case studies across five continents to demonstrate the state of knowledge among TFWs and identify commonalities and differences among settings. Intertidal mangroves are the best-defined of the TFWs thanks to decades of research on their geomorphology, hydrology and ecology across their broad distribution. Non-mangrove TFW settings, however, demonstrate more diverse hydrological, biochemical and vegetation conditions. In many cases, non-mangrove TFWs are situated at upper intertidal or supratidal elevations, where surface waters and groundwater are subject to interactions between astronomic tides, meteorological tidal anomalies, and freshwater inputs. Salinity datasets, where available, show variations ranging from tidal freshwater forested wetlands and 'low-salinity mangroves' to mesohaline or marine salinities, often with high temporal variability. While the floristic composition of non-mangrove TFWs varies among biogeographic regions, locally dominant TFW species are commonly distributed beyond the tidal niche into non-tidal wetland and upland forests. This presents challenges for traditional remote sensing approaches to ecosystem mapping.

The landscape position and forested structure of TFWs supports provision of timber, fuel, foods and other culturally-important products, as well as maintenance of aquatic and coastal services and greenhouse gas regulation. Growing evidence of these ecosystem service values can help motivate arrest and reversal of contemporary and extensive historic losses of TFW. Major knowledge gaps regarding the roles of tidal processes and biophysical controls – and the implications of sea-level rise and climate change – should be addressed to maintain these ecosystem services given contemporary and extensive historic losses of TFW distribution. This need is particularly significant in major river deltas (including the Amazon and Niger) and lowland peat swamp forests of Southeast Asia. Continued collaboration across diverse settings, and the incorporation of non-mangrove TFWs into mangrove and blue carbon initiatives presents new opportunities for improved outcomes for all TFWs across local to global scales.

1. Introduction

Wetlands across the world's coastal zones exhibit diverse vegetation structures and compositions, reflecting the complex interactions of marine and fresh waters, climatic, geomorphic and other biogeographic drivers, and legacies of anthropogenic influence. Among the array of coastal wetland types, there is increasing awareness of the diversity and function of tidal forested wetlands (TFWs): forested wetland ecosystems that are subject to the influences of tides. These TFWs span ecosystems experiencing regular surface inundation by tides, including most intertidal mangrove forests, tidal freshwater forested wetlands, and Sitka spruce TFWs (among others), to forested wetlands only occasionally subject to tidal inundation, or those receiving only indirect impacts of the tides via their influence on surface hydrological regimes, water table depths and groundwater salinities (Wolanski et al. 1992, Duberstein et al. 2013, Adame et al. 2024). That is, diverse TFWs may be distributed across 'intertidal' or 'supratidal' positions of sheltered coasts and estuaries, as well as occurring as 'transitional' forested wetlands situated immediately upslope or upstream of mangrove forests or salt marshes, where hydrological connection and/or salinity gradients with adjacent mangroves or marshes may occur (Ewel 2009, Martínez-Camilo et al. 2020, Cejudo et al. 2022).

In some settings, tidal influences may interact with rainfall or flooding events (seasonal or episodic) and/or coastal storm surges to create compound flooding conditions (Goodman et al. 2018, Kumbier et al. 2018) which likely influence TFW distribution, structure and function. Understanding the relative importance and interaction of these biophysical drivers is of particular importance for understanding and managing stressors associated with climate change, sea-level rise and saltwater intrusion, as well as anthropogenic impacts and management interventions (Schuerch et al. 2018, Tran et al. 2022, Visschers et al. 2022). For mangroves – the most broadly distributed and well-researched TFW type – knowledge of biophysical drivers and ecological function have been greatly advanced in recent years due in part to the global interest in 'blue carbon' and their role in climate change mitigation (Friess et al. 2019, Macreadie et al. 2021). For many other TFW types, however, significant knowledge gaps remain, despite emerging evidence of their potential for provision of blue carbon and other ecosystem services (Krauss et al. 2018, Kauffman et al. 2020, Adame et al. 2024).

Research into the distribution, biophysical processes, and ecosystem service provision among TFWs is currently in its infancy in most settings and remains absent for many regions. Such paucity of knowledge is limiting understanding, protection and restoration of these specific ecosystems, as well as TFWs collectively. Understanding and managing for the implications of human impact and climate change on TFWs requires knowledge of: (1) the diversity and distribution of TFW ecosystems and their component biota; and (2) the dominant biophysical processes which influence TFW distribution, ecological structure and ecosystem function.

Together, TFWs have a distribution spanning multiple continents (Adame et al. 2024), that extends beyond the latitudinal distribution of mangroves alone. Throughout their range TFWs are mostly defined by regional names and descriptions, many of which we explore and describe in this article. We synthesise the state of knowledge of such TFWs through 12 case studies from relatively better-studied settings, while compiling available information from other settings. We describe the dominant biophysical conditions of each of these settings and review the ecosystem service values, threats and opportunities across these ecosystems. We then synthesize commonalities and differences among these global TFWs and present lessons from the mangrove blue carbon experience as a blueprint for the improved valuation and management of all TFW ecosystems across multiple scales.

2. Classification and terminology

For consistency and clarity, we propose a three-tiered hierarchy of terminology for describing forested wetland ecosystems from broad to specific circumstances (Figure 1), which we follow in this article:

1. 'Coastal forested wetlands' (CFW) refers to all forested wetland ecosystems in the coastal zone, regardless of their hydrological regime (i.e. tidal and non-tidal; permanent to infrequent inundation) or salinity regime. This term is broadly used in the literature, including to link both tidal and non-tidal settings (Conner and Day 1988, White et al. 2021, Conroy et al. 2022). Non-tidal CFWs may include forested wetlands associated with floodplains of non-tidal rivers, dune swales, non-tidal lakes and lagoons, non-tidal lowland peat swamps, as well as forested wetlands behind anthropogenic structures which exclude direct or indirect influences of tides.

2. 'Tidal forested wetlands' (TFW) refers to all coastal forested wetlands whose structure, composition and function are influenced by tidal processes. Such influence may range from regular or occasional surface inundation by astronomic or other tides, to indirect influence of tides on wetland water tables and/or saline groundwater intrusion. Although the influence of astronomic tides is better known, TFW also includes wetlands which may be subject to anomalies of astronomic tides due to atmospheric conditions (e.g. low-pressure systems; wind tides), as well as forests influenced by compound events (i.e. co-occurrence of tidal and non-tidal hydrological events such as seasonal river flow fluctuations and storm surge). By definition, TFW is inclusive of intertidal mangrove forests. In instances where mangroves are to be specifically excluded, such as for comparative purposes, we suggest and use the term ‘non-mangrove TFWs’. The name TFW is used in preference over the arrangement ‘Forested Tidal Wetlands’ (e.g. Williams et al. 2019) to maintain the symmetry of TFW with existing terms of CFW, ‘tidal freshwater forested wetlands’ (TFFW), and ‘tropical coastal freshwater forested wetlands (TCFFWs)’.

3. Setting-specific terms of TFW types such as mangrove forest, TFFW, TCFFW, transitional forests, supratidal forest and maritime forest (among others) are often descriptive of the conditions in which these ecosystems are distributed. The use of such terms may be crucial to capture the nuances among ecosystems and enable differentiation, when needed, based on their geomorphic, biochemical or ecological attributes. In some cases, geographic descriptors are also used to differentiate between settings (e.g., ‘Atlantic’; ‘Pacific North West’) and are used in our case studies below to specify where current knowledge pertains to.

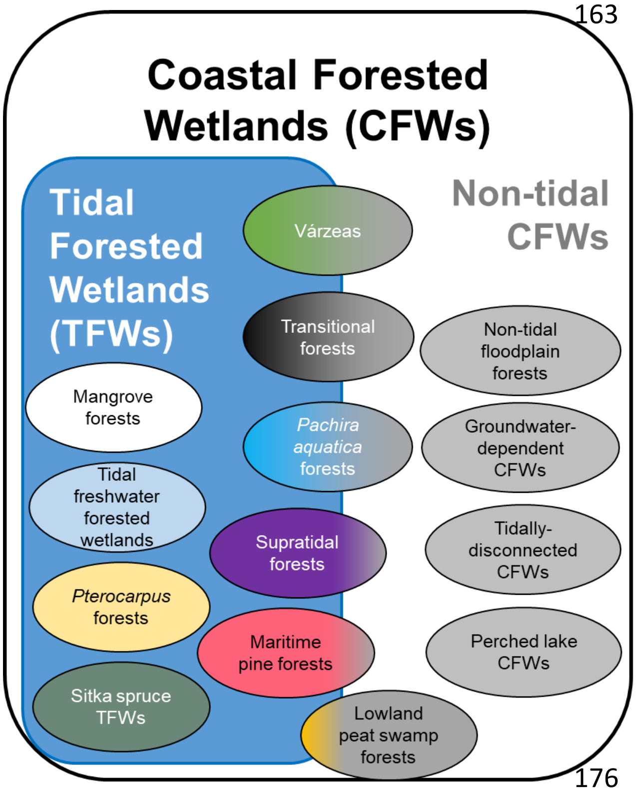

Figure 1. Hierarchy of forested wetland terminology in the coastal zone, across broad (‘CFW’), intermediate (‘TFWs’, ‘non-tidal TFWs’ and setting-specific names and ecosystem descriptors (ovals). This list of ecosystem types is not exhaustive at the setting-specific level. Note the existence of diverse non-tidal forested wetlands in the coastal zone which are not reviewed in this paper, and gradient of many setting-specific terms across both tidal and non-tidal classes.

3. Case studies from specific TFW settings

In this section we utilise a series of case studies from TFW settings that are among the best represented in the existing and emerging scientific literature. For each, we review the known distribution, biophysical controls, and dominant plant taxa of the ecosystem. While these case studies are far from comprehensive, they demonstrate the broad similarities and differences among TFW settings at regional to global scales.

Mangrove forests

Spatial distribution: The term 'mangrove' is used to refer to both (1) a broad collection of woody plant species; and (2) an intertidal ecosystem; distributed along tropical, subtropical and some warm temperate coastlines worldwide. Mangrove forests cover approximately 145,000 km^2 across 120 countries and territories (Bunting et al. 2022, Jia et al. 2023). Large areas of mangroves are found in Southeast Asia (Indonesia holds about a quarter of the world's mangrove area), the Amazon Macrotidal Mangrove Coast, the Sundarbans in the Bay of Bengal, Niger Delta in Africa, and the coastlines of Australia. At a global scale, the geographic distribution of mangroves is primarily limited by temperature and aridity (Osland et al. 2016). Mangroves are generally found between the latitudes of 25° N and 25° S, where sea surface temperatures remain above 20°C throughout the year (Duke et al. 1998), though some species extend beyond this latitudinal range – for example, up to 38°S in southern Australia – with expansion or thickening near the latitudinal limits observed across multiple continents (Saintilan et al. 2014, Giri and Long 2016). Substantial mangrove-forest expansion has also occurred in New Zealand's numerous upper North Island estuaries due to estuary infilling with eroded soils, associated with catchment deforestation and conversion to pastoral agriculture since the mid-1800s (Morrisey et al., 2010, Swales et al., 2020). Across their distribution mangroves can form dense forests along low energy coastlines, estuaries, river deltas and lagoons, where they play crucial roles in coastal protection, carbon sequestration, and supporting biodiversity (Rovai et al. 2018, Friess et al. 2020).

Biophysical controls: Mangrove forests are composed of salt-tolerant tree and shrub species, and typically occur within the upper half of the tidal frame, that is, from about mean sea-level and above (Krauss et al. 2008). Mangrove forests are therefore periodically inundated by tidal surface waters, though the frequency and period of inundation will vary according to local geomorphic and hydrologic factors, including tidal range, elevation, and the influence of non-tidal inputs such as riverine flooding and storm or wind surges (Krauss et al. 2009).

Mangrove species may exhibit distribution patterns based on their tolerance to hydroperiod and salinity, with certain species occupying specific elevations relative to sea level (Crase et al. 2013). Mangroves exhibit a variety of adaptations to cope with saline environments, including specialized root systems, salt-excreting leaves, and physiological mechanisms to maintain water balance (Madhavan et al. 2024). However, salinity tolerance varies among different mangrove species, influencing their distribution within estuarine and deltaic settings (Barik et al. 2017, Dittmann et al. 2022). In areas with high salinity, such as hypersaline lagoons, mangrove diversity may be lower, with only the most salt-tolerant species able to survive. While mangroves most commonly occur within saline or brackish, estuarine settings, 'freshwater' mangrove forests have been described from low salinity locations in South and Central America (Martínez-Camilo et al. 2020, Bernardino et al. 2022). A recent estimate suggests inclusion of previously unmapped 'freshwater mangrove', comprising both mangrove-obligate and facultative-wetland species, represents a ~20% increase in the total mangrove area in the Amazon Delta (Bernardino et al. 2022), though distribution elsewhere is poorly constrained.

Significant plant taxa: The term 'mangrove' is also used in reference to the collection of woody plants with necessary physiological and morphological adaptations for living in intertidal environments, with many from diverse evolutionary lineages (Tomlinson 1986). Definitions of mangrove species are therefore subjective, with global counts ranging from 51 to >80 species, across ~20 plant families (Tomlinson 1986, Duke et al. 1998, Kathiresan and Dagar 2024). Species definitions differ mostly due to uncertainty in whether low-salinity back-mangrove species should be counted within the mangrove ecosystem. Nevertheless, taxonomic diversity is greater in the Indo-West Pacific relative to the Atlantic-East Pacific, though the dominant genera *Avicennia* and *Rhizophora* contain species across both regions (Duke et al. 1998).

Many mangrove species are viviparous, meaning seeds germinate while still on the parent plant, while the buoyancy of these propagules enables distribution with tides and currents (Tomlinson 1986, Madhavan et al. 2024). This reproductive strategy is less common among other TFW types, where contributions via seedbanks or vegetative reproduction may dominate (Infante Mata and Moreno-Casasola 2005, Salter et al. 2010). Some classifications refer to selected species as 'mangrove associates', based upon differences in salinity or inundation tolerances, and/or their distribution in 'transitional' ecosystems (Tomlinson 1986).

There may be overlap in the inclusion of 'mangrove' and 'mangrove associate' taxa with other TFW settings, including some of those described below.

Tidal freshwater forested wetlands (TFFW) of southern and eastern USA

Spatial distribution: Tidal freshwater forested wetlands (TFFW; also known as tidal swamps) are a TFW that occur in every coastal state from Texas on the Gulf Coast to New York on the Atlantic Coast of the U.S. (less common north of Delaware; Duberstein et al. 2014). TFFWs are found in the upper estuary of rivers and streams of the North American Coastal Plain, where sufficient freshwater discharge from the watershed meets ocean tidal forcing (Doyle et al. 2007). Tidal freshwater rivers are a significant part of North American Coastal Plain water bodies totalling ~3,000 km in length from Florida to New Jersey alone (Ensign and Noe 2018). Watershed geomorphology, primarily size and slope, along with tidal range play a significant role in determining the extent of TFFW along tidal rivers. For example, TFFW occupy nearly the entire 5-km wide floodplain, and cover nearly 75 km^2, along the large Savannah River in Georgia and South Carolina (Krauss et al. 2008), whereas TFFW width along the small Mattaponi River in Virginia reduces to nearly 10 m near the head-of-tide (Kroes et al. 2023).

Biophysical controls: As suggested by the name, TFFW are located in the tidal freshwater zone. Tree and shrub richness and evenness decreases as the tolerance thresholds of individual species to salinity and sulfide is exceeded at chronic salinities of 1-2 psu, leaving a monoculture of *Taxodium distichum* trees (if present, see below) in areas with chronic interstitial salinities of 2-4 psu (Krauss et al. 2007, Hackney et al. 2007). TFFW transition to tidal freshwater marsh lower in the tidal frame and downriver in the tidal freshwater zone, and transition to tidal oligohaline marsh downriver as prolonged inundation or salinization causes lower diversity of trees and thin canopies that allow the establishment of herbaceous and graminoid understory species. Upriver of TFFW is typically bottomland hardwood (nontidal) floodplain forest, and upslope laterally is low elevation *Pinus taeda* tidal forest (described below) or more commonly terrestrial forest, agriculture, or human development. Many TFFW have a topography consisting of low slope base elevation (i.e., the extensive hollows) that are typically equivalent to mean high water, get inundated most tidal cycles, and drain slowly (Day et al. 2007, Krauss et al. 2009). Amid the hollows are slightly elevated hummock islands (15 – 20 cm; Anderson and Lockaby 2007), ranging 1 – 10 m^2 in size, and comprising 20-30% of the landscape (Duberstein 2011). Most tree species are found in greater numbers on hummocks as compared to hollows (Duberstein 2011), likely because hummocks are inundated briefly only during higher spring tides (Day et al. 2007). Groundwater is rarely deeper than 10 cm below the wetland soil surface (Krauss et al. 2009) (Figure 2).

Significant plant taxa: TFFW includes a large species pool of trees, shrubs, and emergent vegetation. Duberstein et al. (2014) identified four common plant communities among TFFW: *Nyssa aquatica* (water tupelo), *Nyssa biflora* (swamp tupelo), *Sabal minor* (dwarf palmetto), and *Sabal palmetto* (cabbage palm). *Taxodium distichum* is common in most TFFW, except at latitudes north of Virginia and Maryland. Co-dominant trees and shrubs also can include *Acer rubrum, Fraxinus* spp., *Quercus nigra*, *Liquidambar styraciflua*, *Alnus serrata*, and *Morella cerifera*. Nearly all taxa have distributions that extend beyond TFFWs, especially those species common to non-tidal floodplain forests.

