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Ecohydrology of coastal aquifers in humid environments and implications of a drying climate

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Abstract

Coastal groundwater-dependent ecosystems (GDEs), such as wetlands, estuaries and mangrove forests, are globally important habitats that promote biodiversity, provide climate regulation and serve as refugia for plant and animal communities. However, global warming, coastal development and over-abstraction threaten the availability and quality of groundwater in coastal aquifers and, by extension, the ecohydrological function of dependent ecosystems. Because ecohydrological knowledge of coastal groundwater is disparate across disciplines and habitat types, we begin by summarising the physiochemical, biological and hydrological processes supported by groundwater across coastal watersheds. Groundwater makes a significant but poorly recognised contribution to the function and resilience of coastal ecosystems and will play an essential role in climate change mitigation and adaptation. This review then explores how critical ecosystem processes supported by groundwater will be affected in areas of the humid subtropics that are expected to be impacted by climatic drying. Where rainfall is predicted to decrease, reduced groundwater recharge will interrupt the hydrology of coastal GDEs, while anthropogenic pressures, such as land-use intensification and pollution, will diminish the quality of remaining groundwater. The challenges of managing groundwater for multiple purposes under climate change predictions are highlighted. To improve the management of coastal GDEs, research should be aimed at developing robust conceptual models of coastal groundwater systems that quantify biophysical linkages with ecological communities across relevant spatiotemporal scales.

KEYWORDS

climate change, coastal ecosystems, coastal groundwater, coastal resilience, ecohydrology, groundwater dependent

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1 | COASTAL GROUNDWATER, DEPENDENT ECOSYSTEMS AND CLIMATE CHANGE

In coastal areas, groundwater provides a reliable source of freshwater for humans and ecosystems (Eamus & Freund, 2006; Wada et al., 2020). Over 2 billion people rely on coastal groundwater for direct consumption (Ferguson & Gleeson, 2012), and many more depend on ecosystem services provided by highly productive groundwater-dependent ecosystems (GDEs) (Taylor et al., 2013). Despite the enormous value of GDEs, they have degraded globally due to changing hydrological factors and anthropogenic influences, impacting their ability to sequester atmospheric carbon, moderate climate extremes and provide habitat for a range of species (Griebler & Avramov, 2015). Due to their position in the landscape, coastal GDEs are susceptible to both oceanic and atmospheric climate change-related drivers, such as sea-level rise, increasing rainfall variability and anthropogenic pressures associated with coastal development. An understanding of the ecohydrological function of coastal

aquifers is needed to accurately predict and mitigate impacts associated with climate change and ensure the longevity of these important systems.

GDEs are ecosystems that require access to groundwater to meet their water needs on a permanent or intermittent basis (Richardson et al., 2011). The degree of groundwater dependency can vary in space and time between individuals, species and communities (Boulton, 2020; Eamus et al., 2006). In coastal settings, GDEs include a variety of habitats and the ecological communities they support (Erostate et al., 2020) (Figure 1). Examples of coastal GDEs include upland freshwater habitats such as wetlands and coastal river systems, habitats within the tidal interface including mangrove and salt-marsh areas, and near-shore marine environments. We use the term 'coastal' to describe GDEs that exist across coastal catchments and not exclusively GDEs directly influenced by the ocean.

Changes in the timing, intensity and magnitude of rainfall due to atmospheric warming are predicted to alter groundwater regimes: being the timing, magnitude, frequency, duration and rate of change in groundwater quantity and quality (Ferguson & Gleeson, 2012; Kath

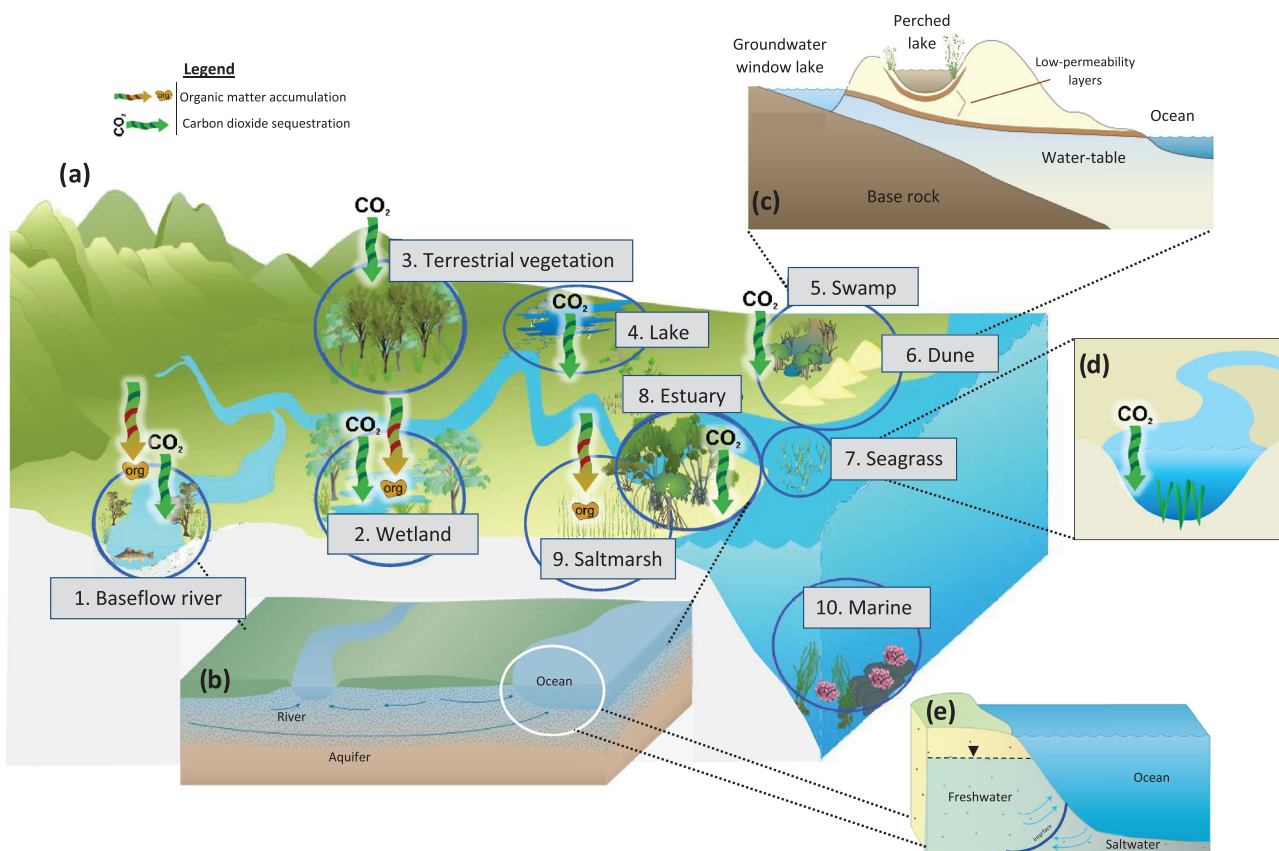


FIGURE 1 (a) Examples of coastal habitats and ecosystems that are supported by groundwater (coastal GDEs). Landscape features and associated habitat types are numbered, and biogeochemical and biological processes supported by groundwater in these habitats are described in Table 1. (b) Simplified representation of a gaining river receiving baseflow from an adjacent perched aquifer. (c) Coastal dune system adjacent to shoreline can host groundwater in perched, unconfined aquifers where low-permeability layers permit. Groundwater window lakes occur where low-lying parts of the dune system intersect the groundwater table. (e) Simplified representation of the freshwater-saltwater interface critical to groundwater quality in coastal aquifers and the maintenance of near-shore coastal habitats. (d) Discharge of groundwater into shallow marine environment (seagrass meadows, reefs and other benthic habitats)

et al., 2018). However, it is important to note that changes in rainfall due to global warming are not uniform across all humid subtropical coastlines. Total annual precipitation has decreased, and consecutive dry days have increased since the 1950s across humid subtropical regions in China, India, Africa and Australia (IPCC, 2021). Yet, in humid subtropical coastlines of North and Central America, total annual rainfall has increased since the 1950s (IPCC, 2021). Changes in rainfall do not always reflect climatic drying in humid subtropical coastlines, and there will be differences in the response of groundwater tables to precipitation in these areas (Kotchoni et al., 2018; Taylor et al., 2012). However, declining groundwater availability as a result of climatic drying and over abstraction is a critical issue to coastal GDEs globally and remains the primary focus of this review (Cuthbert et al., 2019).

