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REVIEW ARTICLE

Nutrientscape ecology: a whole-system framework to support the understanding and management of coastal nutrient connectivity

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Abstract
Context Nutrient connectivity across landscapes and seascapes plays a fundamental role in shaping the structure and function of coastal ecosystems. A whole-system understanding of the spatial–temporal dynamics and ecological significance of nutrient connectivity is essential for developing more effective coastal management strategies.

Objectives The aim of this study is to summarize the recent state-of-science in coastal nutrient connectivity research and identify future research needs. We then propose an integrated and solution-oriented scientific framework to advance a landscape ecology approach to address the research needs.

Methods We conducted a systematic literature review of 77 studies on nutrient flows in tropical and subtropical coastal marine environments (coral reefs, mangroves, and seagrasses) that have been conducted over the past decade.

Results Few studies considered interlinkages between multiple coastal habitats. Most (73%) studies that examined ecological impacts of nutrient connectivity focused on anthropogenic terrestrial runoff and indicated negative ecological responses to nutrients. Few studies adopted landscape ecology concepts and methods. We identified 15 research needs for advancing coastal nutrient connectivity research. Urgent research needs include the impacts of climate change on nutrient connectivity, the interactions between multiple nutrient pathways across habitats, and the social-economic drivers and impacts of change. An integrated framework that we term nutrientscape ecology is presented as a way forward.

Conclusions The nutrientscape ecology framework emphasizes the spatially explicit study of pattern-process relationships across multiple scales and leverages concepts and methods from landscape ecology and systems thinking. We seek to inspire interdisciplinary research collaborations and the development

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of a predictive science of nutrient connectivity that informs coastal management.

Keywords Systematic literature review · Nitrogen · Phosphorus · Seascape · Landscape ecology · Social-ecological systems

Introduction

Nutrients are the critical building blocks of all living organisms (Vitousek and Howarth 1991; Fennel and Testa 2019). In both terrestrial and aquatic environments, the availability of key nutrients such as nitrogen and phosphorus is the most common limiting factor for primary productivity (Ryther and Dunstan 1971; Elser et al. 2007; Bristow et al. 2017). Indeed, nutrient availability can produce cascading effects in the food web from primary producers to higher trophic levels, thereby fundamentally shaping ecosystem structure and function (Vitousek and Howarth 1991; Peñuelas et al. 2020). Nutrient availability is often determined by nutrient connectivity, defined here as the nutrient flows that connect locations in space and time, forming spatial–temporal linkages between entities such as food webs, habitats, and ecosystems (Loreau et al. 2003; Galloway et al. 2004; Tuerena et al. 2022). Nutrient flows within and across ecosystems are highly complex as they operate and interact across multiple spatial and temporal scales (Shantz et al. 2015; Fong and Fong 2018; Graham et al. 2018; Wang et al. 2018b; Adam et al. 2020).