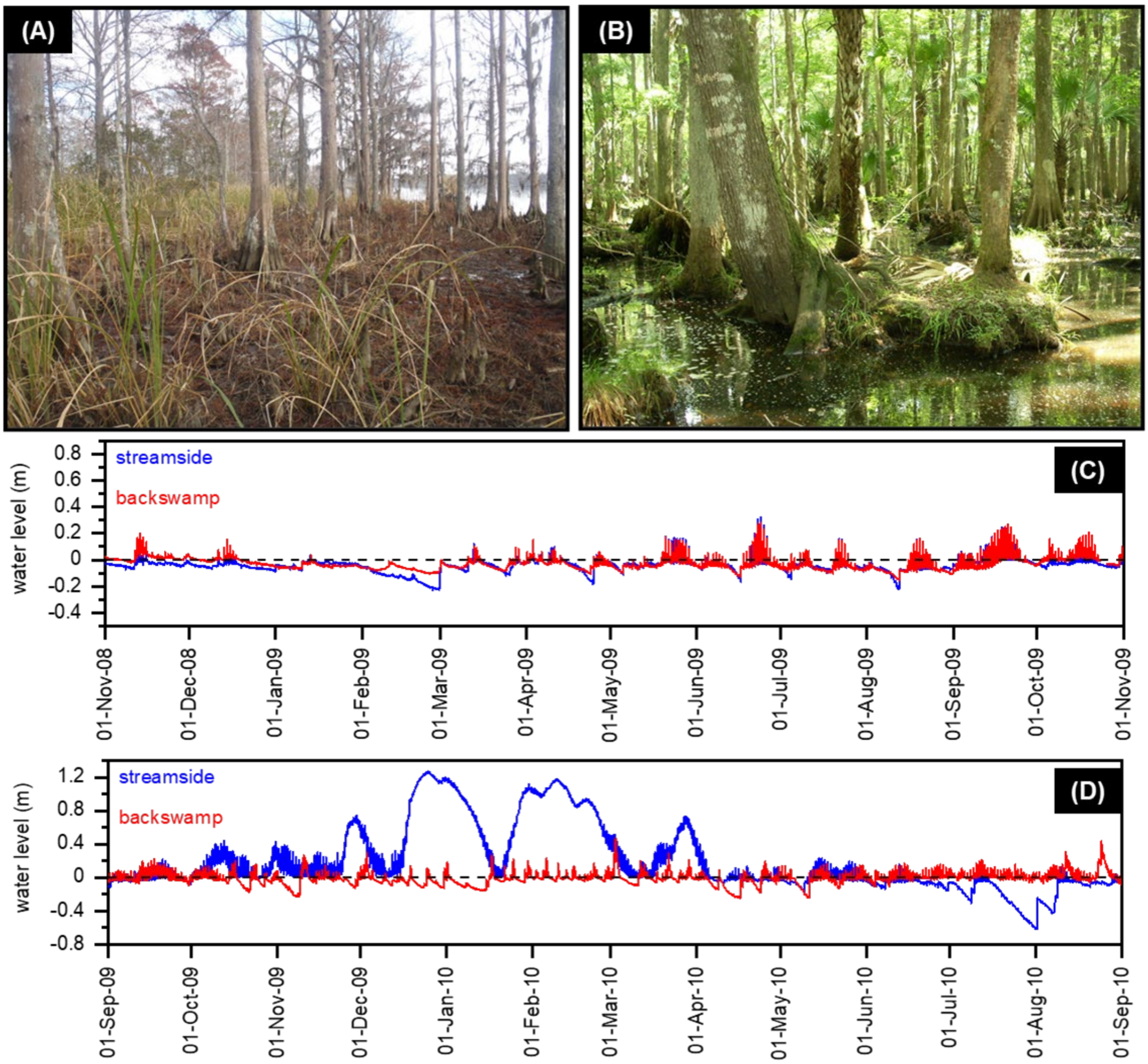

Figure 2. Southern and eastern USA tidal freshwater forested wetlands as a monoculture of baldcypress due to salinity stress along the Waccamaw River (A); as a relatively diverse

broadleaf tree community situated in a backswamp location with extensive hummock and hollow topography along the Suwannee River (B). Hydrographs for TFFW in streamside (~250 m from the river) and backswamp (> 1 km from the river) sites along the Savannah River (C) and Altamaha River (D). Dashed lines at 0 m represent ground surface in each hydrograph. Credits / sources: KW Krauss (A), JA Duberstein (B); Duberstein 2011 (C, D).

Várzea floodplain forests

Spatial distribution: Várzea floodplain forests are distributed from the mouth of the Amazon and Tocantins rivers to the western Amazon lowland floodplains (Figure 3). Várzea floodplain forests cover approximately 150,000 km^2 (da Silva Marinho et al. 2010) and tidal influence along the Amazon River extends throughout the lowland floodplain and has been suggested to reach up to 1,000 km inland along its tributaries (Freitas et al. 2017). The extensive inland influence of the tidal frame is due in part to the macrotidal range at the mouth of the river, the weak slope bed of the river, and substantial annual variations in discharge (Fassoni-Andrade et al. 2023). Tidal influences vary substantially throughout the year and it is only during low flow periods that the tidal influence is expressed so far inland (Fassoni-Andrade et al. 2023). The high tidal range at the mouth, variation in flow rates over the year and overall high discharge of the river results in three distinct hydrological regimes along the estuarine gradient in the Amazon River: (1) a river flow dominated regime during high flow periods with tidal influence only during low flow periods in the upstream watershed (1,000 km – 670 km from the mouth); then (2) a section dominated by both river and tidal influences throughout the year (albeit with seasonal variation in the dominant hydrology, 670 km – 270 km from the mouth), and finally (3) a tidally dominant stretch at the mouth of the river from 270 km to the mouth of the river including *furos* (rivers and creeks dissecting the mouth of the estuary) around Ilha de Marajó (the largest fluviomarine island in the world) (Fassoni-Andrade et al 2023).

Biophysical controls: The várzea ecosystem has historically been poorly studied, in part due to its inaccessibility as a result of seasonal flooding, low population density and limited transport infrastructure. There is a biodiversity gradient running from west to east with the highest diversity found in the west and lowest diversity found at the mouth of the Amazon River (Parolin et al. 2004). In the east, particularly around Ilha de Marajó, there is an ecotone with mixed mangrove and várzea forests found along both the east and west coasts of the island, with true várzea dominant in the south and mangrove in the north of the island, which forms part of the Amazon Macrotidal Mangrove coast (770,000 ha, 77% of the mangroves in Brazil, Lacerda et al. 2022).

The mangrove/várzea ecotone is freshwater dominant at present, but there are occasional influxes of saline water allowing mangroves to compete with the várzea. Over longer time periods, there have been temporal interchanges in marine/freshwater influences resulting in current domination of mangroves in the freshwater outer estuarine environment, particularly in Amapá (to the west of Marajó) (Guimarães et al. 2010, Bernadino et al. 2022). Around Marajó and consequently the lower estuarine reaches of the Amazon River, salinity variations are linked to freshwater inputs and associated seasonal variations. Low flow periods typically run from August to December and high flow periods January to July influencing both the inundation frequency and duration as well as salinity influence, which is minimal in areas dominated by várzea (Cohen et al. 2008). Recent droughts in the Amazon basin have impacted the freshwater flow regime, which combined with damming along the Amazon River and sea-level rise have resulted in increased saltwater intrusion events into the estuary, a situation that looks set to be exacerbated in the future (Lee et al. 2024). The very limited tolerance to salinity of várzea forests is likely to have an impact on their distribution, particularly around Marajó and the mouth of the estuary.

The extremely high average annual discharge of the Amazon River (209,000 $m^3 s^{-1}$; Molinier et al., 1996) and adjacent Tocantins River (13,911 $m^3 s^{-1}$; Von Randow et al., 2019) provide substantial freshwater inputs, as well as sedimentary and suspended organic material ($567 \cdot x 10^6$ tons $year^{-1}$ Amazon; 3.06×10^6 tons $year^{-1}$ Tocantins) (Lima et al., 2005) resulting in rapid rates of carbon sequestration in coastal várzea (up to an order of magnitude greater than global averages for mangroves (Ward et al. in review).

Significant plant taxa: Várzea forests are considered the most species-rich flood forests globally, with over 900 tree species recorded, with diversity varying across a flood inundation gradient with a mix of generalist Amazon forest species within the less frequently flooded edge and much more specialised hydrophytic species occurring in the lower elevation more frequently inundated areas, as well as from east to west (lowest α diversity in the east) (Wittmann et al. 2002, 2006). Species variability can also be linked to vegetation successional stage of the forest, as these forests are an important timber resource that has been utilised extensively since European colonisation (Fortini & Zarin 2011).

Tree species within the várzea ecosystem are well adapted to prolonged inundation, which can reach 7m depth and last for up to 7 months a year in the west, although typically more diurnal in the east (de Assis & Wittmann 2011). Adaptations to extended anaerobic conditions include biomorphological, biochemical and ecophysiological traits (Schlüter et al. 1993, Waldhoff et al. 1998, De Simone et al., 2002, Schöngart et al. 2002, Parolin, 2009). The most common plant families found in várzea flood forests are from the Fabaceae, Arecaceae, Malvaceae, Meliaceae, and Rubiaceae making up 75% of the family importance value index for these forests (de Jesus Veiga Carim et al. 2017). Within the mouth of the Amazon River, the main species that dominate the várzea are *Astrocaryum murumuru*, *Carapa guianensis*, *Euterpe oleracea*, *Hevea brasiliensis*, *Mauritia flexuosa*, *Montrichardia linifera,* *Pentaclethra macroloba*, *Swartzia acuminata*, and *Swartzia racemosa* (Amaral et al. 2023).

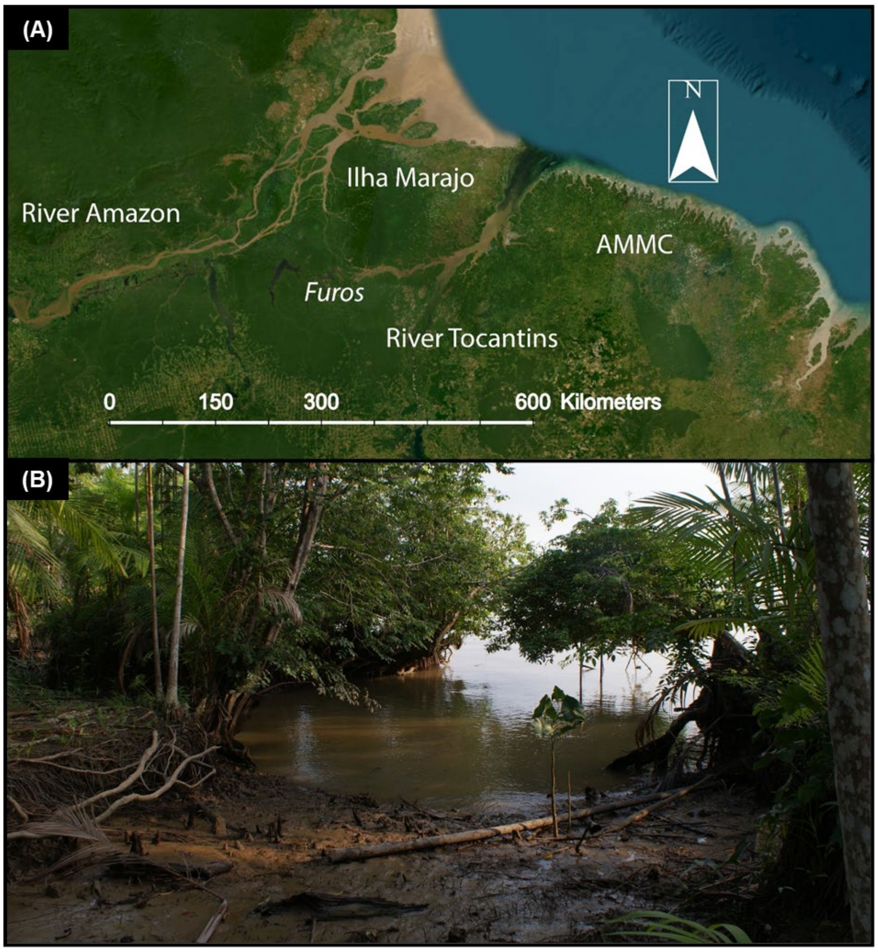

Figure 3. Ilha de Marajó, the largest fluviomarine island at the mouth of the Amazon River, with the *furos* (creeks) in the south. The *furos* can be well over 100 m wide and dissect the land away from the main river channel. The Tocantins River runs to the east of Ilha de Marajó and the Amazon Macrotidal Mangrove Coast (AMMC) runs from the east along to the Amazon estuary (A). The photo shows the highly organic-rich fine sediment in the várzea around Pesqueira (eastern Ilha de Marajó) (B) (Photo R. D. Ward).

Sitka spruce TFWs of U.S Pacific Northwest

Spatial distribution: In the U.S. Pacific Northwest (PNW), TFWs occur in riverine and lagoonal estuaries and embayments, including the outer coasts of Washington, Oregon and northern California, in Puget Sound, and in the Lower Columbia River estuary (Brophy et al. 2019a). Prior to EuroAmerican colonization, PNW TFWs were extensive, dominating the lower-mesohaline to freshwater tidal zones of the region's estuaries (Collins and Sheikh 2005, Thomas 1983, Brophy 2019), but over 90% of these TFWs have been lost, primarily due to logging, diking, and conversion to agricultural uses (Simenstad et al. 2011, Marcoe and Pilsen 2017, Brophy 2019). The information below is based on remaining examples of TFWs in Oregon and Washington.

Biophysical controls: The PNW has semi-diurnal tides, with tide range (MLLW-MHHW) varying from 2.0 m in northern California to 4.4 m in southern Puget Sound, Washington (https://tidesandcurrents.noaa.gov/). PNW TFWs are generally found from approximately mean higher high water (MHHW) to the upper limit of tidal influence at annual high tide (Brophy 2009, Brophy et al. 2011, Janousek et al. 2024); therefore, tidal inundation frequency ranges from many days per month to once a year. Inundation is more frequent in the wet season (winter), when high river flows contribute to elevated total (tidal + fluvial) water levels (Kukulka and Jay 2003, Brophy et al. 2011) (Figure 4). Although salinity tolerances are not yet well-established, *Picea sitchensis* (Sitka spruce)-dominated TFWs studied to date have dry season salinities that can reach as high as the upper mesohaline, about 15 psu (Brophy 2009, Brophy et al. 2011), while other TFW types appear limited to the freshwater tidal zone (Kunze 1994, Christy 2004). Physical structure of PNW TFW channels and wetland surfaces is complex, particularly for Sitka spruce, where *Castor canadensis* (beaver) activity and abundant large woody debris generate forced step-pool channel forms (Diefenderfer and Montgomery 2008). Root platforms of mature Sitka spruce are substantially elevated above the general wetland surface (e.g., 40 cm, Brophy 2009), creating additional structural complexity; these platforms, along with fallen logs, often support the growth of upland shrubs and herbaceous species amidst the otherwise hydrophytic vegetation described below (Brophy 2009, Brophy et al. 2011).

Significant plant taxa: Sitka spruce, an evergreen conifer, is the characteristic dominant tree of fresh to brackish PNW TFWs (Franklin and Dyrness 1988); these regionally distinctive ecosystems are often referred to as "spruce tidal swamps." In freshwater tidal zones -- most extensive in large estuaries such as the Columbia -- other TFW canopy dominants include

Thuja plicata (western redcedar), *Populus trichocarpa* (black cottonwood), *Alnus rubra* (red alder) and *Fraxinus latifolia* (Oregon ash). Understory species vary depending on salinity, with the broadleaf deciduous *Malus fusca* (Oregon crabapple) and *Lonicera involucrate* (bearberry honeysuckle) often dominant in brackish spruce tidal swamps (Christy and Brophy 2007), while in freshwater TFWs the understory is more diverse, including small trees and shrubs such as *Frangula purshiana* (cascara), *Cornus sericea* (red osier dogwood), *Rubus spectabilis* (salmonberry), *Spiraea douglasii* (hardhack), *Sambucus racemosa* (red elderberry), *Myrica californica* (California waxmyrtle), *Vaccinium* spp. (huckleberries), *Salix* spp. (willows) and others (Kunze 1994, Christy 2004). Herbaceous understory vegetation also depends on salinity; in brackish TFWs the herb layer can be similar to PNW high tidal marsh, while the herb layer in freshwater TFWs is similar to that of nearby non-tidal forested wetlands (Christy 2004). In fact, nearly all taxa found in both brackish and freshwater TFWs of the PNW are also found in non-tidal forested wetlands upslope, although dominants differ in brackish versus fresh environments.