This review aims to outline the ecohydrological importance of groundwater in subtropical coastal regions to ecosystem function and summarise threats presented by declining rainfall as a result of climatic drying. Specific aims are to (1) outline the vulnerabilities of coastal GDEs in the humid subtropics while considering key differences in the function of arid and humid GDEs; (2) synthesise the literature on groundwater's role in supporting ecosystem functions in humid environments; (3) investigate climate change impacts on the quality and quantity of groundwater available to support ecosystems, with a focus on declining rainfall and (4) consider how the management of coastal GDEs should be approached under conditions of climatic drying.

2 | FOCUSING ON COASTAL GROUNDWATER IN THE HUMID SUBTROPICS

The presence of GDEs in coastal environments relies on hydraulic connectivity to aquifers, the location and extent of recharge and discharge areas, the direction and velocity of flow and the infiltration capacity of surrounding substrate. Coastal groundwater used by dependent ecosystems exists in unconfined, confined and semi-confined aquifers. Unconfined and semi-confined aquifers are typically shallow, and water levels within are exposed to atmospheric pressure; therefore, the water table rises and falls on shorter time scales. These fluctuations are often a reflection of variable rainfall patterns. Confined aquifers are defined by impermeable material above and below the saturated aquifer unit and are held under pressure. Depending on the size of the confined system, recharge may occur outside of coastal proximity, and pressure fluctuations occur over longer time scales.

Within coastal environments, local geology is often comprised of older continental rock units and recent sediments from river discharge and nearshore sediment transport. This combination results in complex aquifer structures, and heterogeneity formed by lateral and vertical variation in permeability (Zamrsky et al., 2020). Unconfined aquifers are generally more susceptible to climate variability than confined systems, especially if the latter is connected to more extensive, deeper groundwater systems. Therefore, depending on aquifer

properties and connectivity to the ocean, coastal GDEs can be exposed to atmospheric and oceanic climate change drivers.

Although coastal GDEs can include subterranean cave systems and karst landscapes, this review focuses on GDEs in predominantly unconsolidated coastal environments within the humid subtropics. Examples of coastal GDEs associated with unconsolidated sediments include the St Lucia estuary in South Africa, the Florida Everglades in the USA and wetland complexes found on Minjerribah (Stradbroke Island), Mulgumpin (Moreton Island) and K'gari (Fraser Island) in southeast Queensland, Australia (Figure 2).

Coastal aquifers formed by unconsolidated sediments, such as quartz derived sand, silts and tidal muds constitute approximately 25% of the coastal ribbon (within 200 km of coastlines) globally (Hartmann & Moosdorf, 2012). An estimated 40% of the human population is concentrated within this coastal ribbon (Zamrsky et al., 2018). Furthermore, a large portion of the human population living in coastal areas relies on groundwater resources stored in underlying unconsolidated groundwater systems (Zamrsky et al., 2020). Unconsolidated aquifers and dependent ecosystems are globally widespread systems under increasing strain from human pressures.

This review focuses on GDEs in the humid subtropics. Outside of the tropics (areas located between 23.5° north and south of the equator) and arid zones, there is a lack of consensus on the response of groundwater to changes in rainfall and recharge dynamics due to climate change. In tropical settings, episodic recharge events can offset drought-driven groundwater table lowering, and higher annual rainfall totals can result in groundwater table rise (Kotchoni et al., 2018; Taylor et al., 2012). Comparatively, however, the relationship between climate change, rainfall and recharge remains less understood in subtropical settings. This warrants concern given much of the world's subtropical coastlines and associated GDEs exist in countries experiencing rapid coastal urbanisation (Peel et al., 2007) (Figure 2) and are therefore exposed to unsustainable levels of exploitation and depletion.

2.1 | Why coastal GDEs in the humid subtropics are particularly vulnerable

The effects of declining groundwater availability on ecological communities have been well examined in arid and semi-arid regions (Barron et al., 2014; Máguas et al., 2011; Sommer et al., 2014). Less research has been directed at GDEs and connected groundwater systems located on subtropical coastlines. The reason for such a large discrepancy in research volume is unclear. Erostate et al. (2020) suggest coastal GDE research is constrained by a lack of legal and managerial recognition. Ciruzzi and Loheide (2021) agree that groundwater–forest interaction is largely unexplored in humid climates, perhaps because of the perception that water availability is not a limiting factor in these environments. A relative lack of research means we have a limited understanding of the hydrological and ecological function of humid coastal GDEs despite their ecological and socio-economic importance. This knowledge is critical, particularly