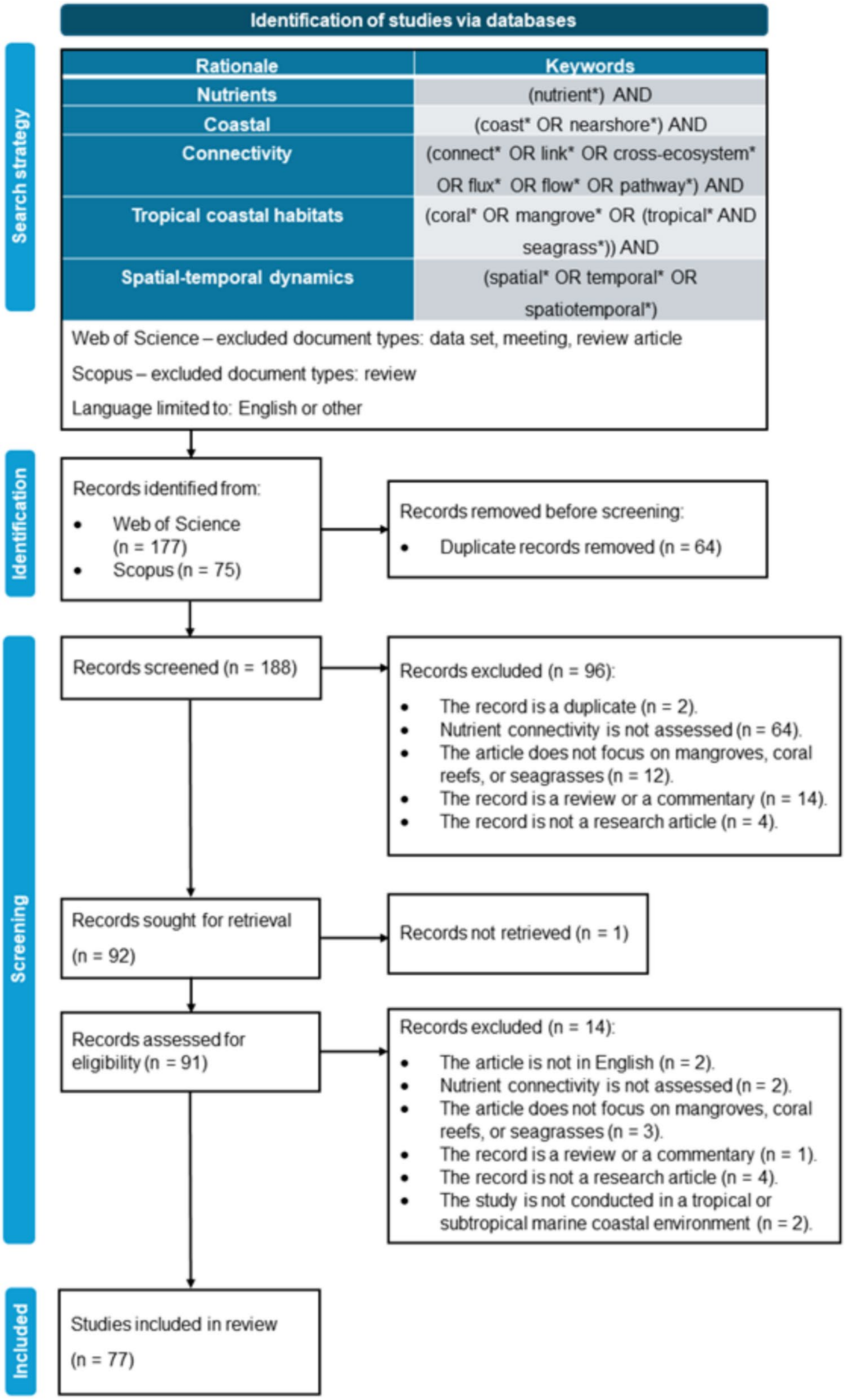
Human activities have significantly modified the flow of nutrients over millennia (Doughty et al. 2016; Peñuelas et al. 2020). Changes to nutrient connectivity across ecosystems include the disruption of animal-vectored nutrient pathways. For example, seabirds foraging at sea transport nutrients through guano to land where they roost and nest (Croll et al. 2005). These seabird-vectored nutrient subsidies can subsequently leach into adjacent coastal waters (Graham et al. 2018; Savage 2019; Benkwitt et al. 2021a). However, on many tropical islands, seabird populations have drastically declined due to the introduction of invasive rats by humans (Jones et al. 2008; Dias et al. 2019). As a result, the magnitude of seabird-vectored nutrient flows between land and sea has diminished (Benkwitt et al. 2021a). In addition to the disruption of animal-vectored nutrient pathways, new anthropogenic sources of nutrients have been created through, for example, the runoff of industrial fertilizers from agriculture, the release of wastewater, fossil fuel combustion, amplified fire regimes, and aquaculture (Seitzinger et al. 2010; Peñuelas et al. 2020; Wang et al. 2020; Tang et al. 2021). Furthermore, various human modifications of the landscape and seascape, such as the building of channels, impervious surfaces, and dredging, have altered the location and speed of nutrient flows (McCann et al. 2021). The human-induced changes in the location, timing, magnitude, and interactions of nutrient flows have had significant and cascading impacts on both terrestrial and aquatic ecosystems (Galloway et al. 2003; Borer et al. 2014). For example, in coral reef ecosystems, changes in nutrient connectivity have altered coral reef biogenic structure, community composition, and ecological functions (Fabricius 2005; Shantz et al. 2015; Benkwitt et al. 2019, 2021b).

Changes in nutrient connectivity may lead to irreversible changes in ecosystems (Steckbauer et al. 2011; Breitburg et al. 2018). For instance, increased anthropogenic nutrient loading to coastal waters has resulted in widespread eutrophication and higher rates of organic matter deposition to the seafloor (Maúre et al. 2021). In some cases, eutrophication has resulted in extreme deoxygenation and the formation of "dead zones", as documented, for example, in the northern Gulf of Mexico (Dodds 2006; Rabalais and Turner 2019). Once a certain threshold of deoxygenation is breached, the resulting biogeochemical feedbacks may lead to hysteresis, i.e., the inability of the ecosystem to recover even when the nutrient load to coastal waters is decreased (Steckbauer et al. 2011). These "dead zones" are becoming increasingly widespread in coastal ecosystems worldwide (Diaz and Rosenberg 2008; Rabalais and Turner 2019; Malone and Newton 2020). The magnitude and geographical extent of eutrophication and hypoxia in coastal waters globally suggest that humanity has already crossed the planetary boundary for biogeochemical flows, increasing the risk of broad-scale abrupt or irreversible environmental changes (Rockström et al. 2009; Bunsen et al. 2021; Richardson et al. 2024; Rose et al. 2024) and indicating an urgent need for improved management of nutrient connectivity worldwide (Nash et al. 2017). Altered nutrient connectivity is a key driver of marine ecosystem regime shifts globally, with impacts compounded by multiple interacting stressors, including global warming and overfishing (Levin and Möllmann 2015; Rocha et al. 2015).