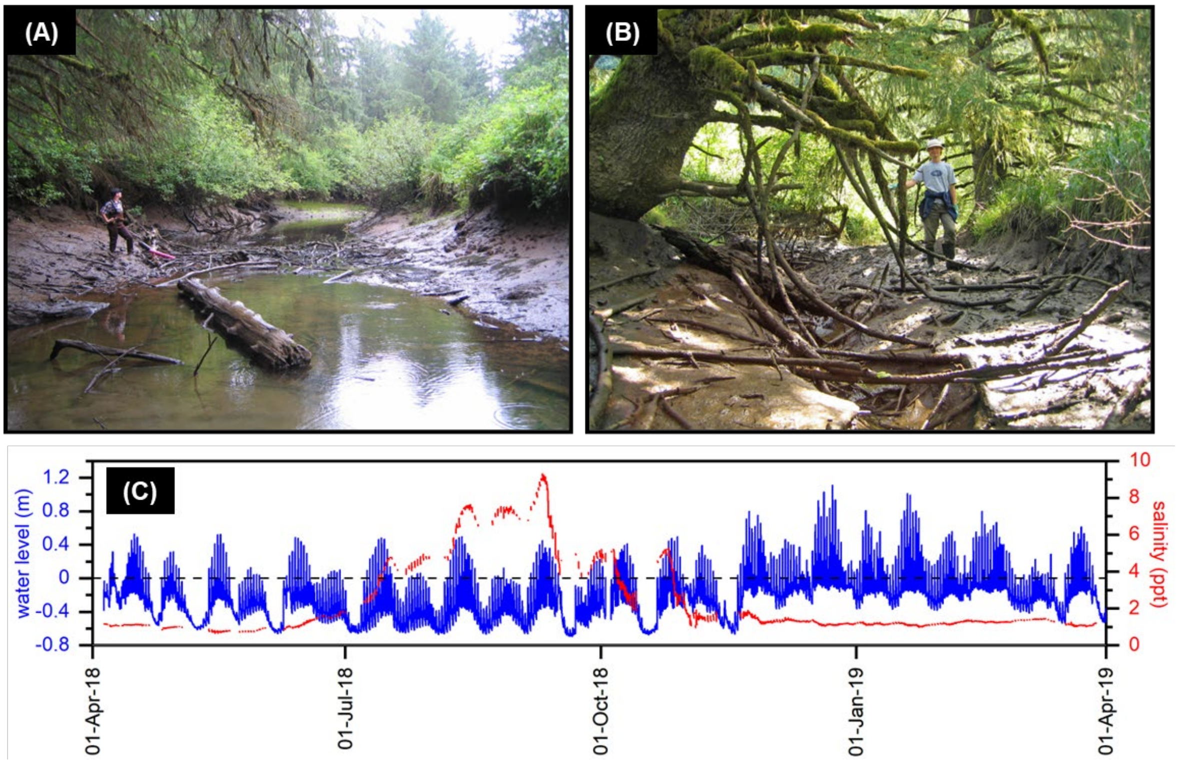

Figure 4. Fringing temperate brackish forested tidal wetland dominated by *Picea sitchensis* (Sitka spruce) with understory of *Lonicera involucrate* (black twinberry) and *Malus fusca* (Pacific crabapple) at Coal Creek Swamp, Nehalem River estuary, Oregon USA (A) and site

Y28, Yaquina River estuary, Oregon USA (B); hydrograph (blue) and groundwater salinity (red) profiles for Coal Creek Swamp (C) (hydrograph and salinity profile at Y28 is similar). Dashed line represents ground surface. Surface inundation occurs during spring tide cycles year-round; elevated salinity during late July through October corresponds to summer low river flows (dry season). Credits / data sources: L.S. Brophy, CC BY-NC 4.0 (A, B); Janousek et al., 2024 (C).

Pterocarpus forests

Spatial distribution: Pterocarpus officinalis forested wetlands (herein, *Pterocarpus* forest) are areas dominated by this woody plant of the Fabaceae family. This forest occurs in monospecific stands in coastal and riverine areas and, in some locations, along riparian corridors of tropical zones of the Caribbean and Central and South America (Bacon 1990; Figure 5). In coastal areas, *Pterocarpus* forests frequently occur landward in the ecotone of the mangrove species *Laguncularia racemosa* to the sea. Historically, *P. officinalis* dominated the brackish and freshwater coastal plains inland, behind mangroves seaward throughout the Caribbean, Central America, northern South America, Brazil, Colombia, Ecuador, and southern Mexico (POWO 2024). Nonetheless, this species also may occur intermixed with mangroves to some extent. For example, on the Caribbean coast of Costa Rica, the importance value of *P. officinalis* (63%) in riverine mangroves reached the highest compared to species of mangroves like *Rhizophora mangle*, *Avicennia germinans*, and *Laguncularia racemosa* (Pool et al. 1977).

Biophysical controls: Hydrologic regimes related to flooding and variations in salinity influence the structure and distribution of stands of *Pterocarpus* forest. For example, individuals of this species have lenticels and adventitious and shallow root systems, which are adaptations to seasonal fluctuations of floods (Saur et al. 1998, Fougnies et al. 2007; López and Kursar 2007). However, they have limited capacity for large fluctuations and levels of salinity: individuals show tolerance to salinity levels usually under 10 psu and lower (e.g., up to 5 psu) throughout the species' distribution (Bompy et al. 2015, Rivera-Ocasio et al. 2007, Rivera De Jesús and Rivera-Ocasio 2022). Among the adaptive mechanisms for salinity in *P. officinalis* are (1) the accumulation of sodium (Na) on the leaf rachis and away from the photosynthetic tissue of the leaf and (2) the capacity to keep high ratios of potassium and sodium (K/Na) in the leaf blades (Medina et al. 2007, Bompy et al. 2015). Also, plants preferentially use surface soil moisture over deeper (>60 cm) water sources, which are more saline (Colón-Rivera et al. 2014). Finally, another related mechanism is its capacity for accretion, which increases the establishment and survival of recruits. For example, sediments and organic matter (mostly leaf litter) accumulate around tree buttresses, which creates mounds of drier soils that facilitate the establishment of seedlings, development of fine roots, and increase soil aeration (Álvarez López 1990, Medina et al. 2007).

Evidence revealed that individuals of *P. officinalis* respond to large changes in salinity in various ways, which influence recruitment and survival (Eusse and Aide 1999, Rivera-Ocasio et al. 2007, Rivera De Jesús and Rivera Ocasio 2022, Colón Rivera et al., 2014). For example, exposure to salinity levels higher than five psu limited reproduction, recruitment of seedlings, growth of juveniles, and forest productivity in coastal areas throughout Puerto Rico (Eusse and Aide 1999, Rivera Ocasio et al. 2007, Rivera De Jesús and Rivera 2022). Also, some of the *Pterocarpus* forest stands in Puerto Rico have reduced their coverage because their individuals have slowly died due to small salinity increases associated with saltwater intrusion (with sea-level rise) in combination with periods of reduced freshwater input (e.g., droughts). For example, decreased recruitment of juveniles and increased tree mortality occurred from 1994 to 2015, with saltwater intrusion explaining most of the pattern of reduced recruitment rather than the mortality rate during that period (Yu et al. 2019). Also, increased salinity increases water use efficiency (WUE) by individuals of *P. officinalis*, resulting in a reduction in gs (Stomatal opening) and A (net carbon assimilation), processes related to low tolerance and recovery capacity to varying water and saline conditions (Rivera De Jesús and Rivera Ocasio 2022). Furthermore, evidence suggests that increased salinity influences responses from mutualistic symbionts of the species limiting the establishment of *Pterocarpus* forests and survival plants. For example, increased salinity limits the development of nitrogen-fixing bacteria in root nodules and arbuscular mycorrhizal fungi, which otherwise enhance plant growth and tolerance to flooding regimes in *P. officinalis* (Saint-Etienne et al. 2006, Fougnies et al. 2007, Bâ and Rivera-Ocasio 2015).

Significant plant taxa: Pterocarpus forest stands typically form monospecific stands of trees of *P. officinalis* in the overstory, with the ferns *Acrostichum aureum* and *Acrostichum danaeifolium* covering the understory. In some locations throughout the species' distribution, *P. officinalis* co-occurs with *Annona glabra* (pond apple), which has similar habitat requirements, although *A. glabra* has a higher tolerance to salinity. Trees of *P. officinalis* are frequently found growing inland next to trees of *Laguncularia racemosa* (white mangrove) seaward, along the freshwater-mangrove ecotone. Several woody lianas are also frequently found in these *Pterocarpus forests,* including *Paullinia pinnata, Heteropterys laurifolia, Machaerium lunatum, and Dalbergia ecastaphyllum.*

Figure 5. Brackish *Pterocarpus officinalis* forests at Rio Guajataca, Quebradillas Municipality (A, B) and Punta Viento, Patillas Municipality (C), Puerto Rico. Note the presence of surface water late in the dry season (March 2019) in A; the accumulation of sediment around buttresses and the high-water mark on tree in B (late wet season, October 2023); and the presence of surface water in C (wet season, August 2023). Credits: E. Rivera-Ocasio.

Australian supratidal forests

Spatial distribution: 'Supratidal forests' is a term used in Australia to define a broadly-distributed group of coastal ecosystems on the basis of their (1) position within the coastal landscape and (2) vegetation structure. That is, supratidal forests are named for their typical occurrence at high elevations relative to the tidal frame, near or above the limit of astronomical tides. In reality, however, supratidal forests may occur: (1) in the upper intertidal zone (typically above any adjacent mangrove and saltmarsh); (2) across the supratidal zone; and (3) in 'perched' settings above the tidal frame of intermittently closed or open lakes and lagoons (ICOLLs). Supratidal forests are distributed across Australia's tropical, sub-tropical and temperate climatic zones, though little to no distribution is expected along arid coastlines where unvegetated flats and/or small-statured succulents dominate the supratidal zone.

Biophysical controls: Elevation, inundation and salinity are significant controls on the distribution, productivity and recruitment of supratidal forests, though interactions between the three are not well understood. Variations in vegetation height, composition and health status have been observed across elevation gradients, with tree stress or dieback observed occasionally in lower elevation zones of seaward fringes and/or interior depressions (Conroy et al 2022, Kelleway et al. 2021). Surface inundation is typically infrequent and may be restricted to the highest astronomical tides of the year, or compound flooding events. When inundation does occur, it may influence water table depths and salinity levels for days to weeks (Kelleway et al. In review). Belowground tidal pulses have been also observed in the absence of surface tides across multiple sites and may influence salinity dynamics (Kelleway et al. In review; Figure 6).

Little is known of the salinity regimes of Australian supratidal forests, though recent work has shown groundwater salinities exceed 30 psu in some settings, with recorded site median values ranging from 2.7 to 28.5 psu on temperate coasts (Kelleway et al. In review), while Wei et al. (2013) report a median value of 8 psu in a sub-tropical setting. Groundwater salinities may be highly responsive to rainfall events, and can therefore exhibit high temporal variability (Kelleway et al. In review). Freshwater conditions are likely to occur in sites subject to highly seasonal rainfall. Some settings referred to as 'freshwater' or 'tidal freshwater' wetlands (Grieger et al. 2018, Adame et al. 2019, Iram et al. 2021) are likely to be included within the definition of 'supratidal forests' depending on their position relative to the tidal frame (Adame et al. 2019). In contrast, some taxa common in supratidal forests have been observed in groundwater-dependent wetlands without direct tidal influence (Mensforth and Walker 1996, Carter et al. 2006). Seedling growth studies have shown suppression of plant growth under increasing salinities (Clarke and Hannon 1970, Van Der Moezel et al. 1989, Salter et al. 2007), though vegetative reproduction is common for many taxa, and if often concentrated around the raised hummocks of parent trees.

Significant plant taxa: Australia's supratidal forests comprise multiple species of trees, shrubs, and groundcover vegetation. Despite occurrence across multiple climatic zones, supratidal forests are typically dominated by either of two key genera: *Melaleuca* (family:

Myrtaceae) and *Casuarina* (Casuarinaceae). The genus *Melaleuca*, often collectively termed paperbarks, exhibit diverse growth habits, with some tropical species also extending through parts of southeast Asia (Tran et al. 2015). *Melaleuca viridiflora, M. cajaputi* and *M. leucadendra* dominate supratidal forests in tropical Australia where they may grow as tall forests (Finlayson 2005, Sloane et al. 2019). In contrast, shorter stands or shrubby thickets of just a few metres height of *M. ericifolia* and/or *M. halmaturorum* (SE Australia) or *M. rhaphiophylla* and/or *M. cuticularis* (SW Australia) occupy temperate coastlines (Carter et al. 2006, Turner et al. 2006). Coastal swamp oak forests dominated by the genus *Casuarina* form the landward border of intertidal saltmarshes and/or mangroves, particularly along the east coast of Australia (dominated by *Casuarina glauca*), though *C. obesa* is a significant component of some supratidal forests in southwest Australia, and *C. equisetifolia* has a tropical distribution in Australia (Boon et al. 2016, Kelleway et al. 2021). Other notable tree taxa include *Eucalyptus robusta, E. tereticornis*, *Lophostemon suaveolens*, as well as ‘freshwater mangroves’ (*Barringtonia acutangula*), and a variety of palms (e.g. *Pandanus spiralus*, *Livistonia australis*). Significantly, each of these genera have distributions across terrestrial forests and/or freshwater wetlands over broad areas of Australia.

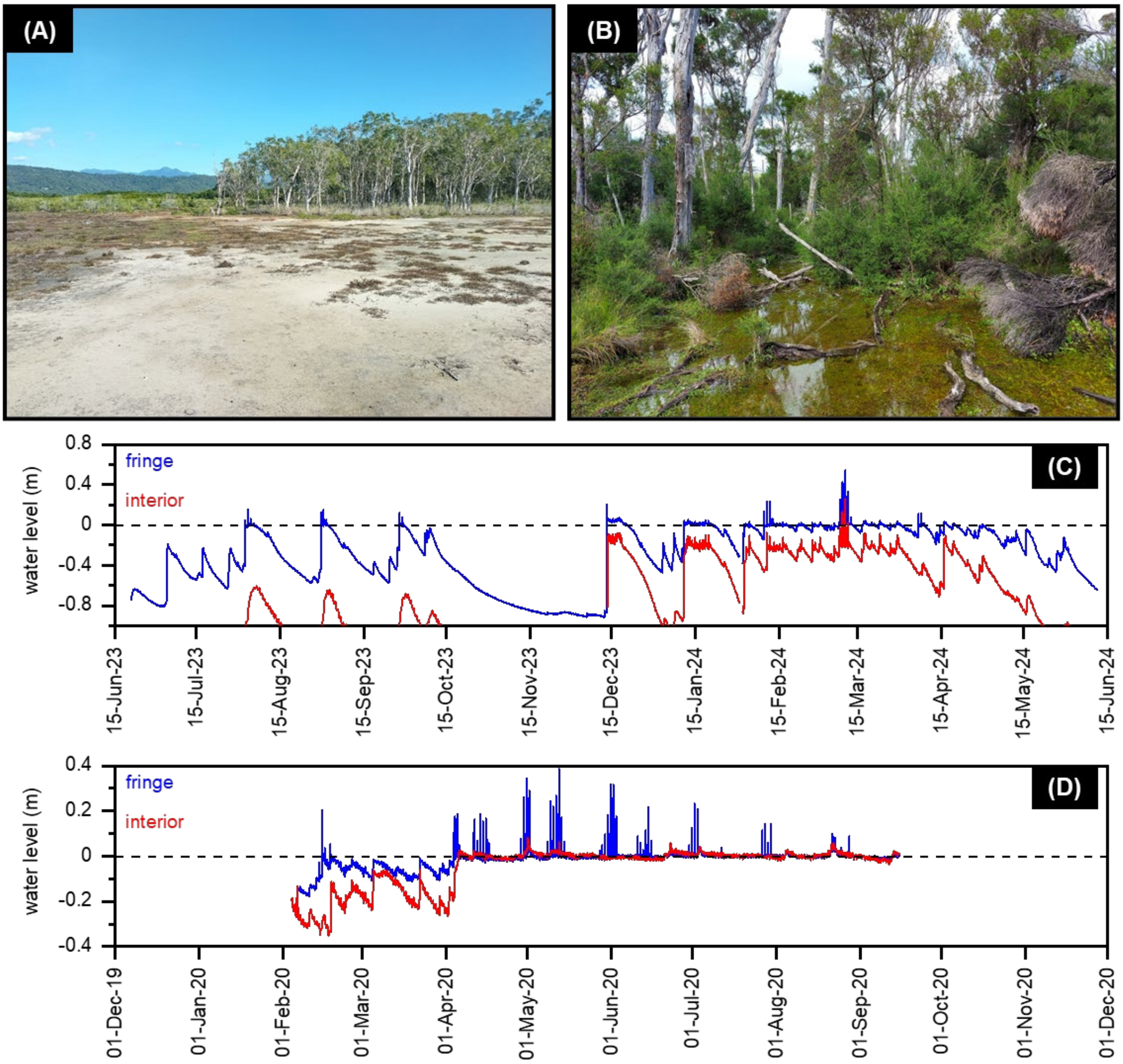

Figure 6. Fringe supratidal *Melaleuca* forest (right mid-ground) adjoining a supratidal salt flat (foreground) and mangrove forest (left mid-ground) during dry season at Port Douglas, tropical Australia (A); interior supratidal *Melaleuca* forest inundated by major rain event in Corner Inlet, temperate Australia (B); hydrographs for fringe and interior groundwater gauges at Port Douglas (C) and Corner Inlet (D). Dashed lines represent ground surface. Influences of storm surge and flooding from tropical cyclone Jasper on 13 December 2023 are clear in panel C. Credits / data sources: J. Kelleway (A, B); J. Kelleway unpublished data (C); Kelleway et al. (In review) (D).

New Zealand supratidal forests

Spatial distribution: The current spatial distribution of supratidal forests in New Zealand is poorly understood. Fragments of these forests occur along the margins of estuaries immediately upslope/landward of saltmarsh and stranded in adjacent lowlands where agricultural land has replaced freshwater tidal wetlands from the mid-1800s. New Zealand's supratidal forests consist of two major types: (1) mānuka scrub-dominated (*Leptospermum hoipolloi*, tea tree, Myrtaceae) and (2) kahikatea (*Dacrycarpus dacrydioides*, white pine, Podocarpaceae) habitats. A notable feature of both these species is that they have broad distributions beyond tidally-influenced systems. Mānuka is widely distributed through New Zealand and south-east Australia, having two main ecological niches: permanent dominance of extreme environments or as a seral/nursery species in indigenous forest succession (Stephens et al. 2005). Kahikatea forest is found in lowland and montane regions to 600 m elevation throughout the North, South, and Stewart Islands. Formerly a common native tree, only fragments of the once extensive lowland kahikatea forests remain (Smale et al. 2005).