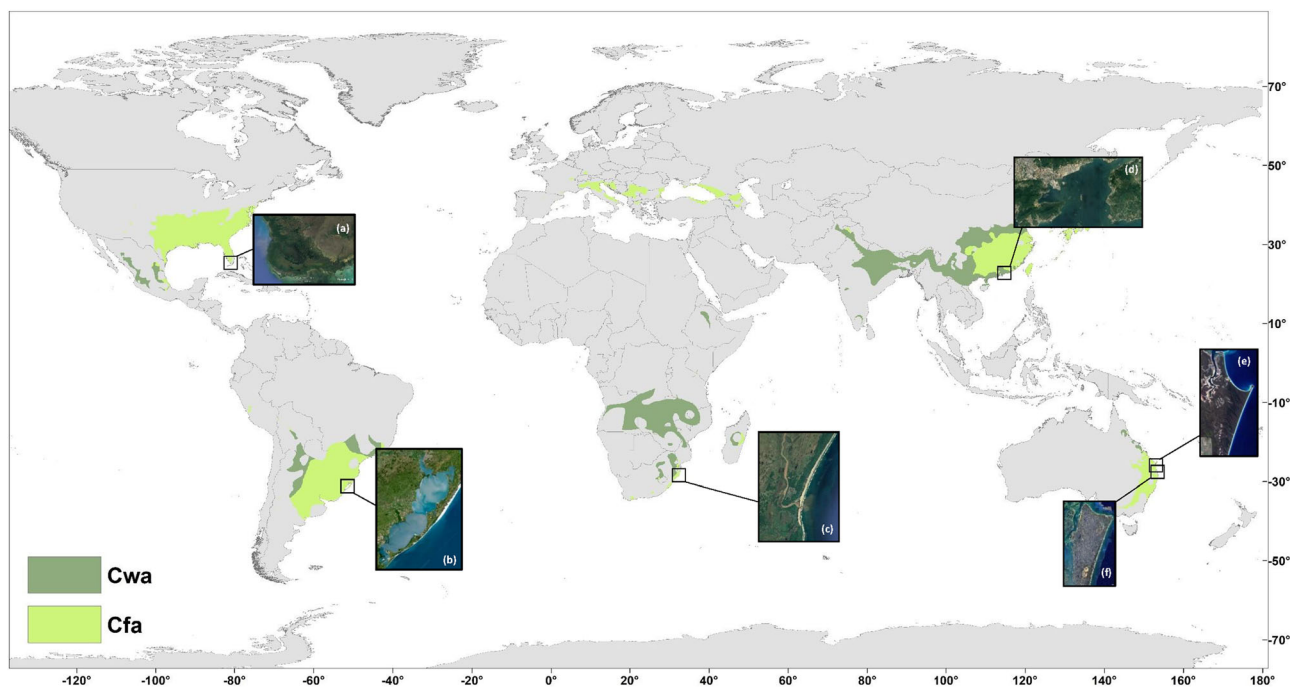


FIGURE 2 Global distribution of humid subtropical climate types and example coastal GDEs. Climate distribution based on Köppen climate classification (Peel et al., 2007). Two subtropical climate types are depicted—Cwa (humid subtropical climate) and Cfa (warm temperature climates). Satellite imagery of example GDEs associated with unconsolidated coastal sediments includes (a) Florida Everglades, USA where groundwater discharge provides an additional source of phosphorus for oligotrophic wetlands (Price et al., 2006). (b) Patos Lagoon, Brazil where seasonal groundwater discharge influences coastal lagoon hydrochemistry (Niencheski et al., 2007). (c) St Lucia Estuary, South Africa where groundwater discharge maintains stream flow during times of drought (Taylor et al., 2005). (d) Daya Bay, China where groundwater discharge influences water quality (viz., heavy metals concentrations) in mangrove swamps (Xiao et al., 2019). (e) Cooloolo Sand mass, Australia where deep regional groundwater discharges into surface waters, regulating stream flow (McDougall et al., 2017). (f) Brown Lake on Minjerribah, Australia where perched groundwater seasonally discharges into a shallow dune lake (Mazzone et al., 2020).

along heavily populated coastlines where development and abstraction will exacerbate climate change impacts (Erostate et al., 2020; Kløve et al., 2014).

Unlike humid GDEs, arid GDEs are considered important vestiges of evolutionary understanding often being labelled climate refugia (Cartwright et al., 2020; Davis et al., 2020). For instance, in arid parts of central Australia, groundwater-dependent spring ecosystems fed by large artesian aquifers are routinely studied for their unique taxonomy and evolutionary insights (Fensham et al., 2021). The effective decoupling of arid GDEs from rainfall suggests that long-term stability is mediated by larger watersheds and larger aquifers with minimal heterogeneity (Figure 3). Arid GDEs respond to changes in climate over extended periods (decades and millennia), contingent on the response of more extensive, basal aquifers to changes in recharge and discharge (Davis et al., 2020). As a result, arid GDEs connected to larger groundwater systems are considered more resilient to climate variability.

Humid GDEs, however, are more likely to experience rapid changes in hydrology and ecology due to climate influences or abstraction (Figure 3). The heterogeneous nature of unconsolidated coastal sediments exacerbates the vulnerability of subtropical GDEs to climate change. GDEs in the humid subtropics commonly rely on groundwater held in aquifers bound by impermeable or low-

permeability material, such as indurated sand, palaeosol horizons or peat (Richardson et al., 2011). These low-permeability layers are unique features of humid coastal landscapes formed by intermittent or near-permanent water-logging in areas of low relief (Tibby et al., 2017). Due to these layers, shallow unconfined aquifers are tightly coupled with climate and are highly exposed to rapid climate-induced hydrological change (Rama et al., 2018).

Though coastal groundwater systems generally contain small heterogeneous aquifers, rivers, lakes and wetlands in humid regions can receive groundwater input from more stable, regional groundwater sources (McDougall et al., 2017). Similarly, arid GDEs may utilise shallow, seasonal groundwater when available (Zencich et al., 2002). However, flow paths that influence hydraulic connectivity to regional groundwater sources can be spatially discontinuous and temporally dynamic in humid climates. For many GDEs in the humid subtropics, the groundwater system that they relies on is small, shallow and highly exposed to degradation.

There remain significant gaps in our understanding of humid groundwater systems and reliant ecosystems relative to arid regions where much of the extant literature is focused. These gaps centre on (1) the complexity of assessing climate change impacts on the hydrogeology and ecology of GDEs that rely on dynamic (sometimes

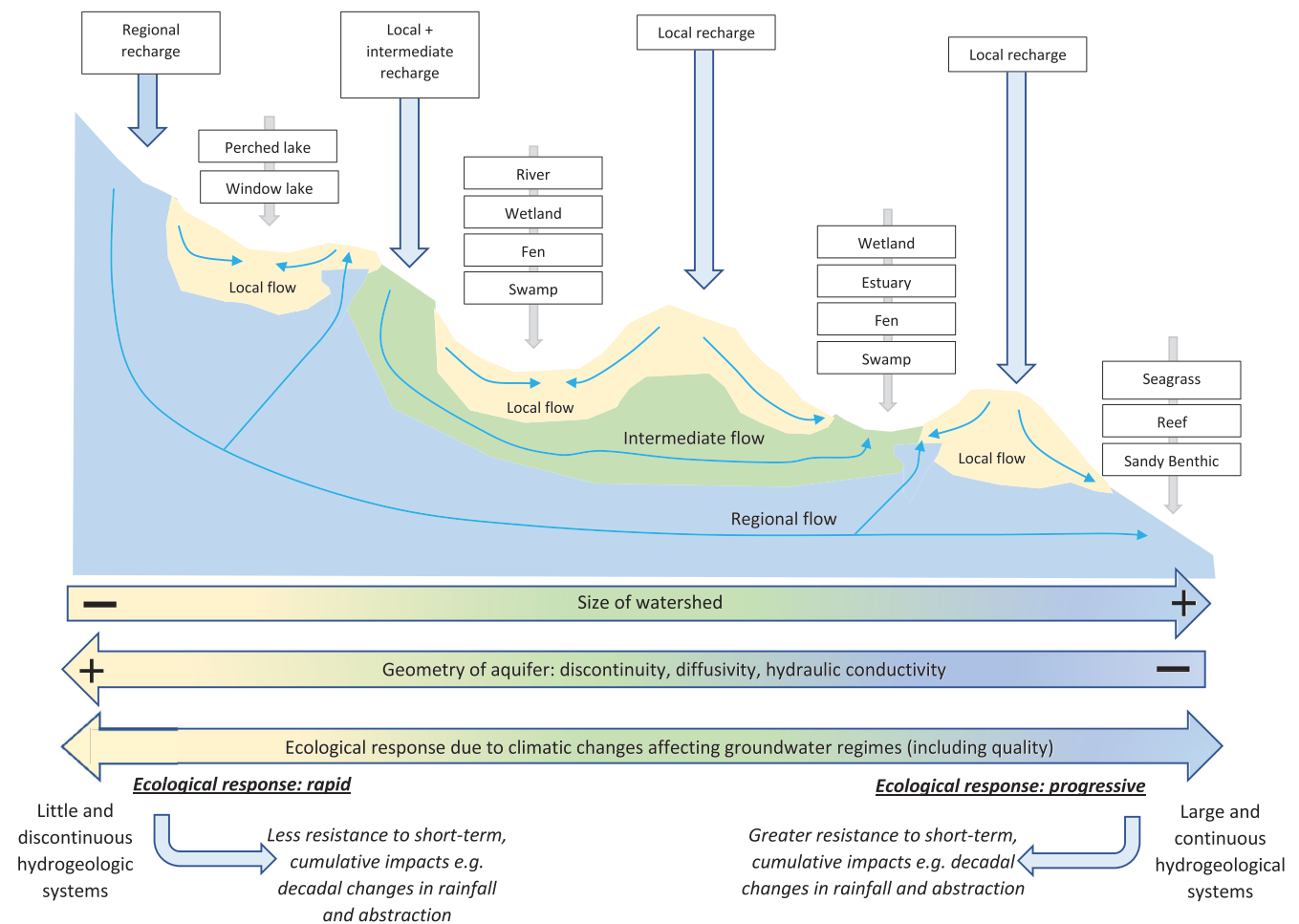


FIGURE 3 A conceptual diagram of the linkages between watershed characteristics, aquifer geometry and the sensitivity of associated ecosystems to changes in hydrology. This concept was theorised for groundwater systems by Tóth (1963), with subsequent iterations by Kløve et al. (2014) and Bertrand et al. (2011) to include ecohydrological implications of climate change for GDEs. Where ecosystems rely on aquifers recharged by smaller watersheds, with greater variation in discontinuity, diffusivity and hydraulic conductivity, changes in hydrology and ecology are likely to be rapid. Conversely, larger watersheds with greater homogeneity in aquifer geometry (and consequently lower variation in water-level changes and nutrient and heat fluxes) are likely to experience progressive changes in hydrology and ecology.

multiple) groundwater sources differently throughout space and time, (2) predicting the timeframe between hydrological change and unidirectional ecological change and, (3) improving the ability to mitigate impacts before irreversible ecosystem degradation is reached.

3 | BIOGEOCHEMICAL AND ECOLOGICAL PROCESSES SUPPORTED BY GROUNDWATER IN HUMID, COASTAL ENVIRONMENTS

Ecosystem services provided by GDEs are well documented (Griebler & Avramov, 2015; Kløve et al., 2011; Murray et al., 2006). However, the underlying biogeochemical processes governed by groundwater and their influence on ecosystem function are poorly described in coastal environments. This section aims to briefly summarise key biogeochemical processes maintained by groundwater in

coastal settings that contribute to ecosystem function and resilience (Table 1). We recognise that this is not an exhaustive list, but have aimed to provide key examples to highlight the ecohydrological role of groundwater in subtropical coastal landscapes. Armed with an understanding of the ecological processes supported by groundwater, we can then assess how climate change drivers are likely to affect GDEs.

The movement of groundwater through coastal landscapes contributes to the functional coupling of habitats, food webs and biogeochemical processes (Singer et al., 2014). Connectivity is facilitated by baseflow-fed rivers, subterranean estuaries and hydraulic connectivity between aquifers. Across coastal catchments, groundwater connects inland watersheds with near-shore marine environments (Wada et al., 2020). Even in instances where GDEs are not hydraulically connected, groundwater supports connectivity by contributing to the function of discrete habitats across the landscape (Sanchez-Higuero et al., 2020).

TABLE 1 Biogeochemical and physical processes maintained by groundwater in coastal environments and influence on the function of coastal ecosystems.

Habitat	Biogeochemical and physical processes maintained by groundwater	Influence on communities and ecosystem functions
River and riparian	<ul style="list-style-type: none"> Vertical and lateral groundwater gradient influences hyporheic zone (ecotone between surface stream and groundwater where exchange of water, nutrients and organic matter) (Hancock et al., 2005). Groundwater discharge provides perennial source of water (McGregor et al., 2018). Cooler groundwater discharge influences temperature of receiving aquatic habitats (Menberg et al., 2014). Groundwater discharge delivers additional nutrients and solutes to rivers (Murray et al., 2003). Facilitates movement of nutrients and solutes throughout the landscape. 	<ul style="list-style-type: none"> Groundwater table and soil moisture gradient regulates riparian ecotone, contributing to habitat creation and maintenance (Lawson et al., 2015). Groundwater discharge (baseflow) provides low-flow regulation, allowing key processes to occur at times of reduced rainfall and surface water flow. Depth to groundwater influences riparian plant community structure and function (Zeng et al., 2020; Zolfaghar et al., 2014). Influences species distribution and diversity throughout the landscape.
Wetland, heathlands and fens	<ul style="list-style-type: none"> Presence of groundwater table maintains water quality in fens and wetlands (Williams et al., 2020). Saturated groundwater table maintains anoxic environments, allowing build-up of organic material. Groundwater discharge influences temperature of receiving aquatic habitats (Menberg et al., 2014). Groundwater discharge delivers additional nutrients and solutes to wetlands and fens (Sanchez-Higuereado et al., 2020). 	<ul style="list-style-type: none"> Groundwater input can stabilise water levels and maintain anaerobic environment allowing the build-up of organic material (Drexler et al., 2013). Build-up of organic material contributes to soil development, increasing the moisture holding capacity and nutrient levels of otherwise oligotrophic, porous material soils (Tibby et al., 2017). Shallow groundwater can drive physiological adaptation in mesic plant communities (Fan et al., 2017). Groundwater chemistry affects distribution of microbial and macroinvertebrates communities, influencing food web dynamics, water purification and primary productivity (Griebler & Avramov, 2015).
Terrestrial phreatophytic vegetation	<ul style="list-style-type: none"> Groundwater table provides alternative source of water when rainfall decreases (Zencich et al., 2002). Shallow groundwater table maintains soil moisture gradient within the vadose zone (Rodriguez-Iturbe et al., 2007). 	<ul style="list-style-type: none"> Shallow groundwater creates and maintains hydrological niches by partitioning space along fine-scale soil-moisture gradients (García-Baquero et al., 2016). Water table depth is a determinant of phreatophytic vegetation structure, composition and patterning. Increasing depth to groundwater has been shown to significantly limit plant community structure (Adams et al., 2015; Zeng et al., 2020; Zolfaghar et al., 2014). Access to shallow groundwater increases growth of woody vegetation, increasing productivity of vegetated ecosystems (Ciruzzi & Loheide, 2021).
Groundwater window lake	<ul style="list-style-type: none"> Stabilises water levels, despite variability in rainfall and evaporative demand (Smerdon et al., 2007). Cooler groundwater discharge influences temperature of receiving aquatic habitats (Menberg et al., 2014). Groundwater discharge delivers additional nutrients and solutes to oligotrophic lake environments (Kidmose et al., 2015). 	<ul style="list-style-type: none"> Supports lakes as refugia during periods of drying (short and long-term) (McLaughlin et al., 2017). Stratification of temperature, influencing nutrient cycling at varying depths (Lewandowski et al., 2015).
Perched lakes and swamps associated with sand dunes	<ul style="list-style-type: none"> Intermittent water-logging and fluctuation in shallow water table (Curreli et al., 2013). 	<ul style="list-style-type: none"> Influences successional dynamics and dune stabilisation over short and long-term periods (Curreli et al., 2013). Provides water source sandy unconsolidated substrate, increasing landscape connectivity. Development of plant communities adapted to specific set of hydrological conditions (Antunes et al., 2018). Contributes to the maintenance of unique habitat for a range of rare and endemic species adapted to these environments.
Estuarine (including mangrove forests and saltmarshes)	<ul style="list-style-type: none"> Groundwater provides less saline water source for transpiration (Krauss et al., 2014) Ameliorates highly saline conditions in surface soils due to tidal inundation and high evaporative demand (Lovelock et al., 2017). 	<ul style="list-style-type: none"> Increases productivity of vegetated coastal areas such as mangrove forests (Santini et al., 2014). Potentially increases diversity of mangrove forests (Lovelock et al., 2017).

TABLE 1 (Continued)

Habitat	Biogeochemical and physical processes maintained by groundwater	Influence on communities and ecosystem functions
	<ul style="list-style-type: none"> Groundwater discharge and movement of groundwater at coastal interface provides additional solutes and nutrients. Groundwater discharge maintains boundary between freshwater and saltwater (Acworth et al., 2020). 	<ul style="list-style-type: none"> Contributes to maintaining balance between mangrove encroachment and replacement of saltmarsh (Saintilan et al., 2019).
Marine (i.e. benthic, seagrass, rocky reefs, coral reefs)	<ul style="list-style-type: none"> Delivery of land-based nutrients and solutes into ocean (Luijendijk et al., 2020) Facilitates material flux into coastal ocean (typically considered oligotrophic environment). 	<ul style="list-style-type: none"> Modifies marine habitats via temperature and delivery of land-based nutrients and solutes, increasing habitat heterogeneity and potentially species diversity (Leitão et al., 2015). Influences food web dynamics (submarine groundwater discharge can contribute to increased macroalgae growth and fish biomass) (Basterretxea et al., 2010) Increases primary productivity of near-shore habitats by sustaining enhanced phytoplankton biomass (Babu et al., 2021).