Biophysical controls: Drivers on the control of distribution of supratidal forests is a data gap in New Zealand but it is likely that salinity and inundation both play a part. Mānuka scrub and Kahikatea habitat have wide distributions that include a broad range of biophysical conditions, with both found from lowland to sub-alpine elevations. Mānuka scrub occurs in freshwater and fringing estuarine wetlands, geothermal areas, alpine, and areas with high rainfall (Stephens et al. 2005, Saunders 2017). Kahikatea is present in floodplains and the saturated margins of the lowland wetlands (Smale et al. 2005). There is little research on salinity or inundation of supratidal forests in New Zealand. The porewater salinity tolerance of these supratidal forests is currently being investigated at the Omaha-Taniko Scientific Reserve (Auckland; Figure 7), in the Future Coasts Aotearoa research programme (NIWA 2024).

Significant plant taxa: Based upon the first detailed vegetation survey of Omaha-Taniko Scientific Reserve (Figure 7; data file provided in Figshare upon acceptance), New Zealand's supratidal forests include:

1. Mānuka shrubland: Native wetland facultative Mānuka shrub *Leptospermum hoipolloi* and previously named *Leptospermum scoparium*. In the Omaha-Taniko Reserve, *L. hoipolloi* has an average cover of 30% and a maximum height of 5.5 m. Tussock swamp twig rush *Machaerina juncea* is the next most predominant species in this habitat with 45% cover. *Apodasmia similis, Ficinia nodosa*, *Cordyline australis*, *Coprosma tenuicaulis, Gahnia xanthocarpa* and *Machaerina articulata* are present at <5% covers.

2. Kahikatea mixed podocarp and hardwood forest: Supratidal indigenous White pine Kahikatea *Dacrycarpus dacrydioides* forest habitat is the most diverse of the four ecotones and it is mostly represented by non-salt tolerant plants. In the Omaha-Taniko Reserve, Kahikatea shows a maximum cover of 50% within the ecotone with maximum height of 25 m. Multiple other tree, shrub and sedge species are present: *Lotus pedunculatus, Cordiline australis, Gahnia xanthocarpa, Freycinetia banksii Microsorium pustulatum, Hedycarya arborea, Leucopogon fasciculatus, Rhopalostylis sapida, Podocarpus totara, Coprosma rhamnoides, Microsorium scandens, Myrsine australis.* The other three predominant species of the Kahikatea Forest are: *Gahnia xanthocarpa* indigenous wetland facultative sedge occupying up to 80% cover; *Freycinetia banksii* indigenous wetland facultative climber occupying up to 10% cover; and *Cordyline australis* indigenous wetland facultative tree occupying up to 8% cover, while the rest of the species represent <5% cover.

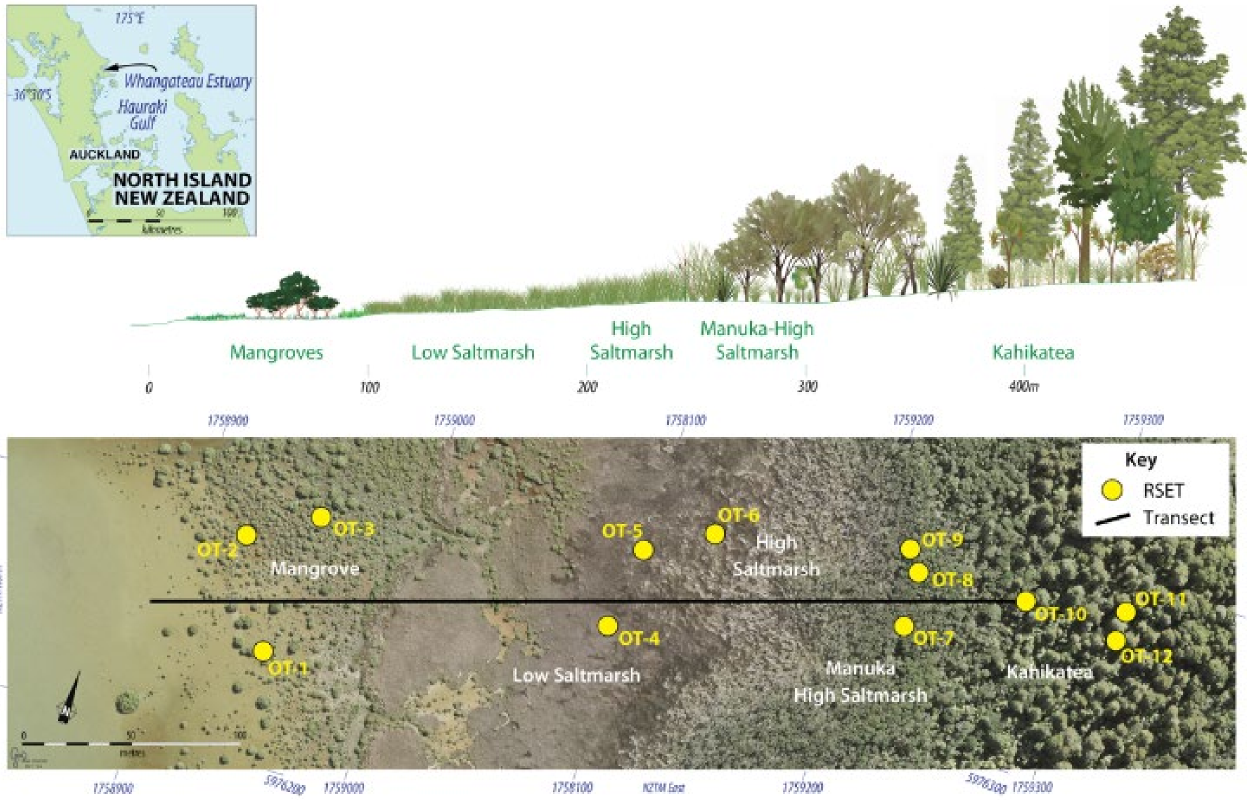

Figure 7. Experimental transect established in the Omaha-Taniko Scientific Reserve (Auckland Region, NZ). The transect includes the full sequence of coastal wetland habitats observed in the upper North Island, including supratidal Mānuka Scrub and Kahikatea Forest that were once common around estuarine margins prior to the establishment of pastoral agriculture since the mid-1800s.

North Atlantic maritime pine forests

Spatial distribution: In the low elevation and shallow-sloping North American Coastal Plain of the North Atlantic, maritime pine forests occupy an elevation range upslope of dune and tidal marsh ecosystems, in poorly drained soils of the supratidal zone of barrier islands and estuaries (Brinson et al. 1995; Figure 8). These saltwater-influenced forests reside downslope of mixed hardwood and pine forests or adjacent to seasonally flooded (freshwater) non-tidal forested wetlands that are referred to by regional names such as Delmarva bays, Carolina bays, or pocosin wetlands (Moorehead and Brinson 1995).

Biophysical controls: Maritime forests are irregularly flooded by seawater from adjacent brackish or saline water sources (ocean, estuaries, or tidal creeks) (Hussein and Rabenhorst 2001, Nordio et al. 2024), and groundwater is also influenced by tides and lateral seawater intrusion. For example, in a maritime pine forest in the Eastern Shore of Virginia, storm surges reaching less than 1 m above mean sea level, mostly from unnamed storms, inundated the forest between two and four times per year from 2019 to 2022 (Nordio et al. 2024) (Figure 8c). Inundation events, and to a lesser extent lateral saltwater intrusion into groundwater, create a variable environment for plants with salinities averaging approximately 3 to 13 psu over time (Jobe and Gedan 2021) and peaking at the adjacent waterbody's salinity level during flooding events (Nordio and Fagherazzi. 2022). The dissipation of groundwater and soil porewater salinity is dependent on the volume of unsaturated soil during a flood, which can make the effects of a single flood event unpredictable (Yang et al., 2018; Nordio and Fagherazzi. 2022). Drought appears to influence these systems as well, with the saltwater wedge in the groundwater moving inland during drought and affecting a larger area of maritime forest (Ardon et al. 2013). As maritime forest systems occur in very flat areas of coastal plain, understanding the accumulation of soils or sediments (i.e. accretion) and patterns in drainage may require the development of new models and model experiments (Moorhead and Brinson 1995).

Significant plant taxa: North Atlantic Maritime pine forests tend to be less speciose and more ruderal than upland forests of the same regions and contain a more constrained set of dominant species than adjacent upland pine forests (Heaton et al. 2023). *Pinus taeda* (loblolly pine) is the dominant species in the Mid-Atlantic US region, sometimes mixed with *Quercus alba* or other oaks. *P. taeda* is replaced by *P. rigida* (pitch pine) in the northeastern US (Payne et al. in review) and by southern pine species *P. serotina* (pond pine), *P. palustris* (longleaf pine) and *P. elliottii* var. *elliottii* (slash pine) in the southeastern US (Faber-

Langendoen et al. 2013 NatureServe). Ruderal tree species, such as *Liquidambar styraciflua*, *Prunus serotina*, and *Nyssa sylvatica*, are also common. Subcanopy evergreen trees of *Ilex opaca* and *Juniperus virginiana* can be abundant and share the subcanopy with shrubs of *Morella cerifera* (Sward et al. 2023). At the edge of the forest closest to tidal marsh, the common reed *Phragmites australis*, an invasive lineage from Europe, is abundant in monotypic stands (Shaw et al. 2022). Another notable feature at this edge of the forest is a reduction in live trees and an increasing number of tree snags (i.e. 'ghost forest'), resulting from greater salinity stress and higher flood frequencies at the tidal marsh edge (Ury et al. 2020, Taillie et al. 2019, Payne et al. in review).

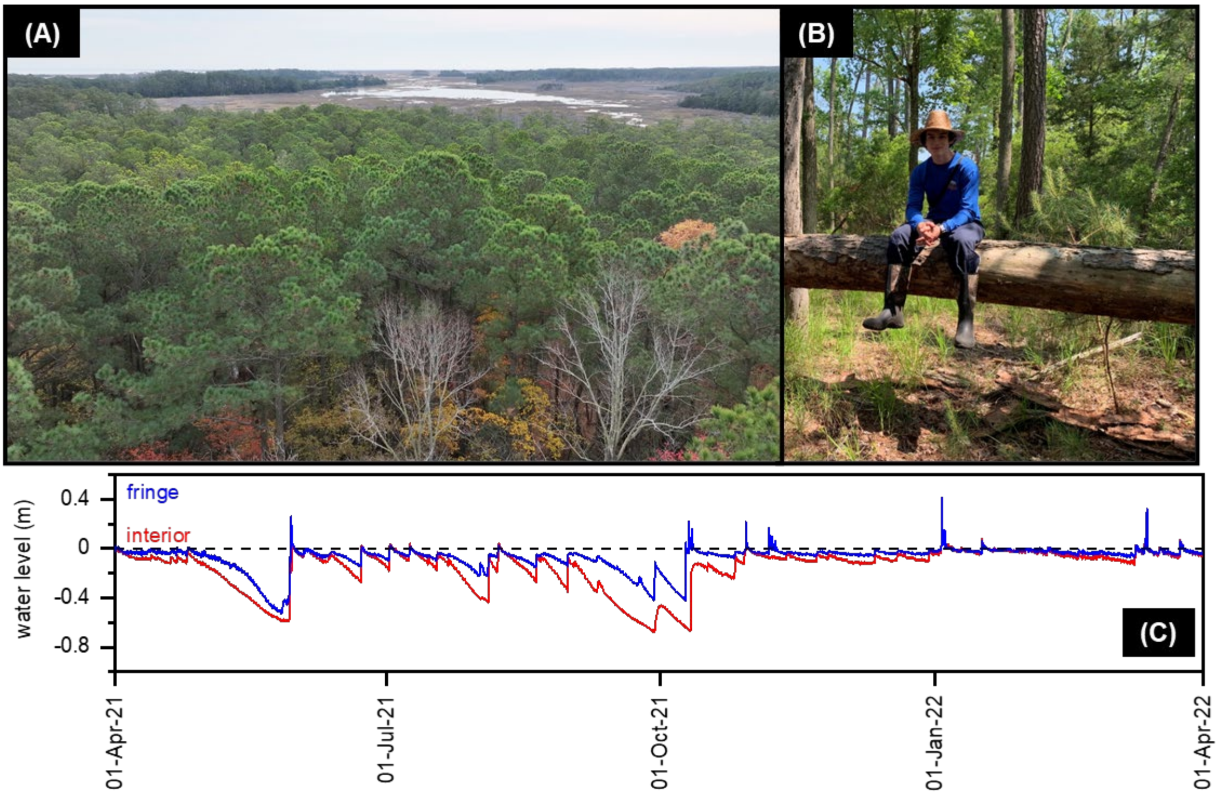

Figure 8. Maritime pine forest of Brownsville Preserve, Nassawadox, Virginia, showing habitat succession from a drone with the camera facing towards the estuary (A); Monie Bay National Estuarine Research Reserve in Princess Anne, Maryland (B); hydrographs for fringe ('low') and interior ('high') North Atlantic Maritime pine forests at tidal wetland at Brownsville forested area, Virginia (C). Dashed line represents ground surface. Credits / data sources: R. Leff and J. Callaghan 2024 (A); K. Gedan 2021 (B); Fagherazzi and Nordio (2022) (C).

Transitional forests of the Niger Delta

Spatial distribution: The Niger Delta is the third largest wetland in the world (Uluocha and Okeke 2004), has the most extensive swamp forest (inclusive of mangrove and freshwater) ecosystems in Africa (Igu and Marchant 2016), and is a biodiversity hotspot (World Bank 1995). Diverse vegetation is found in the region; with the major formations distinguished as: brackish water swamps (made up of the mangrove forest and coastal vegetation), freshwater swamp forests, lowland rainforest and riparian forests. Transitional forests across the Niger Delta, like other transitional zones, act as a bridge between diverse biogeographic units across the region. Among the various transitional forest types in the region, this case study focuses on the notable and extensive transitional forests which occur between mangrove and freshwater ecosystems. Broadly, these forests are located between the Cross River and the Niger River of western Africa.

Biophysical controls: The Niger Delta transitional forests are shaped by a range of factors (mainly biophysical) which largely determine (and/or constrain) its composition, distribution, diversity and structure. These include climate, topography, hydrology, soil, biodiversity and disturbance regimes. The region is characterized by a tropical climate that experiences a long rainy season which lasts nearly throughout the year, but more pronounced from March/April to October. The peak of the wet season is in July and the dry months are mainly between December and February. Relative humidity rarely dips below 60% and fluctuates between 90 and 100% for most of the year, with average monthly maximum and minimum temperatures between 28 to 33 ^{o}C and 21 to 23 ^{o}C, respectively (Imevbore et al. 1997). The Niger Delta transitional forests occur in low relief zones which normally experience annual flooding regimes and are hence made up of alluvial rich soils deposited after floods. The soils are broadly classified as hydromorphic soils (Areola 1982) which are either seasonally or permanently water-logged. The forests are found between saline and freshwater environments and so have varied saline conditions in different locations, depending on their proximity to mangrove (saline) zones or freshwater zones. Such patterns suggest an important role of tidal influence, either through surface or sub-surface expression, however, no quantification of such influence is currently available. Site conditions, disturbance regimes, water quality and nutrient content of the soil likely also play roles in the variations seen across the ecosystem.

Significant plant taxa: Plants in transitional zones in the region are adapted to the prevailing environmental conditions where they are found. The composition of the transitional forest is largely determined by biogeographic region and environmental conditions. Mangrove-freshwater transitional regions are for example characterized by species that are found in the two biogeographic zones at different degrees. They are not as diverse as other tropical forest ecosystems (especially the lowland forests) due to constraints in dispersal, germination and establishment due to flooding and seasonal extremes (Igu 2016). Species such as *Rhizophora racemosa*, *Elaeis guineensis*, *Raphi*a spp, and *Lannea welwitschii* were dominant in a mangrove-freshwater zone (Igu 2019), with most of these taxa occurring in mangrove ecosystems in the region. The Arecacea family - mainly *E guineensis* and *Raphia* spp - dominated the transitional zone, reflective of their presence in both mangrove and freshwater ecosystems, especially because the sites were disturbed ecosystems and had sufficient moisture to support their dominance (Igu 2019). Other dominant species in another transition forest in the region include: *Strombosia pustulata*, *Strombosia grandifolia*, *Erythrophleum ivorense*, *Diospyros crassiflora*, *Nauclea stipulosa*, *Cleistopholis patens*, *Celtis zenkeri*, *Diospyros mesipiliformis*, *Sterculia rhinopetala*, *Sterculia oblonga* (Igu and Marchant 2016). These species are also known to grow in the freshwater and lowland rainforest in the region.

Pachira aquatica **wetlands of tropical America**

Spatial distribution: *Pachira aquatica* (family: Malvaceae) is originally from tropical America and grows in wetlands locally known as "Zapotonales" in Mexico (Adame et al. 2024), and recently categorised within 'tropical coastal freshwater forested wetlands (TCFFWs)' by Barrios-Calderón et al. (2024). Wetlands of *P. aquatica* have been described in the Gulf of Mexico, the Mexican Pacific, and the Amazon basin (Adame et al. 2015, Infante Mata et al. 2011, Barrios-Calderón et al. 2024). *P. aquatica* is also cultivated worldwide for ornamental and commercial purposes (Daim Costa et al. 2023).