Groundwater has been shown to be a significant nutrient and carbon source pathway for sensitive coastal ecosystems, such as wetlands, estuaries (Lagomasino et al., 2014) and nearshore marine habitats (Luijendijk et al., 2020). Similarly, shallow groundwater provides a source of freshwater in coastal environments where sandy soils characteristically have poor water storage capacity and nutrient availability (Ciruzzi & Loheide, 2021). Submarine discharge of fresh groundwater delivers land-based solutes into coastal oceans and has been linked to habitat modification, food web dynamics and primary productivity in highly valuable but vulnerable near-shore coral reefs (Lilkendey et al., 2019).

Shallow groundwater tables in coastal environments provide a water source for ecological communities but can also mediate access to other water sources, such as soil moisture or surface water (Rodriguez-Iturbe et al., 2007). For example, perched groundwater can support hydrological connectivity with surface water by contributing to base-flow (Rains et al., 2006). During times of reduced rainfall, groundwater discharge can maintain water levels in lakes and regulate flow regimes in rivers (Kurylyk et al., 2014).

Another critical role of groundwater in coastal settings is its ability to support habitat stability and heterogeneity (both at a habitat and landscape scale). For example, groundwater can alter habitat in-stream temperatures at discharge points within river and stream ecosystems, creating micro-habitats for species to colonise (Briggs et al., 2018). Thermoregulation of habitats via groundwater discharge creates habitat heterogeneity within rivers, streams and wetlands, and these sites can act as potential climate refugia in future.

Coastal groundwater has contributed to the development and maintenance of diverse and productive plant and animal communities in otherwise oligotrophic environments (Hesp, 1991). Vital metabolic functions are sustained by direct access to shallow groundwater tables. In wetland systems, plant species richness has been shown to peak where groundwater levels maintain favourable nutrient conditions (Audet et al., 2015). Similarly, reefs that receive submarine groundwater discharge (SGD) show higher levels of primary productivity due to the delivery of dissolved solutes (Pisternick et al., 2020).

In intertidal environments, groundwater increases the growth and productivity of mangrove forests (Hayes et al., 2018; Lovelock et al., 2017; Wei et al., 2013). Due to its role in controlling hydrology and productivity in coastal ecosystems, groundwater will play an important role in mitigating the impacts of global warming (Serrano et al., 2019).

4 | IMPACTS OF CLIMATIC DRYING ON SUBTROPICAL COASTAL GDES

A description of climate change impacts on coastal GDEs must include impacts to aquifers and connected ecosystems. However, climate change impacts on coastal aquifers and groundwater systems at large are well discussed (see Ferguson & Gleeson, 2012; Vandenbohede et al., 2008; Werner et al., 2011) owing to the importance of groundwater resources to coastal communities and industries and the threat of saltwater ingress (Werner et al., 2013) (Figure 4). Here, we focus on how ecosystem functions outlined in the previous section will be interrupted by a drying climate—a topic that has received less attention, particularly within the humid subtropics (Figure 4).

Climatic drying is likely to have multiple, complex impacts on subtropical coastal GDEs. To aid this discussion, we have delineated ecosystems into zones to examine climate vulnerability (Figure 5). Zones have been delineated based on proximity to the ocean within coastal catchments and the hydrogeological support mechanisms that support ecosystem function that are vulnerable to oceanic and atmospheric climate change-related effects.

4.1 | Impacts to near-shore, intertidal and marine GDEs

Saltmarsh, mangrove, sea grass and reef habitats can be reliant on terrestrial groundwater discharge and SGD for the delivery of solutes and nutrients and the maintenance of hydrological settings. Near-

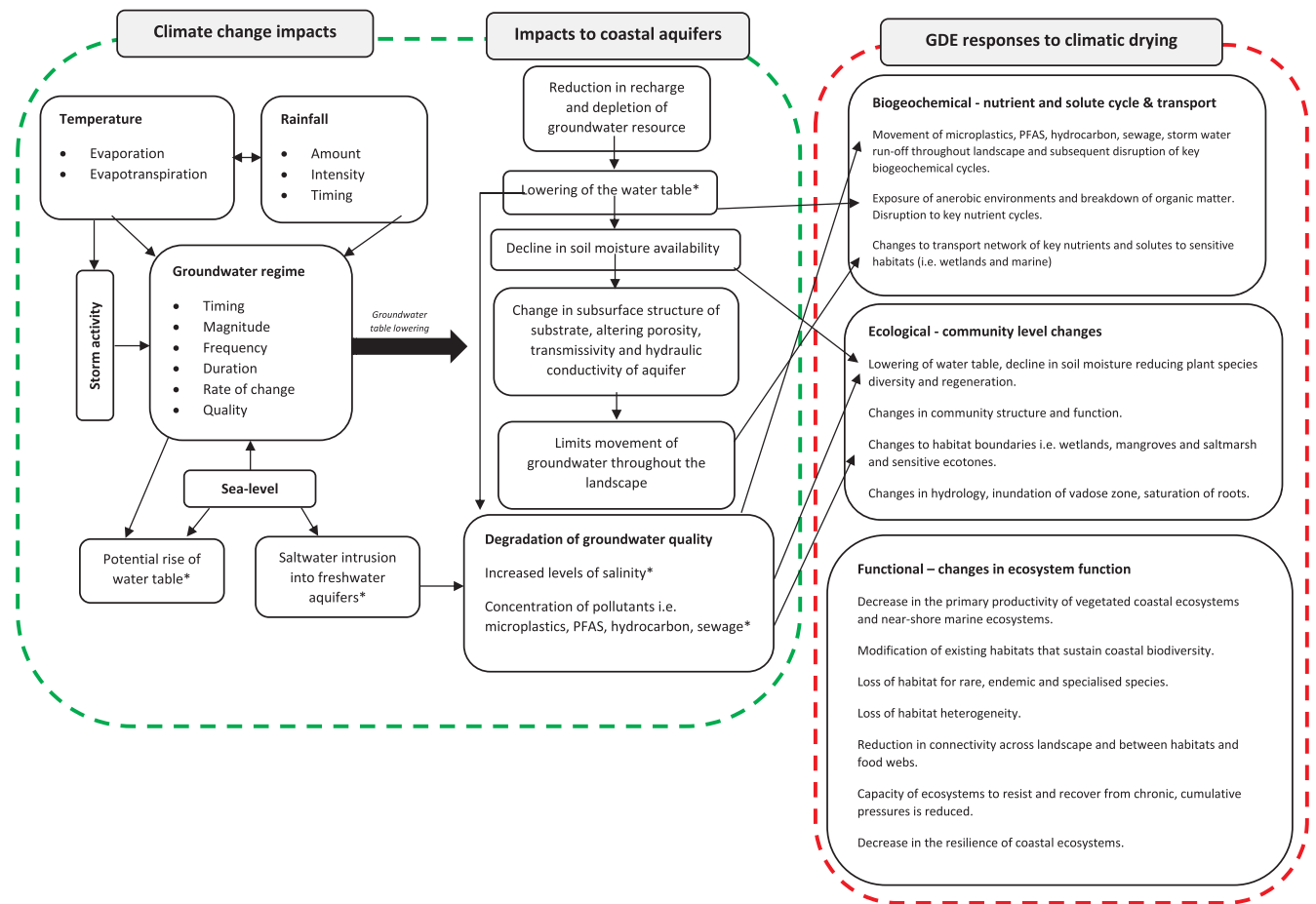


FIGURE 4 Climate change impacts on groundwater levels in coastal aquifers in humid regions, with a focus on GDE responses to climatic drying. Interactions framed by green outline are well-studied, but subsequent ecohydrological responses (red outline) require further research. Asterisks (*) indicate where anthropogenic activities are likely to compound climatic drying.