Biophysical controls: Wetlands dominated by *P. aquatica* are usually located in river floodplains and dune depressions of coastal areas adjacent to mangrove forests; they are regularly or seasonally inundated from river overflow, runoff, or groundwater (Infante Mata et al. 2011; Figure 9). The overlap in salinity and annual hydroperiod estimates between some *P. aquatica* wetlands with adjacent mangrove forests in some settings (Cejudo et al. 2022) is suggestive of some degree of tidal influence, though this is currently unquantified. *P. aquatica* wetlands have also been found in regions of relic marine incursions, such as the western Amazonia region, in what is now Colombia, Ecuador, and Brazil (Bernal et al. 2019). In general, the soils of *P. aquatica* wetlands are waterlogged and are inundated for months at a time during the wet season (Sánchez-Luna et al. 2022). As a result, soil redox changes drastically between dry and wet seasons, with values ranging from highly anoxic soils with -

200mV in the wet season to oxic conditions of > 300mV during the dry (Infante Mata et al. 2011). Although *P. aquatica* is not a highly salt-tolerant species, it can grow where superficial and groundwater salinity range from 0.2 to 2 and 0.2 to 11 psu, respectively (Infante Mata et al. 2011). Soil texture is dominated by sand or clay, organic carbon is high, with values ranging from 5 to > 30%, and the organic matter layer is at least one meter (Adame et al. 2015, Infante Mata et al. 2011).

Significant plant taxa: *P. aquatica* can form forests with tall trees > 20 m in height, an aboveground biomass of 162 ± 11.6 Mg ha^{-1} and a downed wood biomass of 25.0 ± 5.6 Mg ha^{-1} (Adame et al. 2015). Estimated belowground biomass is 43.5 ± 6.8 Mg ha^{-1}, with trees in anoxic conditions having lower belowground allocation (Adame et al. 2015, Infante-Mata et al. 2019). *P. aquatica* can reproduce rapidly through seedlings, which disperse through water (Vázquez-Benavides et al. 2020). However, their dispersal can be severely limited by competition with the grass *Leersia hexandra*, which impedes dispersal and outcompetes seedling growth (Vázquez-Benavides et al. 2020). The management of grass biomass has been successful in helping the establishment of the saplings (Sánchez-Luna et al. 2022). *P. aquatica* distribution also extends beyond areas of tidal influence, including non-tidal freshwater swamps.

Figure 9. *Pachira aquatica* forest / Zapotonales within Biosphere Reserve La Encrucijada in Chiapas, Mexico (A); partial surface inundation of the forest associated with tidal influence (B); *P. aquatica* foliage and flower (C). Credits: M.F. Adame

South African Swamp Forest

Spatial distribution: South Africa has 3431 ha of East African Swamp Forest associated with 32 estuaries in the subtropical and tropical zones (Van Niekerk et al. 2019). In the temperate estuaries reeds and sedges occupy this habitat. The five estuaries with swamp forest area greater than 100 ha are iMfolozi/uMsunduze (1683 ha), Kosi (869 ha), uMgobezeleni (417 ha), aMatigulu/iNyoni (195 ha) and uMlalazi (104 ha) (Riddin and Adams 2022). These systems are located in the Maputaland coastal plain where there are gentle gradients and a high water table associated with the primary aquifer (Grundling et al., 2013, Kelbe and Taylor, 2019). The remaining 27 estuaries have less than 20 ha of swamp forests and are mostly perched estuaries intermittently closed to the sea and characterised by fresh to brackish conditions (Riddin and Adams 2022). Even though 62% of the areal extent of swamp forests occur in protected areas they are considered Critically Endangered because of removal due to illegal slash and burn agriculture and reduction of water level and freshwater inflow from surrounding forestry and settlements (Grundling et al. 2021, Van Deventer et al. 2021)

Biophysical controls: Swamp forests occur where there is low-salinity waterlogging and only brief desiccation as they are typical lentic ecosystems (Mucina et al. 2021). They are associated with an accumulation of clay or peat sediments, having a regular oceanic tidal regime on soft sedimentary coasts (Grundling et al. 2013; Kelbe and Taylor 2019). Swamp forests are found in altitudes between 20 to 60 m where annual precipitation ranges between 1000 to 1500 mm (Van Deventer et al. 2021). In Kosi Bay (an estuarine lake) water level fluctuations of 0.53 m occur at the fringe of the swamp forest close to the location of water level recorder W7T003 at KZN Wildlife Maklangula Jetty (Figure 10). This site shows very little tidal range with only a 5 cm difference observed for the neap-spring cycles. However, for the downstream water level recorder (W7T005 in the Mtando Channel between Lake 2 and Lake 3) the neap tide amplitude is 0-5 cm and spring tide 15-20 cm (Department of Water & Sanitation, 2016). Swamp forest is dominant where salinity is less than 5 psu. Salt-water intrusion following the development of a port in the Richards Bay area resulted in the mass mortality of *Phoenix reclinata*, *Hibiscus tiliaceus* and *Barringtonia racemosa* (Cyrus et al. 1997, Riddin and Adams 2022). In the uMgobezeleni Estuary high seas in 2007 introduced saline marine water into the lower portion of the estuary killing swamp forest (Taylor 2016). Studies have shown the optimal salinity for *B. racemosa* to be 0 to 3.5 psu , while death of individuals was recorded at 35 psu after 53 days (Kelbe and Taylor 2019).

Significant plant taxa: Swamp Forest in South Africa have thirteen key indicator tree species (Van Deventer et al. 2021) and are considered an azonal regional biome (Mucina et al. 2021). The tree species are *H. tiliaceus* (lagoon hibiscus), *Syzgium cordatum* (water berry), *B. racemosa* (powderpuff tree), *Voacanga thouarsii* (wild frangipani), *Ficus trichopoda* (swamp fig), *F. sur* (broom-cluster fig), *Bridelia micrantha* (coastal golden-leaf), *Casearia gladiiformis* (sword-leaf), *Cassipourea gummiflua* (large-leaved onionwood), *Macaranga capensis* (wild poplar), *P. reclinata* (wild date palm), *Raphia australis* (kosi palm) and *Rauvolfia caffra* (quinine tree) (Wessels 1991a, b, Van Deventer et al. 2021, Riddin and Adams 2022). Thickets of the sedge *Scleria angusta* and the sword fern *Nephrolepis biserrata* can form a dense understorey, and the sedges *Cladium mariscus* and *Typha capensis* are common associates at the water's edge (Taylor 2016). *B. racemosa* and *H. tiliaceus* are dominant in the perched closed estuaries. *R. australis* is endemic to South Africa and is found in Maputaland, where it occurs at Kosi Bay and the Siyaya Estuary (Kelbe and Taylor 2019, Riddin and Adams 2022).

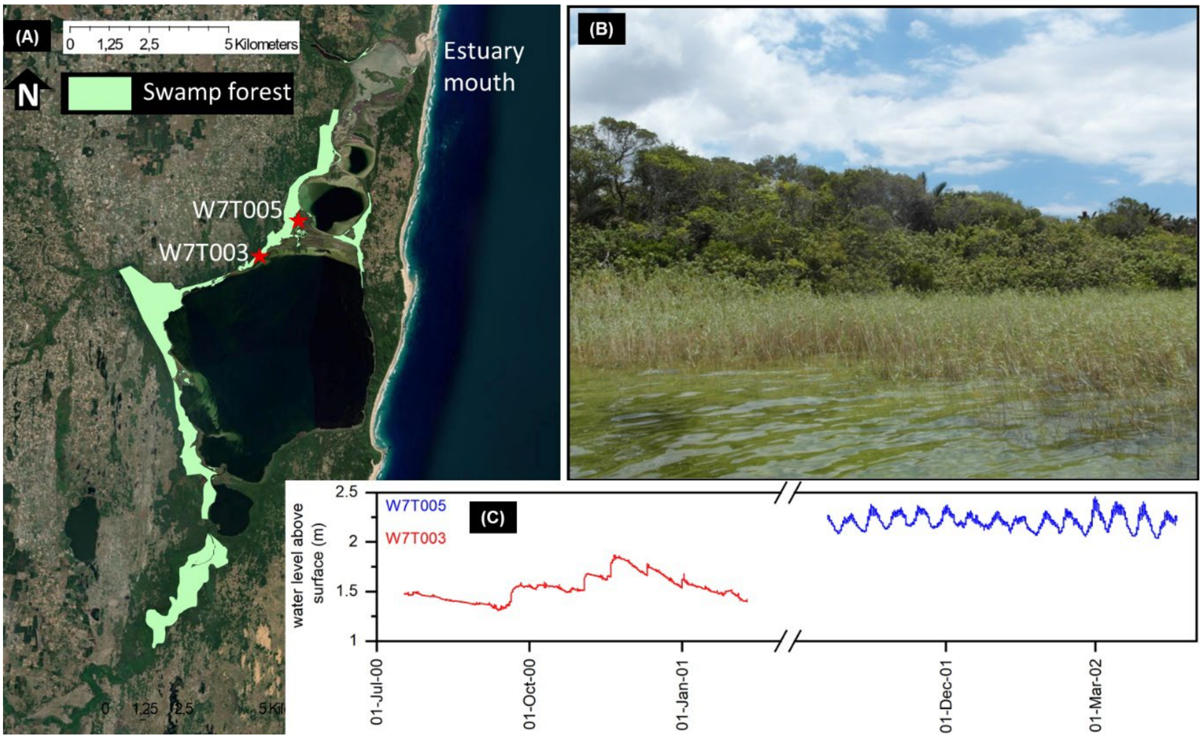

Figure 10. Swamp forest in the Kosi Estuary, South Africa: Satellite imagery overlaid with the distribution of swamp forest (green) and location of water level logger (red stars) (A); *Hibiscus tiliaceus* fringed by *Phragmites australis* in Lake Nhlange, within Kosi Bay Estuary (B); and recorded water level fluctuations at swamp forests fringing the water at starred location in A (C). Image and data credits: JB Adams.

Lowland peat swamp forests of Southeast Asia

Spatial distribution: In Southeast Asia, peat swamp forest is the terminology used to define forested peatlands – general land formed through actively accumulating peat or partly decomposed plant materials (Page & Rieley 2016, United Nations Environment Programme 2022). Most of the peat swamp forests in this region are naturally waterlogged with some areas receiving tidal inputs and distributed across the lowland near coastal area of Sumatra, Borneo, and Peninsular Malaysia (United Nations Environment Programme 2022, Anda et al. 2021). In some areas, peat swamp forests occur behind mangrove forests with large areas of overlapped mangrove and peatland distributed along coastlines in southern Sorong and Bintuni Bay (Murdiyarso et al. 2024), and peatland dominated by *Nypa fruticans* along coastal eastern Sumatra and western Kalimantan coastlines (Murdiyarso et al. 2009). Peatland distribution mapping remains challenging with high uncertainty especially in the tropics

(Gumbricht et al. 2017, Melton et al. 2022) and further research is needed on the identification and mapping of tidally influenced peat swamp forest area in Southeast Asia to improve their conservation management strategy along with other blue carbon ecosystems (Adame et al. 2024).

Biophysical controls: Lowland peat swamp forests are commonly distributed on a peat formed dome located between two rivers (Page and Rieley 2016). While peat swamp forests are mostly rain-fed ecosystems with low pH (<5), a small portion of them may receive tidal influence several times in a year during high astronomical tide events, particularly along the edge of the peat dome where elevation is lowest (e.g. Figure 11) (Adame et al. 2024, Arisanty & Rahmawati 2024). Some paleoecology assessment of these coastal peat swamp forests suggests that their peat soils were primarily formed by mangrove species during the late Holocene (Dommain et al. 2014, Fujimoto et al. 2019, Ruwaimana et al. 2020).

Significant plant taxa: Peat swamp forest vegetation is commonly characterised by tall closed-canopy trees and palms. In some edge zones, the contemporary vegetation composition can be dominated by mangrove genera (e.g. *Avicennia*, *Rhizophora, Bruguiera*) and/or other widespread TFW species (e.g. *Melalueca leucadendron*) (Omar et al. 2022). Overall, most peat swamp species are categorised into lowland Dipterocarp families which typically can reach up to 40-70 m height. Similar to mangrove species, most peat swamp forest vegetation trees commonly have breathing roots including prop-roots, knee-roots and pneumatophores to ensure oxygen input in the waterlogged condition during wet season and high astronomical tide events. Other non-woody vegetation such as *Nypa* palms and pandanus species dominate the riparian areas of the blackwater coloured peat swamp forest streams. Pitcher plants (*Nepenthes* spp.) are dominant in peat swamp forests where pH in this system is very low.

Figure 11. Blackwater coloured and pandanus dominated coastal peat swamp forest stream in Tanjung Puting National Park, Central Kalimantan, Indonesia. Streams at the edges of peat domes may regularly receive tidal input during high astronomical tides and/or compound flooding events. Photo: Sigit Sasmito.

4. Synthesis of biophysical drivers controlling TFWs

The above case studies demonstrate the broad distribution of TFWs at a global scale and the diversity of coastal settings and abiotic conditions across which they occur. In Figure 12 we demonstrate the approximate range of tidal influence and salinity regimes in which a variety of CFWs occur, based upon existing data, or inference from their landscape position(s) as described in the case studies. Together, these case studies highlight several important points regarding mangrove and non-mangrove TFWs:

(1) TFWs have a global distribution that spans tropical and temperate climatic zones, beyond the latitudinal limits of mangroves alone;

(2) mangrove forests occupy much of the higher-salinity, frequently tidal niche (i.e., the top right corner of Figure 12), despite being limited in their latitudinal range, though non-forested tidal ecosystems including tidal marshes and/or unvegetated flats also occupy this niche along temperate, semi-arid and arid coastlines;

(3) diverse non-mangrove TFWs converge in biophysical space where tidal inundation is infrequent and salinities are fresh or low. Importantly, however, some TFWs extend at least

partway along axes of frequent tidal inundation (e.g. TFFWs and freshwater mangroves), increasing salinity (especially Australasian supratidal forests), or both (e.g. PNW sitka spruce TFWs).

(4) TFWs occur across multiple gradients at multiple spatial scales. At one extreme, the structure and composition of TFWs vary over the scale of kilometres to hundreds of kilometres along riverine-estuarine gradients in major coastal systems such as the Amazon basin, the Niger delta, and the lower Columbia River estuary (Oregon and Washington, USA). Gradients in the expression and influence of tides and salinity can also be observed across the scale of tens of metres, as observed in contrasting hydrographs in ‘fringe’ versus ‘interior’ locations in the same study site for several of the case studies. The growth and recruitment on tree species on hummocks, root platforms, and/or raised sediments around tree buttresses (as identified in multiple case studies) represents response to tidal influences at an even finer spatial scale.

Some of the above patterns are partly a reflection of the semantics of ecosystem definitions, whereby highly salt-tolerant intertidal tree species have typically been grouped as ‘mangroves’ across broad geomorphic settings and regardless of the taxonomic lineages or composition of their dominant species. Nevertheless, there remain important distinctions between mangrove and non-mangrove TFWs, as the case studies demonstrate. For example, a common theme among many of the non-mangrove TFWs described above is the distribution of many locally dominant TFW species beyond tidal and beyond wetland settings. Distribution extending into terrestrial/upland ecosystems demonstrates such species are not obligate halophytes, though many will be facultative halophytes. While the halophyte status and salt tolerance mechanisms of many true mangroves and some mangrove associates are well documented (Parida and Jha 2010), this is not currently true for many of the dominant species of non-mangrove TFWs. Critically, several TFWs described in the case studies – potentially representing significant spatial extents – are not represented in Figure 12 due to lack of data on inundation and salinity regimes, further highlighting the information gaps regarding biophysical drivers of non-mangrove TFWs.

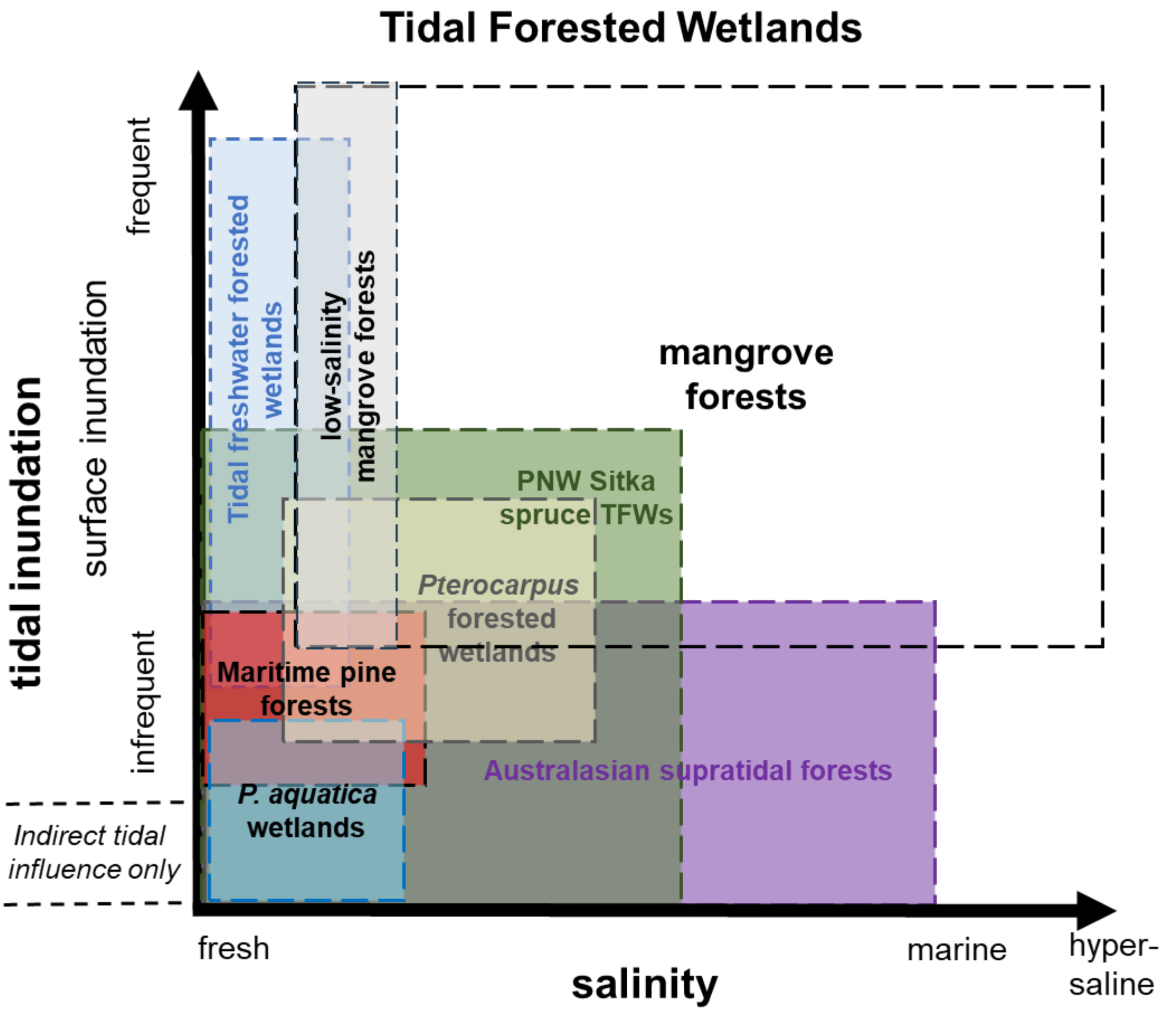

Figure 12. Range and overlap of known tidal influence and salinity regimes for selected Tidal Forested Wetlands classes, based on datasets and references detailed in case studies above. Note that several of our case studies are not represented here due to a lack of suitable data.