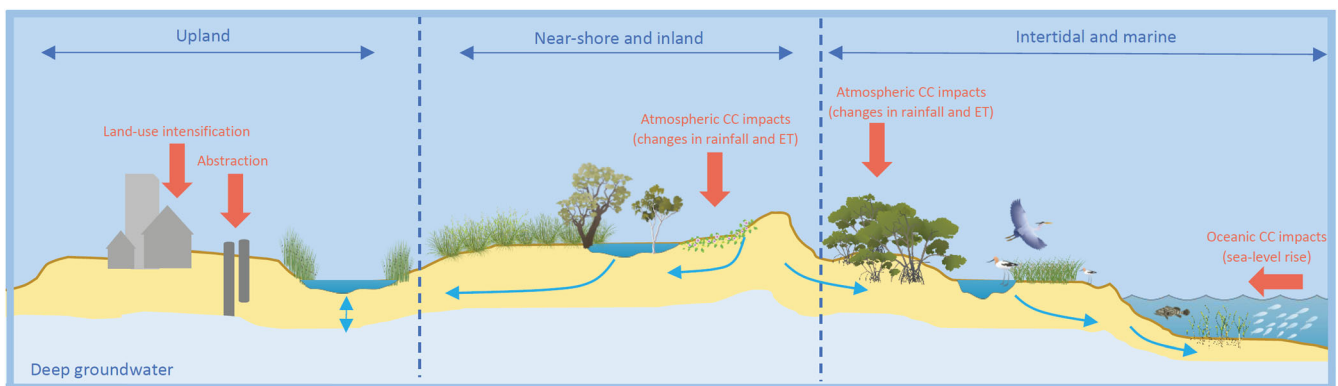


FIGURE 5 Representation of a coastal watershed and zones where GDEs occur. Zoning is based on landscape position and groundwater connectivity. The vulnerability of GDEs within each zone to climate change is described in Section 4. Red arrows indicate major threats (CC = Climate change, ET = Evapotranspiration). Blue arrows indicate groundwater movement. Examples of intertidal and marine GDEs include mangroves, estuarine environments, saltmarsh, seagrass, coral and rocky reefs. Groundwater input can be discharge from deep regional groundwater and shallow adjacent unconfined groundwater sources. Discharge volume and quality are dependent on seasonality, sea-level and tidal inundation. Examples of near-shore and inland coastal GDEs include wetlands, fens, swamps and lakes. Groundwater inputs via discharge from deep regional groundwater and shallow adjacent unconfined groundwater sources or interaction with groundwater table (i.e., groundwater window lake). Upland GDEs include freshwater wetlands, rivers, lakes and creek systems where groundwater is discharged from unconfined aquifers or deep regional groundwater sources.

shore, intertidal and marine GDEs are exposed to oceanic and atmospheric climate change drivers that affect groundwater discharge volume and quality. In this zone, GDEs are vulnerable to subtle changes in hydrology and water chemistry, affecting geochemical cycling and the timing of magnitude of groundwater fluctuations.

Numerous studies have modelled the effect of sea-level rise on coastal groundwater systems (Rotzoll & Fletcher, 2012), yet ecohydrological implications remain elusive. Sea-level rise is predicted to prolong tidal inundation and alter hydro-periods of intertidal environments, affecting soil properties, oxygen availability and species co-occurrence. Where sea-level rise leads to groundwater inundation, coastal habitats are likely to experience substantial changes in root-zone saturation leading to widespread successional changes in species composition and alteration of critical habitat features (Masterson et al., 2014).

Mangrove forests are a good example of the vulnerability of intertidal GDEs to sea-level rise as they are at the frontline of the freshwater-saltwater interface and are principally controlled by surrounding hydrology. Ecologists have studied soil accretion in mangrove forests as a means of combatting sea-level rise by sustaining elevation within tidal ranges. Plants, such as mangroves and wetland species, have been shown to enhance resilience in low-lying coastal habitats by improving mineral sediment trapping and retention (Cahoon et al., 2020). Because groundwater can increase above-ground growth in mangrove forests in the humid tropics (Hayes et al., 2018), it is likely to play an essential role in supporting vertical accretion and coastal resilience to sea-level rise.

While acknowledging saltwater intrusion is a slow phenomenon in most cases, reduced aquifer volumes from climate induced-drought and over-abstraction will exacerbate the inland movement of the saltwater wedge, particularly in low-lying coastal areas (Werner et al., 2011). The ecohydrological impact of saltwater intrusion and climate-induced drought will differ significantly depending on aquifer properties and hydraulic gradient (Lagomasino et al., 2014). Acworth et al. (2020) demonstrated that the net movement of the saltwater wedge in a subtropical coastal dune system is landward, only reversing during periods of heavy rainfall and associated freshwater discharge. The missing dilution effect of discharge coupled with tidal regimes and increased run-up of waves during storm events, potentially reversing the hydraulic gradient, may also force the saline wedge landward (Acworth et al., 2020). Coastal freshwater discharge is predicted to decrease as a result of a drying climate, having a consequential impact on the capacity of freshwater discharge to depress saline intrusion and mitigate the effects of sea-level rise (Huizer et al., 2018).

Fresh groundwater discharge into subtropical marine and intertidal habitats is important for ecosystem resilience to climate change. For instance, on the shoreline of the subtropical Lake St Lucia estuary in South Africa, Taylor et al. (2006) reported that salt intolerant species took refuge in groundwater discharge zones during times of drought. Simulations of groundwater discharge rates indicated that discharge persisted during drought for at least a decade, highlighting the importance of groundwater discharge in facilitating long-term refuge zones and supporting ecosystem resilience (Taylor et al., 2006).

Recent studies have suggested that reef-building foraminifera species can recover from de-calcification when exposed short periods (3 days to 1 month) of acidic conditions (Charrieau et al., 2022). While ocean acidification continues to affect calcifying species, fresh groundwater discharge may mitigate the effects of ocean acidification in some areas (Rheuban et al., 2019).

As a result of sea-level rise, saltwater intrusion into coastal aquifers will elevate salinity levels and alter the ecohydrology of ecotonal GDEs such as salt marshes. Salt marsh ecosystems are susceptible to changes in hydrochemistry over diurnal (tidal) and multi-decadal times scales (Tobias & Neubauer, 2019). The movement of saltwater into predominantly freshwater aquifers is predicted to reduce the accumulation of organic matter in shallow soil profiles by disrupting biochemical cycling. This will limit the ability of marshes to build soil volume and keep up with changing sea-levels (Neubauer, 2013). Global assessments have concluded that coastal wetlands and saltmarshes are likely to succumb to sea-level rise and associated saltwater intrusion without measures that ensure the capacity of ecosystems to accrete sediments (Vafeidis et al., 2008). Groundwater discharge into saltmarsh ecosystems could play a key role in facilitating resilience to sea-level rise by depressing saltwater intrusion, ensuring the longevity of these habitats.

In the humid subtropics, declining rainfall has the capacity to render groundwater flow paths dormant. This will limit the movement of freshwater and associated solutes into connected habitats such as wetlands and near-shore marine environments like seagrass meadows and reefs (Gilfedder et al., 2015). Without the delivery of solutes via groundwater discharge to coastal GDEs, fundamental ecological processes such as nutrient cycling and primary productivity will be disrupted. La Valle et al. (2021) demonstrated that SGD variability strongly influenced benthic algae community structure in reefs. The authors concluded that even subtle changes to the volume or quality of SGD altered primary productivity and food web dynamics in marine environments. Changes in the productivity of near-shore marine habitats due to reduced groundwater discharge or quality will have broad-reaching consequences for coastal fisheries (Lecher & Mackey, 2018). At a landscape scale, a breakdown in hydraulic conductivity due to drought will ultimately reduce the linkage between inland watersheds and coastal environments and eliminate key transport pathways.

4.2 | Impacts to inland coastal GDEs

Moving inland of the intertidal and subtidal zone, climate change impacts on inland GDEs in coastal regions will be driven by changes in rainfall and evapotranspiration. Indirect impacts from oceanic processes are likely to occur where saltwater intrusion moves into and beyond connected aquifers and surface water bodies. In this zone, inland habitats such as wetland, stream and riverine GDEs continuously or seasonally rely on groundwater discharge from unconfined and semi-confined aquifers. In many instances, groundwater sources are shallow and directly accessed by groundwater-dependent vegetation (phreatophytes). Phreatophytes represent important proxies for

discerning early changes in groundwater dynamics (Hultine et al., 2019). We therefore focus this section on impacts on phreato-phytic plant communities.

Variability in water availability has long been considered a key driver of community assembly and persistence. In mesic environments, species are locally adapted to a narrow range of ecohydrological conditions (Brotherton & Joyce, 2014). The modification of hydrogeological regimes will interrupt hydrologically controlled physiological, successional and functional dynamics in sensitive mesic habitats (Froend & Sommer, 2010). Dune slack vegetation assemblages, in particular, have shown a strong association with distinct groundwater regimes and community composition. Curreli et al. (2013) concluded that a predicted 100 cm reduction in a shallow groundwater table would substantially alter dune slack plant community assemblage. Changes to the structure and composition of groundwater-dependent plant communities could reduce the ability of coastal ecosystems to endure further disturbance, recover and adapt to new conditions.

Receding groundwater tables will impair vital metabolic processes that regulate growth, productivity and biomass in plant communities (Balestrini et al., 2021). For instance, where groundwater tables have steadily declined, long-term monitoring showed larger woody species replaced herbaceous vegetation with more uniform stand development and greater water requirements (Sommer & Froend, 2011; Specht et al., 2011). In a low-lying subtropical sand island, Fan et al. (2014) found that a highly transmissive aquifer allowed a large volume of groundwater to be used by water-intensive vegetation at levels above recharge by local rainfall. This subsequently altered the lateral subsurface flow of groundwater and reduced discharge to adjacent native wetlands. The encroachment of woody tree species in replacement of herbaceous species is likely to occur in subtropical regions as shallow groundwater tables recede (Stewart et al., 2020). Sustained declines in groundwater levels beyond the reach of deeper rooted species will induce stomatal closure and eventually vegetation dieback (Antunes et al., 2018; Hultine et al., 2019).

The rapid drawdown of shallow groundwater tables can result in progressive and unidirectional conversion to an alternative ecohydrological state, resulting in community re-structuring (Sommer et al., 2014; Sommer & Froend, 2011). Even small changes in water fluxes between groundwater and the saturated sediments of adjacent riverbeds can alter the dynamics of the hyporheic zone, impeding the recruitment and structure of sensitive riparian vegetation (Hancock et al., 2005; Krause et al., 2011). Decadal changes in rainfall patterns may provide some reprieve for ecosystems to respond, but for small coastal aquifers drying trends will be relatively extreme and compounded with development and saltwater intrusion may further reduce the adaptive capacity of ecosystems.

In humid climates, the development of low permeable layers is critical to groundwater storage and movement (Osland et al., 2016). However, lowering of groundwater tables will increase oxygen availability in coastal sediments, leading to the degradation of existing perched layers via oxidation of peat and the cessation of organic matter accumulation (Swindles et al., 2012). Changes to coastal aquifers' transmissivity, storativity and porosity will ultimately influence the

water balance of sensitive GDEs such as wetlands and fen systems. For example, Niswonger and Fogg (2008) found that the rate of perched groundwater discharge was proportional to the hydraulic conductivity of surrounding sediment. Similarly, the duration of discharge was closely linked to the hydraulic conductivity of the sedimentary unit. Continuous and seasonal groundwater discharge is vital to GDEs. Following a decline in groundwater discharge, Drexler et al. (2013) reported a 10% to 16% decrease in fen area over an 80 year monitoring period in Sierra Nevada. Land-use intensification and groundwater abstraction will act to further reduce groundwater recharge and discharge rates already affected by climate change drivers.

Climate change is predicted to affect dissolved organic carbon (DOC) content in shallow coastal groundwater as well as temperature-dependent reactions such as reduction-oxidation (redox) (McDonough et al., 2020). Furthermore, degradation of organic matter via changes in hydrology, pH and iron concentrations will alter the bioavailability of DOC in coastal groundwater systems (Meredith et al., 2020). Few studies have attempted to explain the ecohydrological implications of these changes in coastal GDEs. However, it is widely acknowledged that the bioavailability of DOC in groundwater has important implications for biogeochemical cycling and microbial abundances (Chapelle et al., 2012), particularly in shallow wetland environments (Nath et al., 2013). Therefore, changes in DOC content can alter water quality for GDEs while also affecting the carbon budget of connected coastal ecosystems (Daud et al., 2015).

4.3 | Impacts to upland GDEs within coastal catchments

Upland GDEs are an integral component of coastal watersheds that take many forms, including wetlands, rivers and lakes. Though substantively disconnected from the ocean, these ecosystems link terrestrial and marine realms, making them critical to the function of coastal watersheds and the integrated management of groundwater. Much like inland GDEs adjacent to oceans, upland GDEs rely on various groundwater sources, including unconfined groundwater and discharge from deep semi-confined aquifers. Many of the drying impacts discussed above also apply to ecosystems in this zone. However, more relevant to upland GDEs is declining water quality from land-use pressures. Coincidentally, a decline in groundwater volume due to drought will jeopardise the quality of groundwater stored in coastal aquifers by increasing the concentration of nutrients and pollutants with a missing 'dilution' effect provided by rapid recharge.

Global land-use change results in the conversion of vegetated land to agricultural, industrial and urban land uses, each influencing groundwater recharge within coastal catchments. When estimating the impact of land cover on groundwater recharge in a humid subtropical watershed of the Lower Mississippi River Alluvial Valley, Ouyang et al. (2019) demonstrated that forested land increased groundwater recharge compared to agricultural land. Rapid urbanisation across subtropical coastlines continues to threaten groundwater recharge.

Ghimire et al. (2021) revealed that groundwater recharge is expected to decrease in areas of India experiencing high and medium urbanisation rates. Furthermore, climate change predictions exacerbated declines in recharge due to increasing urbanisation. Preserving recharge mechanisms and capture zones is pivotal to mitigating climate change impacts on upland GDEs and downstream connected ecosystems.

Eutrophication in coastal aquifers will further undermine the quality of groundwater. The sources and contaminant pathways of nitrogen and phosphorous are well studied in aquifers downstream of agricultural land use (Wada et al., 2020). However, the mechanisms leading to nutrient enrichment in coastal aquifers that are not abstracted from, but are important water sources for ecosystems, remain understudied. What is apparent is that the movement of pollutants through groundwater systems will be affected by the flux of groundwater discharge and should be evaluated in the context of climate change-related reductions in groundwater recharge (Andersen et al., 2007). Disentangling the effect of reduced recharge and increasing groundwater demand on eutrophication is difficult without a detailed conceptual understanding of coastal groundwater systems.

Groundwater contamination continues to be a pervasive issue worldwide, particularly near centres of development (Gorelick & Zheng, 2015). Yet the rate and occurrence of groundwater contamination are likely underreported worldwide. Hartmann et al. (2021) calculated that the risk of groundwater contamination is substantially more than estimated where rapid recharge occurs across Europe, North Africa and the Middle East. Climate change and anthropogenic factors will work in unison to influence the concentration of pollutants in upland coastal aquifers and downstream connected GDEs.