5. Ecosystem services

Coastal ecosystems provide myriad direct and indirect benefits to human populations and have been identified among the most significant providers of ecosystem services. For example, past global assessment has ranked coastal wetlands (defined there as including ‘tidal marsh, mangrove and salt water wetlands’) as second only to coral reefs in their mean total monetary value of ecosystem service provision per unit of area (de Groot et al. 2012). Such assessments have also highlighted the disproportionate value of ‘swamps/floodplain’, ‘tropical forests’ and ‘temperate/boreal forests’ – each likely to have at least some classification overlaps with TFWs – in the total global flow of ecosystem service value (Costanza et al. 1997, de Groot et al. 2012).

Several ecosystem service classifications exist, that largely build off categorizations introduced in the Millennium Ecosystem Assessment (MEA, 2005). In this review, we use the Common International Classification of Ecosystem Services (www.cices.eu), that groups ecosystem services into those related to: (1) the provisioning of material and energy needs; (2) regulation and maintenance of the environment for humans; and (3) cultural significance associated with non-material characteristics of ecosystems. In most instances we expect that ecosystem service types or quantity across and between TFWs will vary associated with the degree of tidal inundation, physicochemical conditions, and the unique flora and fauna, structure and distributions of each TFW type. Mangrove forests are the most studied in terms of ecosystem services, and for existing overviews we refer readers to previous work covering mangroves in a variety of contexts (Camacho-Valdez et al. 2014, Lee et al. 2014, Friess 2016, Kelleway et al. 2017, Friess et al. 2020).

Provisioning services

TFWs support substantial and diverse provisioning services, reflecting the forested structure, high productivity, and composition of plant and animal species within these ecosystems. There are, however, few detailed studies of the provisioning services specific to TFWs other than mangroves. Significantly, TFWs and adjacent transitional / freshwater swamp forests are a major contemporary source of timber in many regions, via small-scale or large-scale extraction, including the Amazon floodplain (Fortini and Zarin 2011), Niger Delta (Igu 2017) and lowland peat swamps of Southeast Asia (Page and Rieley 2016), and the Southeastern United States in the past (Conner et al. 2007). Igu (2016) identified that swamp forests (inclusive of transitional forests; see case study above) of the Niger Delta are used as the main sources of timber, non-timber forest products such as forest fruits, sources of fuel (firewood), medicine (herbs) and used for hunting bushmeat. Together these provision services may represent a major source of sustenance and income generation, with most forest sites used very frequently (i.e. daily and weekly basis), though remote locations might only be used occasionally (e.g. seasonally). Provision services may also vary between swamp areas which support fishing and other forest types supporting agriculture (Igu 2016).

An ethnobotanical investigation in the Klang district of southeastern Thailand reported broad use of 30 TFW-associated species (out of 48 identified in the survey area) by local community members, primarily for food, food additive and material uses (Panyadee et al. 2022). Interestingly, the most ecologically important species *Melaleuca cajuputi* was not reported to be used, though this species is used as a building material and medicinal plant across southeast Asia and northern Australia (Brophy et al. 2013). Instead, uses were reported across a diversity of herb, shrub, aquatic, and tree species, while the most economically valuable plant from the tidal forest was *Schoenoplectiella mucronata*, a sedge used for weaving mats and baskets. Many respondents received income from selling tidal forest plant products, ranging from ~$US75 to more than $US4,000 annually (Panyadee et al. 2022).

In addition to supplying plant-derived resources, TFWs provide habitat for a diversity of wild fauna across their global distribution (for iconic examples see Fig. 4 of Adame et al. 2024). Some of these animal species may represent important food resources for local communities and/or important economic opportunities. For example, in the Pacific Northwest of the United States and Canada, TFWs support diverse life history strategies and seasonality among aquatic fauna, including providing foraging habitat for juvenile salmonids with high-energy prey, resulting in rapid growth potential (Davis et al. 2019, Woo et al. 2019). In northern Australia, the corms of *Eleocharis dulcis* – a freshwater sedge associated with Melaleuca swamps at the interface of saltwater instruction - provide an important food source for iconic magpie geese (*Anseranas semipalmata*) and Aboriginal people, with magpie geese and their eggs also being valuable cultural resources (Bayliss and Ligtermoet 2018, Sloane et al. 2019). Overall, however, knowledge of the contribution of non-mangrove TFWs to wild food resources - including potentially significant contributions to coastal fisheries – is limited, in contrast to long-established knowledge for mangrove and tidal marsh ecosystems (e.g., Odum 1980, Nagelkerken et al. 2008).

Regulation & Maintenance services

The position of TFWs in the coastal landscape, at the interface of land, freshwater inputs and the influence of tides and the sea, is of importance to the regulation and maintenance of many natural cycles and processes. Despite this, the specific contributions of TFWs remain largely unquantified and unknown, with the exception of an emerging body of evidence on the disproportionate contribution of TFWs to climate regulation relative to their extent (see below). Like most wetlands, TFWs are expected to regulate water supplies, including the recharge of coastal aquifers and mitigation of the impacts of both floods and drought on local communities (Williams et al. 2016, Callahan et al. 2017). The coastal protection role of TFWs against both short-term pulses (storms and associated water-level surges) and longer-term stressors of sea-level rise and coastal erosion, is likely significant to coastal zone infrastructure, adjoining land uses and adjacent and upstream ecosystems (van Zelst et al. 2021) though little quantification is available for non-mangrove TFWs. Other physical services likely include the provision and maintenance of habitat structure for nursery populations (see provisional services above); habitat for ecosystem engineers such as beavers that may contribute to ecosystem and landscape climate change resilience (Diefenderfer and Montgomery 2008); regulation of temperature and humidity including support of cold water refugia critical for salmonids (Buenau et al. 2024) and connectivity of habitat structure supporting migration of flora and fauna between the mangrove and other ecosystems (Igu 2016). In addition, TFWs may provide wind protection - the supratidal species *Casuarina glauca* has been used extensively as a wind-break (Nasr et al. 2005) - and potentially even resilience to fire impact, with the genus *Melaleuca* (named from the Greek *melas* (black) and *leukos* (white) referring to bark colouration following fire impact) facilitating post-fire recovery vegetation recovery in peat swamps (Tomita et al. 2000, Thai et al. 2024).

There is growing awareness of the diversity of tidal wetlands – including both forested and non-forested ecosystems - which contribute to regulation of atmospheric greenhouse gas concentrations and are therefore worthy of inclusion in blue carbon policy and research initiatives (Adame et al. 2024). This is particularly relevant to TFW ecosystems which support significant carbon sequestration within their significant above and below ground biomass, as well soil carbon pools and sequestration rates often similar to or greater than those of adjacent blue carbon ecosystems of mangrove, tidal marsh and/or seagrass (Krauss et al. 2018, Adame et al. 2019, Kauffman et al. 2020, Kelleway et al. 2021). Quantification of greenhouse gas fluxes across both soil-atmosphere (Krauss and Whitbeck 2012, Livesley and Andrusiak 2012, Iram et al. 2021) and vegetation-atmosphere (Jeffrey et al. 2021a) also point to a net cooling effect of TFWs, though methane emissions might be significant, particularly in freshwater settings (Rosentreter et al. 2021b). Overall, in most TFWs sequestration of soil and biomass carbon is likely to outweigh losses through gaseous and lateral fluxes (Krauss et al. 2018), perhaps even in freshwater mangroves on river deltas where high plant productivity and deposition of vast quantities of sediments likely support substantial carbon burial (Bernardino et al. 2022).

Other chemical regulation and maintenance services of TFWs likely include: regulation of the chemical condition of freshwaters (including aquifers supporting drinking water and/or agriculture), estuarine and/or coastal saltwater bodies via accumulation of sediments, nutrients and heavy metals in substrates (Noe et al. 2016, Yan et al. 2017, Adame et al. 2019); and improvements to soil quality and contribution to food-web energetics via symbiotic nitrogen fixation in the genus *Casuarina* (Mowry 1933, Batista-Santos et al. 2015).

Cultural services

Under the CICES framework, cultural services encompass the natural, abiotic characteristics of nature that enable active or passive (1) physical and experiential interactions; (2) intellectual interactions; or (3) spiritual, symbolic and other interactions. There is likely a high degree of overlap in the physical recreation opportunities of non-mangrove TFWs and other tidal ecosystems, including water-based activities, fishing, birdwatching, and hunting, though the nature and level of participation in such activities may vary geographically (Kelleway et al. 2017). Intellectual, spiritual, symbolic and other interactions are likely to be unique among the specific plants, animals and landscapes of each TFW, and differ among regions and cultural groups. With few exceptions (Panyadee et al. 2022, Suharno and Kadir 2023), such cultural values of TFWs or their dominant taxa are poorly represented in the literature.

6. Losses, threats and restoration opportunities

Land-use change

The position of TFWs within the coastal landscape, including at upper intertidal to supratidal elevations and often in close proximity to human settlements, has led to a long history of land-use conversion and human impact on TFWs. Many TFWs around the world have been disturbed or converted to other anthropogenic land uses (Figure 13), including extensive losses to resource extraction and/or hydrological modification. For example, more than 95% of the pre-colonial tidal forests and scrub-shrub in the U.S. Pacific Northwest have been lost, mostly due to logging and diking (Brophy 2019). These losses have led to recognition of the rarity of TFW in the region; for example, brackish Sitka spruce TFW is classified as “Imperiled because of rarity” in Oregon (Kagan et al. 2019). Similarly, large areas of TFFW in southern and eastern U.S. were converted to diked rice fields following EuroAmerican colonisation (Kovacik 1979). In the Caribbean, large areas of TFW were converted to sugar cane plantations and later to urban areas (Martinuzzi et al. 2009, Rivera Ocasio et al. 2007), while the distribution of *Pterocarpus* forests have been dramatically reduced along its range, mainly due to changes in land use for agriculture and urban development (Cintrón, 1983; Gould, 2007, Feagin et al., 2013, Bomby et al., 2015). Water abstraction, the expansion of timber plantations and a decline in the groundwater table threatens swamp forest habitats in South Africa (Van Deventer et al. 2021).

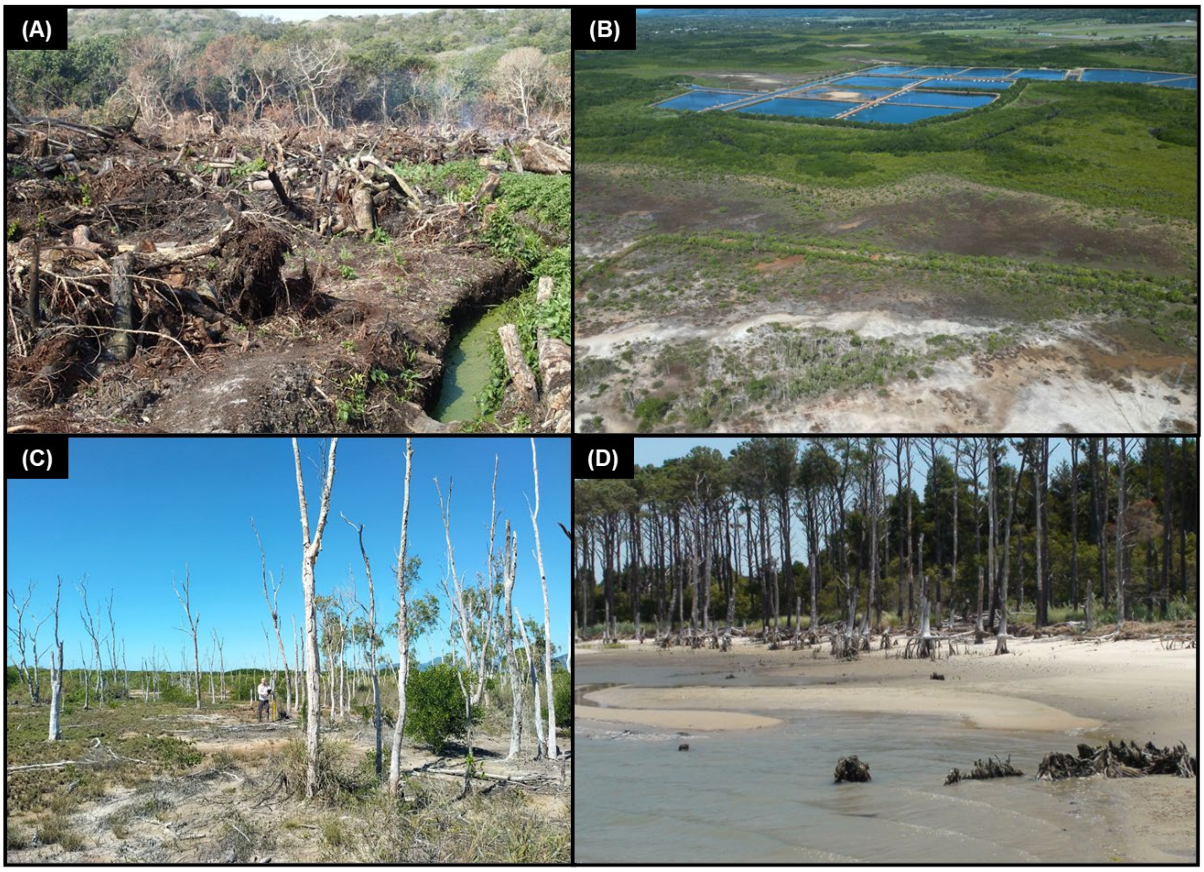

Figure 13. Examples of losses, threats and restoration opportunities in TFWs: a) Illegal slash and burn subsistence agriculture and drainage at uMgobezeleni Estuary destroys Swamp Forest (3 October 2022, JB Adams); b) Example of land-use change with aquaculture facility located on former mangrove, salt marsh and supratidal forest habitat in tropical Australia (R. Carvalho); c) Ghost forest formation and tree stress at the lower elevation fringe of supratidal forest, Port Douglas, Australia (R. Carvalho); North Atlantic Maritime Pine Forest retreat at Skidmore Island, a barrier island off the Eastern Shore of Virginia (Virginia Coast Reserve LTER Catalog, 2008).

Supratidal and associated floodplain forests of Australia’s coastal zone have been subjected to significant historic losses and land-use pressures, including extensive conversion to cane fields in tropical and sub-tropical regions, and conversion to grazing, cropping and residential development across much of their distribution (Boon et al. 2016). Subsequently, several lowland forested wetland types – including some TFWs – are now listed as endangered ecological communities under environmental legislation in Australia (Department of the Environment 2020), though this does not necessarily preclude future land-use conversions.

Land-use pressures remain a significant threat to the extent and condition of TFWs globally. Conversion of coastal lowlands for aquaculture ponds and palm oil in recent decades has likely impacted TFWs in many regions globally, though it is most broadly documented for mangroves (Sidik and Lovelock 2013, Aslan et al. 2016, Oh et al. 2017). Extensive illegal logging has occurred in lowland peat swamps of Southeast Asia (Page and Rieley 2016) and while a decline in mangrove deforestation rates has been observed over the past decade in some regions (Friess et al. 2019), there remains little knowledge on the status or direction of trends in other TFWs.

Impacts of climate change:

Coastal wetlands, including TFWs, are sentinels of the influence of climate change with changes in ecosystem structure and function ascribed to warming temperatures, shifts in precipitation regimes, rising sea levels and/or saltwater intrusion (Gabler et al. 2017, Stahl et al. 2018, Osland et al. 2022). Major shifts in vegetation structure have been observed over recent decades, including encroachment of mangrove forests into tidal marshes (Saintilan et al. 2014), and conversion of non-mangrove TFWs to herbaceous marshes (Kirwan and Gedan 2019), with implications for ecological functions and ecosystem services (Kelleway et al. 2017).