5 | MANAGEMENT IMPLICATIONS

GDEs bolster primary productivity in coastal landscapes and provide habitat for an array of endemic and migratory fauna species (Erostate et al., 2020). In marine environments, coastal GDEs such as seagrass meadows, provide nursery habitat for important fisheries and habitat for endangered marine species. However, their co-occurrence with designated protected areas may exclude them from concerted ecohydrological studies as their land-based features, such as forests and surface waters, are assumed to be protected. Similarly, SGD may be overlooked in marine protected area management where land-sea connectivity is not adequately captured in conservation efforts. Therefore, the existing management of GDEs is not congruent with threatening processes and is instead framed by protecting hotspots of species richness or assessing potential impacts associated with in situ development (Orme et al., 2005).

This is problematic for the management of shared resources like groundwater, where impacts are accumulated off-site and management must be considered beyond the setting or aquifer unit in question (Aldous & Bach, 2014). Groundwater management principles, even those that are deemed sustainable, often aim to mitigate impacts

to these ecosystems via abstraction limits without considering the compounding effect of climate change on the timing and availability of groundwater and the ecohydrological processes it supports (Adams et al., 2015; Rohde et al., 2019; Vandenbohede et al., 2008). This leaves room for the inadequate management of coastal groundwater under a progressively drying climate and ineffective future allocations of groundwater for the environment.

Poor planning in GDE management is exemplified in coastal groundwater systems where much attention has been given to the domestic and industrial allocation of groundwater and little consideration has been given to environmental demand (Noorduijn et al., 2018; Thomann et al., 2020). Compounding this problem is the lack of evidence demonstrating the successful restoration and rehabilitation of groundwater resources and associated ecosystems after disturbances (Boulton, 2020).

Water quality guidelines, trigger level management and flux-based management have also been suggested as tools to abate groundwater decline in coastal aquifers due to drought or over-extraction (Werner et al., 2011). While these management tools have proved useful in avoiding over-extraction, much of the research intent and monitoring infrastructure required is associated with groundwater withdrawal. Furthermore, ecological thresholds based on individual species may not effectively protect from drought-related decline in groundwater quality or quantity (Huggett, 2005). Thresholds will vary within and among species and habitats, making them ineffective for interdependent communities and ecosystems. Likewise, monitoring ecosystem health is meaningless without a consensus on the definition of health and how to measure it (Korbel & Hose, 2017).

6 | FUTURE DIRECTIONS

When hydrogeological knowledge is linked with ecological processes, powerful conceptual models are formed which can uncover the driving processes governing change in GDEs (Orellana et al., 2012). While a substantial volume of literature is focused on anticipating climate change impacts on coastal groundwater systems, subsequent implications to connected ecosystems remain ambiguous. Future research directions should aim to reduce this ambiguity by quantifying biophysical linkages between coastal aquifers and ecological communities.

To preserve the ability of coastal ecosystems to function in the long-term under climate variability, resource managers must identify mechanisms that conserve the capacity of these systems to respond to disturbance. For many coastal wetlands, estuaries, rivers and near-shore marine habitats, groundwater may be key to maintaining the capacity of ecosystems to respond to and recover from disturbance. Similarly, coastal GDEs reliant on base-flow uninterrupted by drought may represent important vestiges of biodiversity under increasing aridity. Protecting the hydrogeological function of coastal GDEs can simultaneously improve environmental outcomes and enhance climate resilience across the broader landscape (della Bosca & Gillespie, 2019; Orellana et al., 2012).

There remains a lack of whole-of-system understanding for GDEs across coastal catchments, limiting the ability to implement hydrosystem-based management that considers landscape connectivity (Erostate et al., 2022). Connectivity principals have proved effective in the past. For example, Wada et al. (2020) found that the preservation of upstream recharge capture zones had a net positive effect on downstream coastal GDEs. To incorporate connectivity into GDE conservation, an in-depth conceptual understanding of the climate-water-ecosystem relationship is needed. For coastal GDEs, this involves the characterisation of groundwater resources, the hydrogeological mechanisms responsible for groundwater expression and the physical and biological processes groundwater sustains. Integrating abiotic and biotic indicators into assessments of groundwater regime modification will prove useful in defining resultant alterations to ecosystem processes (Korbel & Hose, 2017). To preserve ecosystem function, research must aim to uncover the minimum provisions for planning, managing and monitoring groundwater across coastal catchments (Saito et al., 2021).

Episodic rainfall events are an important contributor to groundwater recharge (Crosbie et al., 2011; Lapworth et al., 2012), particularly in coastal settings (Bryan et al., 2020). Numerous studies have demonstrated that the correlation between recharge and rainfall intensity is stronger than the correlation between recharge and annual rainfall volume (Barron et al., 2012; Jasechko et al., 2014). Though episodic recharge from intense rainfall can disproportionately contribute to groundwater recharge in the tropics (Jasechko & Taylor, 2015), there remains uncertainty between the interaction of inter-annual rainfall variation (magnitude and intensity) and recharge in subtropical coastal settings.

For some subtropical groundwater reservoirs, increasing rainfall intensity and magnitude may offset a reduction in rainfall frequency, avoiding groundwater depletion. Bates et al. (2008) suggested that despite heavy rainfall, recharge may be lost to run-off in humid environments (due to saturation of unconsolidated substrate), again highlighting the complexity of changing recharge conditions in subtropical regions. Numerous studies have considered how declining recharge will be exacerbated by increasing evapotranspiration rates, particularly in climates where humidity is predicted to increase (Guo et al., 2017). Studies are urgently needed to understand the dependency of episodic recharge on intense rainfall in subtropical coastal aquifers and how the trajectory of precipitation extremes in regions outside of the tropics will influence recharge and groundwater regimes.

Integration between the disciplines of hydrogeology and ecology will advance stewardship and policy development in GDE conservation (Gosselin et al., 2019). A greater understanding of the ecohydrological function of coastal GDEs provides a greater capacity to identify early warning signs of change, develop effective thresholds and designate allocations of water for the environment. These are global management priorities for GDEs faced with climate change (Rohde et al., 2017) and are particularly urgent for sensitive coastal ecosystems exposed to human development.

7 | SUMMARY

This review summarised the physiochemical, biological and hydrological processes governed by groundwater quality and quantity which support ecosystem function across coastal catchments. Groundwater plays a fundamental role in maintaining key processes that transform and translocate energy and materials across coastal catchments. As groundwater has the ability to bolster the capacity of ecological communities to resist and recover from disturbance, particularly under climate change, it is an essential contributor to ecosystem resilience. To adequately adapt to climate change, we must now seriously consider how changes to groundwater availability and quality will impact the function of coastal biomes and the critical ecosystem services they provide.

Atmospheric and oceanic climate change drivers will affect subtropical coastal GDEs differently, depending on the hydrological mechanisms that support ecosystem function and proximity to the ocean. As highlighted, climate change impacts on coastal GDEs are complex due to numerous feedbacks within the atmosphere-hydrosphere-biosphere nexus (Amanambu et al., 2020). The severity and magnitude of drought impacts on coastal GDEs in humid subtropical regions will remain speculative without focused studies. Local studies can provide critical information to protect ecological flows of groundwater and thus the multitude of regulatory and provisioning services GDEs offer to society and the environment (Esteban & Dinar, 2016). Future research should refine our understanding of the ecohydrological role of groundwater in coastal settings and the implications of climate change in the humid subtropics.

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M.D. led the development and design of the manuscript under the guidance of H. H, D. S, P. M. and R.F. All authors read and approved the final manuscript.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analysed in this study.

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