In southern and eastern United States there has been widespread loss of forested wetlands (including North Atlantic Maritime pine forests, and TFFWs) due to sea-level rise, as these systems convert to shrub-dominated wetlands and tidal marsh; 8% of the forested wetland area was lost between 1996 and 2016 (White et al. 2021). Similarly, areas of forested wetlands dominated by *Pterocarpus* forests through tropical America have decreased significantly in recent decades, due to the synergistic effects of changes in the distribution of the precipitation events and saltwater intrusion related to sea-level rise and global warming (Colón Rivera et al., 2014, Rivera De Jesús & Rivera Ocasio, 2022; Miranda Castro et al., 2023). For example, in Colombia, a coastal *Pterocarpus* forest lost approximately 50% of its cover from 1986 to 2018 (Miranda-Castro et al. 2023). In Puerto Rico, the reduction in the cover of a *Pterocarpus* forest on the northern coast reaches ~90%, with most trees dying and little to no recruits since the last decade. Many remaining stands in Puerto Rico now occur near their physiological limits regarding increased salinity seaward and encroachment that limits inland migration by urban development and infrastructure (Cintrón 1983, Rivera-Ocasio et al. 2007). Where snags accumulate as a result of sea-level rise and saltwater intrusion and the understory grades into tidal marsh, the area is colloquially called a 'ghost forest'. While this term was first related to TFWs along the U.S. Atlantic coast (Penfound and Hathaway 1938, Kirwan and Gedan 2019), it is apparent that this phenomenon has broader relevance.

The impacts of sea-level rise on TFWs may also interact with other climatic, geomorphic and biological factors. In the Caribbean, TFWs have experienced extreme drought events and extreme floods associated with major hurricanes resulting in forest dieback and subsequent vegetation shifts (Rivera-Ocasio et al 2007, Yu et al. 2019). Forest dieback and loss has also been observed across widespread *Melaleuca* floodplain forests of Australia's Northern Territory, attributed to geomorphological changes (expansion of tidal creeks) associated with sea-level rise and feral ungulates (Mulrennan and Woodroffe 1998, Sloane et al. 2019). An increase in sea storms/ surges and saltwater intrusion to normally closed estuaries increases inundation and salinity stress causing die-back of swamp forest. This occurred at Mgobezeleni Estuary (South Africa) where storm swells after two cyclones caused strong winds and waves that scoured open the estuary mouth. Large swamp forest (*Ficus trichopoda*) trees died in the lower floodplain (Taylor 2016). Biological drivers of forest stress and dieback, such as fungal disease (e.g. 'myrtle rust' infestations of *Melaleuca quinquenervia*) or pests (e.g. defoliation of Green-ash dominant TFFW by the Emerald Ash Borer) also require attention, including potential for synergistic impacts under changing climatic conditions.

The capacity of coastal wetlands to build surface elevation is central in their resilience to sea-level rise. Decades of field-based measurement has demonstrated that mangroves have a high capacity to build surface elevation through both the accumulation of tidal-borne sediments and/or the production and preservation of belowground biomass (i.e., roots) (Krauss et al. 2014, Rogers 2021). Palaeo-stratigraphic records, however, suggest that even mangroves (which are among the most inundation- and salt-tolerant of all TFWs) are susceptible to in situ losses under higher rates of sea-level rise which may be experienced in coming decades (Saintilan et al. 2020). For most non-mangrove TFWs there is little understanding of rates or processes of surface elevation maintenance, though research is emerging in some settings (Krauss et al. 2023, Saintilan et al. 2023). High rates of shallow zone subsidence in TFFWs of eastern USA (Krauss et al. 2023), combined with radiometric dating (Craft 2012) and broadscale observations of forest decline, suggest these ecosystems are commonly not maintaining elevation compared to relative sea-level rise rates and are currently in transition and will be reliant on upstream and upslope migration for survival in the longer-term.

Restoration opportunities

Efforts to manage, restore and/or enhance the resilience of TFWs are driven, in part, by growing recognition of their role in ecosystem service provision. Effective management approaches require knowledge of the specific stressors that limit desired ecosystem attributes and can be successfully ameliorated by a restoration or enhancement approach. For TFWs, restoring hydrology, replanting trees, addition of sediment, and establishing migration corridors for sea-level rise transgression are all being used or considered (Recht et al. 2024) (Kelleway et al. 2020, Lovelock et al. 2022). Restoration of tidal flows (including both inundation and drainage across the tidal cycle) through dike removal or notching can be used to restore tidal ecosystems including TFWs (Diefenderfer and Montgomery 2008), often with the benefit of greenhouse gas abatement (Kroeger et al. 2017). However, subsidence or low sediment supply in diked areas have led to loss of elevation compared to current (and future) sea-level (Drexler et al 2013), generating uncertainty about how and where tidal influence can be restored to allow re-establishment of TFWs and avoid drowning to an aquatic ecosystem (Brophy 2019). Reintroduction of freshwater through river diversions can reduce salinities and is being planned in Louisiana (White et al 2023) and may favour lower salinity TFWs. Replanting is frequently used to reestablish TFW following conversion or logging (Conner et al. 2007b, Recht et al. 2024), sometimes in association with building microtopography for tree establishment (Diefenderfer and Montgomery 2008). Although we are not aware of implementation of thin-layer sediment addition to TFWs, relatively low sediment availability for many settings (Kroes et al. 2023) suggests that the extra elevation capital gained through this restoration approach could be effective for increasing ecosystem resilience to sea-level rise, as has sometimes been shown in tidal marsh (Raposa et al. 2023). Finally, conserving or managing the landscape adjacent to current or past TFW and other tidal wetlands could facilitate ecosystem migration upslope in response to sea-level rise (Kelleway et al. 2020).

The inclusion of tidal forests within blue carbon and other environmental crediting schemes may present significant support for TFW restoration opportunities. In Australia, supratidal forests have been explicitly incorporated into the country’s first blue carbon crediting scheme (Lovelock et al. 2022), an action which has also subsequently raised the profile and research status of these ecosystems. In the USA, the Oregon Global Warming Commission's Natural and Working Lands Proposal recognizes TFW restoration as an important strategy for climate mitigation (Oregon Global Warming Commission 2021). Globally, there is also scope to include TFWs within existing or emerging voluntary market mechanisms. For example, the Verra VM0033 Methodology for Tidal Wetland and Seagrass Restoration is inclusive of 'tidal forests' (including but not limited to mangroves), however, does not provide default accounting values for non-mangrove TFWs, due to a lack of data availability at the time of development (Needelman et al. 2018). Overall, there have been relatively few attempts to restore non-mangrove TFWs to date, and further research is needed to predict and evaluate outcomes following management.

7. Information and research needs

Building knowledge across diverse settings

This review, along with earlier works by Duberstein et al. (2013a) and Adame et al. (2024), has demonstrated the widespread global occurrence of diverse TFWs. Despite this broad distribution, much of the current knowledge for non-mangrove TFWs (including our case studies) stems from the United States, and to lesser extent Australasia and the tropics of the Americas. Even in the US, however, knowledge of non-mangrove TFWs remains in infancy relative to the tidal marshes and mangrove forests which have been subject to decades of research.

For TFFWs of southern and eastern USA, the first scientific descriptions emerged in the mid-1980s (Brinson et al., 1985), with a small pulse of additional publication in the early 1990s (e.g., Hackney and Yelverton 1990, Rheinhardt and Herchner 1992). Up to that point, non-mangrove TFW descriptions were observational but not treated distinctively until trees died and transitioned to a more definable landscape feature as 'ghost forests'. Further steps toward describing these ecosystems were made in 2007 through an edited volume that synthesized various upper estuarine studies underway in the southern and eastern USA (Conner et al. 2007).

In Australia, research of non-mangrove TFWs has been rare, with a longer focus instead on *Melaleuca* and *Casuarina* CFWs in non-tidal settings. For example, early research focussed on vegetation dynamics of non-tidal CFWs (Williams 1984, Finlayson et al. 1993, Franklin et al. 2007), though some exceptions included tidally-influenced settings (Clarke and Hannon 1970, Clarke and Allaway 1996). More recent research of non-mangrove TFWs in this region has focussed largely on carbon cycling capacity (Adame et al. 2019, Kelleway et al. 2021), though clarification of the tidal processes and appropriate terminology for non-mangrove TFWs and non-tidal CFWs is underway (Tozer et al. 2022, Carvalho et al. 2024, Kelleway et al. In review). Similarly, while diverse forested wetlands have been described across the American tropics – spanning Mexico to Brazil – little quantification exists of the influence of tidal processes or salinity regimes, or resilience to sea-level rise among these ecosystems.

The current paper has highlighted and summarized specific TFW case studies, ranging from the well-studied to the poorly understood. While our definition of TFWs (Section 2) is intentionally broad, and these TFWs occur along a broad gradient of inundation and salinity gradients, refinement of definitions and terminologies according to the specific influence of tides may be warranted. For example, should specific thresholds or classifications of "tidal influence" be applied in relation to their influence on the ecology and function of TFWs (Williams et al. 2016)? Should TFWs subject to regular inundation by astronomical tides or regular, predictable combined fluvial/tidal forces be categorised separately from TFWs subject only to belowground tidal expressions, or those experiencing only occasional flooding from abnormally high tides? Such questions will be particularly pertinent to TFWs located at higher elevations relative to the tidal frame (e.g. supratidal forests, transitional forests, and some maritime forests) (Kirwan and Gedan, 2019). For many settings, including the vast lowland peat swamps of Southeast Asia and transitional forests of the Niger Delta and tropical Americas, there is currently little to no data on tidal influence variables such as salinity and ground water level gradient along the continuum of mangrove to non-mangrove TFW to non-tidal CFW. This limited understanding of the role of tides and sea-level change in shaping belowground and aboveground biophysical characteristics of these specific ecosystems, and also curtails effective classification of TFWs and CFWs at a global scale.

Clearly there is need for more detailed knowledge, both within already-studied settings, and across the diversity of TFWs globally. A more systematic and complete knowledge of the distribution and drivers of TFWs and non-tidal CFWs, developed through global comparison and synthesis, will be critical to improving terminologies, definitions and classification systems. This broadened understanding will also enable better inclusion of diverse TFW types within emerging and revised ecosystem typologies. For example, while the current version of IUCN Global Ecosystem Typology is gaining traction within environmental accounting and decision-making frameworks (e.g. Farrell et al. 2021), mangroves are the only tidal forests specifically described and included in this framework, under 'MFT1.2 Intertidal forests and shrublands' (Keith et al. 2020). Similarly, while there is a functional group ('MT2.1Coastal shrublands and grasslands') for low-statured supralittoral vegetation subject to periodic disturbance from exceptional tides and coastal storm events, an analogous group for forested settings is missing. Elsewhere, Adame et al. (2024) provide an attribute classification scheme which will be useful for the refinement of a typology of TFWs (among other blue carbon ecosystems), though knowledge gaps currently restrict such an approach for many TFW settings.

Data needs first described in the mid-1990s have been advanced into four primary research needs at present. These themes include the need for maps on the distribution of TFWs, further insight into biophysical controls of TFWs and their response to environmental change, improved understanding of TFW biogeochemistry and associated ecosystem service provision, and defining actionable management opportunities. Additional study of all four of these themes is needed for TFWs around the world.

Mapping

Global research and management efforts on TFWs are limited by incomplete and inconsistent maps. As a result, the threat of climate change and opportunities for blue carbon are unrealized for TFWs at the global scale. Earth observation satellites have been leveraged extensively over the past several decades to map and quantify landscape change at the global scale. In particular, coastal vegetated ecosystems such as mangrove and saltmarsh are routinely mapped with increasing precision and inclusion of the worlds vegetated intertidal environments (e.g., Giri et al. 2011, Bunting et al. 2022, Murray et al. 2020, Worthington et al. 2024, Maxwell et al. 2024). However, demarcating non-mangrove TFWs remains challenging for multiple reasons. First and foremost, differentiating tidally-influenced forests from other adjacent forest ecosystems via remote sensing is confounded by overlapping distributions of dominant TFW taxa with terrestrial forests, non-tidal CFWs, and even mangroves (as observed in many settings in Section 3) (Bernardino et al. 2022). Traditional land use/landcover mapping approaches like pixel-based classification algorithms (e.g., support vector machines, random forests, maximum likelihood) and object-based image analysis perform best when the targeted land use/landcover types have minimal overlap in spectral reflectance and physical properties between classes. Other coastal ecosystems like mangroves and saltmarsh have been extensively mapped at a global scale due to the relative homogeneity in landscape positioning and vegetative expression. In contrast, some geographically-extensive map products based primarily on aerial photograph interpretation, such as the U.S. National Wetland Inventory (Dahl et al. 2020), have inadvertently omitted many TFWs, often erroneously characterizing them as non-tidal forested wetlands or upland forests (Endris et al. 2024). This is particularly challenging in upper elevation TFWs (e.g., supratidal forests and North Atlantic Maritime Pine Forests) which may have a 'light touch' of tidal influence that can be difficult to discern via imagery, because of the low and/or unpredictable frequency of flooding and potential influence of groundwater (see sections 3 & 4). The forested nature of TFWs also complicates the use of spectral approaches which might otherwise be used to differentiate inundation or wetness conditions among tidal and non-tidal settings.

Despite the challenges, a number of approaches and potential solutions have been advanced. Recently, methods that utilise models of elevation, inundation and/or hydrological connectivity, rather than relying on spectral differentiation of vegetation types alone, have shown specific promise for TFWs (Brophy et al. 2019b, Carvalho et al. 2024, Endris et al. 2024). For example, the combination of high water level data, water level spatial models, LiDAR-based digital elevation models, and land cover datasets has been used to identify extensive areas of likely TFWs in areas where these had previously been poorly mapped, including the U.S. Pacific Northwest and some U.S. Gulf Coast and southeast coastal plain estuaries (Brophy et al. 2019b, Endris et al. 2024), and to map their historical extent and losses (Brophy 2019). A similar approach, combining elevation and hydrological connectivity is also being used to develop first continental scale mapping of supratidal forests in Australia (Carvalho et al. 2024). At smaller scales, deployment of water level recorders and extrapolating to imply tidal influence has also been used at small scales (Krauss et al., 2018; Kroes et al., 2023). Regardless of scale, these inundation-based approaches are reliant upon suitable elevation and/or hydrological data, which may not be available in many TFW settings, and need to consider the influence of complex tidal hydrology (e.g. propagation or attenuation of tides) along dendritic pathways and/or across broad vegetated plains, associated with some TFWs (Figure 14).

Advances in remote sensing technology, data availability and analytical methods will continue to provide new mapping opportunities for TFWs in the future. Improved resolution of satellite sensors to characterize vegetation and hydrology, the generation of new geospatial predictor datasets (such as national scale predictions of the extent of the annual highest high tide and high-resolution elevation models) and additional field studies (e.g., elevation, hydrology surveys; UAV-based surveys) of diverse TFWs will all offer opportunities for improvement. Advances in the use of existing remote sensing datasets to map flooding regimes in other forested wetland settings (Gašparović and Klobučar, 2021; Oakes et al., 2024; Tsyganskaya et al., 2018), also offer potential approaches to improve mapping of TFW distribution and hydrological processes. For example, the combination of remote sensing observations of water with statistical approaches to account for forest canopies (Lymburner et al. 2024) may offer new opportunities to quantify inundation dynamics and improve differentiation of TFWs and non-tidal CFWs. Similarly, expansion of LiDAR data availability – through spaceborne, aircraft and UAV instruments – provides opportunities for improving models of vegetation structure and, potentially, sub-canopy water levels (e.g., Thomas et al. 2023).

The inherent spectral and spatial complexity of TFWs may make them good candidates for the new frontier of remote sensing research that leverages the advancement of machine learning algorithms, adoption of deep learning approaches, and accessibility of more powerful computing resources. Deep learning algorithms like convolutional neural networks are well suited to process gridded data from satellite imagery for land use/landcover classification and can handle complex patterns. Convolutional neural networks have the potential to be paradigm shifting for TFW mapping by extracting and leveraging additional information in imagery to form more consistent boundaries for each class. The biggest challenge to its adoption for TFWs is the need for pre-tagged images for model training, which there is no available dataset for right now. Integration of new TFW data collection with existing coastal training datasets (e.g., Murray et al. 2022) will be of broad benefit to coastal ecosystem mapping efforts. A global map of TFWs will have a significant impact on the research and policy advancement that better capture their value in broader ecosystem functioning.

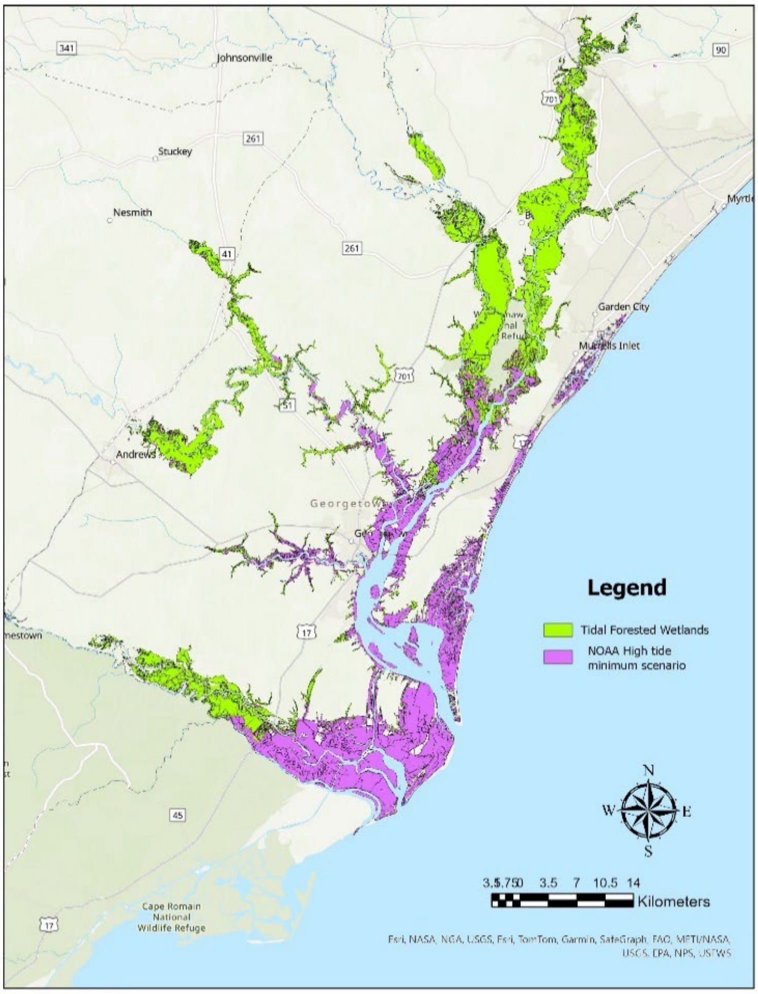

Figure 14. Potential distribution of tidal freshwater forested wetlands within the Winyah Bay Estuary of South Carolina, USA showing the dendritic patterns of upper estuarine tidal forest development that needs to be accounted by future mapping efforts. (Andrew S. From, U.S. Geological Survey).

Biophysical controls and response to environmental change

Fundamental knowledge of the biophysical controls on TFW ecosystems and their biota is required to understand the structure and function of ecosystems, and their potential changes in response to climate change and other disturbances. We summarized the distribution of different CFW types along salinity and inundation gradients based upon current knowledge (Figure 12). In general, better understanding of the role of tidal influences and salinity in groundwater and porewater is needed, especially for settings with little to no data at present. Disentangling the individual or interactive effects of increased inundation and increasing salinity associated with sea-level rise and saltwater intrusion will be challenging, and likely setting- and taxa- specific, given the high variation amongst settings (Figure 12). Although salinity and inundation are clearly important controls for TFWs, other factors are also likely important including geomorphic position, temperature, and freshwater availability (Chen and Kirwan 2022; Kelleway et al. In review; Rovai et al. 2018). Most attention has focused on controls of the dominant plant taxa in each TFW type, but there is also a need for better understanding of the biophysical controls for other taxonomic groups (e.g., fish and wildlife).

TFWs occur across substantial biophysical gradients (Craft, 2012) and represent a steady-state that shifts with sea-level fluctuations over millennial time scales. Temporal transitions in ecosystem state are of two types: (1) lateral across the tidal frame, whereby supratidal TFWs eventually transition to ecosystems lower in the tidal frame (intertidal TFWs, tidal marsh or mangrove), and (2) longitudinal along river gradients, whereby TFWs (including brackish TFWs, TFFWs and/or low salinity TFWs) may transition to marsh or mangrove, as saline conditions are pushed upstream. Paleorecords of TFWs and their transitions are rare – and an important area of future research need – though those from the southeast USA document changes in the other direction as well; marsh to TFW (Thomas et al. 2015, Jones et al. 2017). Thus, while transitions are natural, humans can have a heavy hand. For example, within a tidal tributary of the Sampit River, South Carolina, the construction of a paper mill led to greater growth of baldcypress (*Taxodium distichum*) between 1937 and 1975 versus a 1900 reference date, perhaps related to nutrient loading from upland terrestrial tree harvesting; however, growth slowed from 1975, likely related to warm water discharge from a different industry upstream and greater submergence from sea-level rise (Thomas et al. 2015). This same wetland experienced increased accretion during ~1300–1000 cal yr B.P. (roughly corresponding to the Medieval Climate Anomaly) when the climate was drier sea-level rise was slightly elevated (Jones et al. 2017). Much more significant increases were experienced here however in the period 450–300 years BP, coincident with land-use changes and conversion to marsh (Jones et al. 2017). The tree ring chronology from that site began 229 years ago, relative to 2012 (Thomas et al. 2015), and corresponded well to a decrease in woody plant pollen around the same time (Jones et al. 2017).

Lateral and longitudinal transitions are also expected to have produced varied Quaternary and present-day transitional histories. As TFWs in the supratidal zone (e.g. supratidal maritime pine forests, high-elevation TFFWs) transition to marsh with rising sea levels over lateral gradients along the Atlantic US coast, wetland carbon storage and the preservation of pollen down-horizon begins in earnest at the point of conversion to tidal marsh. For Australasian supratidal forests, there is some evidence of a sea-level highstand at c. 6000 years BP (Lambeck and Nakada 1990) which aligns with the contemporary elevation of many supratidal forests in the region (Carvalho et al. 2024), and contrasting the more consistent rise in relative sea level experienced by coastlines in eastern North America (Rogers et al. 2019).

Biogeochemistry and ecosystem service provision

Carbon cycling

As with other aspects, knowledge regarding biogeochemical cycling in non-mangrove TFWs lags that of mangroves and tidal marshes, particularly given advances in blue carbon research over the past decade. While a critical mass of research has warranted the inclusion of many TFWs in blue carbon initiatives (Adame et al. 2024), knowledge and implementation barriers remain. A significant example is a legacy assumption that all freshwater wetlands have high methane emissions, which has countered interest in low salinity TFWs (e.g. TFFWs) as nature-based climate solutions. However, methane fluxes from non-mangrove TFWs have been documented to be far less than assumed (e.g., Krauss and Whitbeck 2012, Williams et al. 2025), and indeed does not, as yet, differentiate from those reported from mangrove ecosystems (Rosentreter et al. 2021a). Tides within regularly flooded TFWs expose soils to the atmosphere often; in fact, with the exception of back swamp areas (sensu, Duberstein et al. 2014), tidal flooding is much less than that of adjacent marshes that are lower in the tidal frame. Methanotrophy can be prominent in TFWs, with Megonigal and Schlesinger (2002), discovering that 52-81% of methane produced in TFFW soils is oxidized to CO_2 before being emitted. From other tidal wetlands, methane oxidation can reach near 100% at high intertidal positions (Wang et al. 2019), while supratidal forests can even act as sinks of methane (Livesley and Andrusiak 2012). Oxidation of tree-stem methane has also been observed in some supratidal forest species (Jeffrey et al. 2021b). Nevertheless, the methane balance of most TFWs remains unresolved to date, with vegetative and lateral aquatic fluxes most poorly constrained, though evidence suggests that soil-atmosphere emissions may be much lower than assumed from salinity alone.

Potential sea-level rise and climate change responses of carbon cycling in TFWs and adjacent ecosystems constitute a significant research question. While global analysis of tidal wetlands has shown a high capacity for preservation of soil carbon under sea-level rise (Rogers et al. 2019), ecosystem transitions can alter soil properties including bulk densities and carbon content (Kelleway et al. 2016, Noe et al. 2016, Jones et al., 2017). Forest dieback (i.e. development of ghost forests) and conversion to marsh has implications for biomass carbon cycling, including the potential for increased methane emissions via vegetative fluxes of methane from snags (Jeffrey et al. 2019). Monitoring of fluxes under such vegetation transitions, along with further quantification efforts of carbon-cycling parameters in general, will provide the evidence base for inclusion of TFWs in carbon trading mechanisms (e.g., Lovelock et al. 2022).

Nutrient cycling

When salinity intrudes into freshwater TFWs, organic matter is mineralized from soils as SO_4-reduction is stimulated (Weston et al. 2006, Marton et al. 2012), and this has presented uncertainty as to what happens to the pulse of additional carbon, nitrogen, and phosphorus mineralized by this physico-chemical change. TFWs accumulate and retain nitrogen and phosphorus through sedimentation (Ensign et al. 2014, Adame et al. 2019), however, mineralization of TFW nitrogen and phosphorus has been observed due to salinization and during ecosystem conversion to salt marsh (Noe et al. 2012, Ardón et al., 2013).

Measurements of nitrous oxide fluxes have been rare in non-mangrove TFWs, with available field studies reporting small, though seasonally variable soil-atmosphere fluxes (Krauss and Whitbeck 2012, Livesley and Andrusiak 2012), similar to findings from the few measurements in mangroves and other coastal wetlands (Rosentreter et al. 2021a). Interestingly, pristine mangrove TFW waters have been found to be a small nitrous oxide sink (Maher et al. 2016). Given the magnitude of potential release of stored nitrogen and phosphorus, and potential implications of future increases in anthropogenic loadings (Murray et al. 2015), additional study and model development from empirical data collections are warranted.

New insights are particularly important in the context of current and future changes in TFW environments. For example, a biogeochemical model (TFFW-DNDC) that incorporates sources (inputs), biological transformations, sinks (storage), and export of nutrients has recently been developed for TFFWs of southeastern USA and their transitions to low-salinity tidal forests and marshes (Wang et al. 2020, Wang et al. 2022, Wang et al. 2023). Other models taking different approaches should be developed, as they have been for mangroves (e.g., Berger et al. 2008). Models will eventually enable large-area scaling of biogeochemical processes and describe changes in nutrient balance as upper estuarine forests retreat.

Information needs for Management

Blue carbon and co-benefit initiatives are increasingly driving enhanced understanding, investment and management outcomes for some coastal wetlands (Macreadie et al. 2021). While mangroves have been at the forefront, opportunities for non-mangrove TFWs have been less common, though this will likely change with increasing awareness of the blue carbon potential of these ecosystems. Incorporation of non-mangrove TFWs into mangrove-oriented initiatives, or at least embracing the management lessons provided through the mangrove experience (e.g., clear policy pathways; institutional readiness; Box) are vital management actions.

There are also management lessons offered through past TFW experiences. For instance, rehabilitation options for TFFWs and transitional habitat have been proposed (Middleton and Jiang 2013, Middleton et al. 2015, Wang et al. 2017), but permitting challenges have been a barrier to implementation. Discussions with stakeholders have identified three realistic management options, including thin-layer sediment placement (c.f., Stagg and Mendelssohn 2010), tidal re-introduction (c.f., Howe et al. 2010, Drexler et al. 2013), and river re-introduction (Das et al. 2012, Wang et al. 2017). All of these actions ameliorate human-facilitated disconnection from sustaining water sources to TFWs, and are focused on restoring flood depth, duration, and frequency requirements in different ways. However, uncertainty regarding management outcomes has led to inaction in some cases.

Historically, tidal restoration projects in Australia have not had a significant focus on non-mangrove TFW outcomes, with some cases causing loss of supratidal forests as tidal, saline water is re-introduced to previously drained and subsided areas (Kelleway et al. 2021). There are early signs of success for TFW restoration, including the conversion of abandoned cane fields to supratidal forests, with associated benefits in water quality and climate mitigation (Iram et al. 2022), though broader demonstration and long-term monitoring is required. Through a survey of TFW restoration practitioners, Recht et al. (2024) documented 14 TFW restoration sites in the U.S. PNW totalling 164 ha (range 1 to 66 ha), with activities focused on tidal reconnection, grading and channel excavation, and often included soil mounds, large woody debris placement, and nurse logs to support woody plantings. All sites reported monitoring at restoration and paired reference sites to inform restoration design and evaluation of restoration effectiveness (Recht et al. 2024). Scaling up from such smaller-scale projects, ambitious large-scale test cases for management action, such as reconnection of the Maurepas Swamp with the Mississippi River in Louisiana (Shaffer et al. 2016) should be launched and science used to guide adaptations in management and/or address stakeholder concerns.

BOX: Mangroves provide a blueprint for the inclusion of tidal forested wetlands in global blue carbon initiatives

Tidal forested wetlands are now considered under definitions of blue carbon (Adame et al. 2024), and some specific ecosystems (mangroves, brackish non-mangrove TFWs, TFFWs, supratidal forests) meet most science and policy criteria of established blue carbon ecosystems (Lovelock and Duarte 2019). However, the scientific basis for blue carbon in other tidal forested wetlands, and their application in blue carbon management and policy shows a lag, though the specific inclusion of supratidal forests in Australia's blue carbon Method is one exception (Lovelock et al. 2022). So far, mangrove forests have received substantially more research attention than other blue carbon ecosystems (de Paula Costa & Macreadie 2022), and have seen more implementation within carbon credit projects (Friess et al. 2022) and national climate change mitigation policies, such as Nationally Determined Contributions to the Paris Agreement (Dencer-Brown et al. 2022, Arkema et al. 2023). This begs the question: **what can we learn from experiences in mangrove blue carbon science and management, to facilitate blue carbon implementation in other TFWs?** Several key turning points were apparent in mangrove blue carbon science and implementation; addressing key research needs such as those described here (*Section 7*) may help strengthen the scientific evidence base for other TFWs and support their more rapid inclusion into blue carbon management actions and climate change mitigation policies.

1. **Clear ecosystem definitions.** Mangrove forests generally have a clear ecosystem definition, based on biophysical setting (generally mean sea level to highest astronomical tide), vegetation structure (forest or shrubby habit contrasting that of tidal marshes and mudflats) or vegetation species assemblage (though mangrove communities show biogeographic variation). This could allow them to be more easily managed and incorporated into policy structures compared to ecosystems with varied or conflicting definitions (*Section 2*).
2. **Agenda-setting research papers.** While carbon dynamics in mangroves have been studied since the 1980s, two key papers played an important role in communicating this science to broad audiences. McLeod et al. (2011) communicated the concept of blue carbon, and showed that mangroves, alongside seagrasses and tidal marshes, exhibited substantially higher carbon burial rates than terrestrial forests. A data synthesis by Donato et al. (2011) estimated mangrove carbon stocks collected in three countries across the Indo-Pacific, showing carbon densities 3-5 times higher than the averages for other terrestrial ecosystems. Similar cross-ecosystem analyses exist for some TFW types in restricted localities (Krauss et al. 2018, Southeast USA;

Kauffman et al. 2020, Northwest USA), but only recently has a broader synthesis of carbon stocks been conducted across a range of TFWs (Adame et al. 2024).

3. **Spatial information on ecosystem extent.** Mangrove research accelerated after the publication of the first global mangrove map in 2011 (Giri et al. 2011). The production of this map quickly led to a range of other global mangrove products (Worthington et al. 2020), including habitat change through time (e.g., Bunting et al. 2022); models of carbon stock distribution (e.g., Atwood et al. 2017); carbon emissions from mangrove loss, both historically and into the future (e.g., Adame et al. 2021); and highlighting areas for potential blue carbon conservation (Zeng et al. 2021) and restoration (Worthington & Spalding 2018). Global mangrove mapping is now a routine activity by several research groups around the world providing regular updates on global mangrove extent (Friess 2023), though mapping remains a key knowledge gap in other TFWs (*Section 7*). Filling this knowledge gap will show the global relevance of TFWs, document change in areal extent and identify the scale of management actions for climate change mitigation.
4. **Clear policy pathways.** Spatial information showed the global relevance of mangrove blue carbon and its potential contribution to climate change mitigation, both globally and at the national level. Consequently, mangroves have been the main blue carbon ecosystem included in Nationally Determined Contributions (NDCs) (Herr and Landis 2016), commitments that countries make to reduce their greenhouse gas emissions as part of climate change mitigation. This in turn has encouraged a number of countries to strengthen national environmental policy around mangrove conservation and establish ambitious restoration targets to achieve NDC goals Sidik et al. (2023).
5. **Institutional readiness.** Mangroves benefited from various long-term international research partnerships that focussed research effort and created substantial evidence for the relevance of mangrove blue carbon, such as The Sustainable Wetlands Adaptation and Mitigation Program (SWAMP), established by the Center for International Forestry Research and the US Forest Service. Amongst other resources, this program led to the creation of a standardised protocol for mangrove carbon stock estimation (Kauffman & Donato 2012), that precipitated a marked increase in published carbon stock assessments. Similar guidance exists for blue carbon management activities such as mangrove restoration (United Nations Environment Programme 2020, Global Mangrove Alliance 2023). Many institutions have also established training programs

and workshops to ensure a pipeline of researchers trained in mangrove carbon assessments. Similar resources and training opportunities focused on other TFWs may increase knowledge and capacity.

8. Conclusions

In this review we have begun synthesis of TFWs by comparing and contrasting the growing body of science on seemingly disparate individual ecosystem types across the globe. In doing so we have demonstrated a critical mass of research and understanding of the occurrence, drivers, values and threats to TFWs across numerous settings globally. Despite differences in their biogeography, extent, plant composition and landscape positions, there are important commonalities among settings. The complex interaction of tidal, non-tidal, surface and sub-surface waters is an important control on ecosystem structure and functions, while salinity regimes – though variable among and within settings – exert a significant control. Similarly, many settings share significant plant flora with adjacent terrestrial/upland and/or non-tidal forested wetlands, presenting challenges for classification and mapping of these ecosystems. For these reasons we have proposed a hierarchy of terminologies - coastal forested wetlands (CFWs) > tidal forested wetlands (TFWs) > setting-specific names – which enable inclusivity or exclusivity as required. While consistency is required at higher levels to consolidate and leverage management opportunities at national and global scales, our case studies demonstrate the importance of setting-specific knowledge and terminologies for improving knowledge and valuation across diverse settings.

In contrast to the long history of research and improving perception of mangrove forests, non-mangrove TFWs have been under-studied and undervalued. Our emerging understanding of their diversity and values needs to be advanced to ensure their sustainability in a time global change and sea-level rise. Critical information gaps include the need to better map and understand the full distribution and character of TFWs, identify and quantify biophysical controls, and better understand TFW biogeochemistry as an important component of ecosystem service provision by TFWs. While some of these challenges will be addressed through improving global capabilities (e.g. refinement of remote sensing approaches), and site-specific studies, integration of local knowledge across scientific, stakeholder and other communities will be vital. Incorporation of lessons from the global mangrove experience, and incorporation of non-mangrove TFWs into mangrove-oriented initiatives – where appropriate

– will be essential for the effective management of diverse TFWs in a time of environmental change.

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