Recent research has shown that effective management of nutrient connectivity and restoration of beneficial animal-vectored nutrient flows and feedbacks could strengthen the resilience of coastal ecosystems to other stressors, such as the increased frequency and magnitude of extreme weather events caused by climate change (Mcleod et al. 2019; Gove et al. 2023; Benkwitt et al. 2024). Due to the contrasting ecological impacts of nutrient flows from anthropogenic and non-anthropogenic sources, the management of coastal nutrient connectivity would ideally consist of mitigative and restorative actions. For example, a mitigative intervention could be the reduction of anthropogenic nutrient runoff from land to sea to decrease detrimental effects on coral reef physiology (Fabricius 2005; D'Angelo and Wiedenmann 2014). An example of a land-sea restorative intervention is the restoration of seabird populations and the associated beneficial seabird-vectored nutrient flows, which can enhance coral reef ecosystem functions and support the recovery of coral reefs from extreme heat waves (Benkwitt et al. 2021b, 2024).

It is increasingly recognized that developing improved management of nutrient connectivity and effective resilience-based management of coastal ecosystems requires a whole-system understanding of the context-specific effects of nutrient flows and their various sources and interactions across multiple spatial–temporal scales (Shantz and Burkepile 2014; Malagó and Bouraoui 2021; Vigouroux and Destouni 2022). However, traditional field-based surveys are typically characterized by data collection at a single spatial scale within a narrow temporal window, thereby only forming a collection of snapshots of the system's patterns and processes (Knee et al. 2016; Wang et al. 2018a). Furthermore, Sitters et al. (2015) suggested that research has largely focused on unidirectional flows of nutrients, with limited consideration of reciprocal nutrient flows between spatially connected ecosystems. Indeed, our understanding of nutrient connectivity, particularly its spatial–temporal patterns, ecological significance, and causative pathways linked to recent human activities, still presents important knowledge gaps (Sitters et al. 2015; Nash et al. 2017; Fong and Fong 2018). To better inform resilience-based environmental management and restoration strategies, integrated research approaches that seek to understand nutrient connectivity from a whole-system perspective are needed (Riechers et al. 2021). Although calls for a more integrated land-sea management are many, a concomitant shift is lacking in the scientific framework and the major funding programs to provide the integrated science at spatial and temporal scales that are required for whole-system decision-making (Beger et al. 2010; Álvarez-Romero et al. 2011).

In this study, we conducted a systematic literature review to understand the dominant approaches to the scientific study of coastal nutrient connectivity, evaluate key knowledge gaps, and systematically identify future research needs. We were especially interested in evaluating the application of landscape ecology concepts and methods to coastal nutrient connectivity. We focused the scope of this study on three major marine coastal habitat types in tropical and subtropical environments: coral reefs, seagrass meadows, and mangroves. These coastal habitat types support high biodiversity and provide essential ecosystem services, yet they are degrading rapidly due to multiple anthropogenic drivers of change (Duarte 2002; Barlow et al. 2018; Goldberg et al. 2020). We anticipate, however, that many of the general recommendations emerging from our literature review will also be applicable to temperate coastal ecosystems (Lønborg et al. 2021). We addressed the following research questions in our literature review: (1) Which nutrient pathways have received the most and the least research attention over the last ten years? (2) What are the dominant methods and spatial–temporal scales of data collection? (3) How prevalent is the use of integrative conceptual frameworks, such as landscape ecology or integrated land-sea approaches, in studying coastal nutrient connectivity? (4) How often do studies consider the ecological impacts of nutrient connectivity or the management implications of their results? Building on the results of the systematic literature review, we then identified 15 future research needs for nutrient connectivity research in tropical and subtropical coastal environments. Finally, to help advance a scientific framework to address these research needs, we propose an integrated, spatially explicit, and multiscale framework for nutrient connectivity studies that we refer to as nutrientscape ecology.



Rationale	Keywords
Nutrients	(nutrient*) AND
Coastal	(coast* OR nearshore*) AND
Connectivity	(connect* OR link* OR cross-ecosystem* OR flux* OR flow* OR pathway*) AND
Tropical coastal habitats	(coral* OR mangrove* OR (tropical* AND seagrass*)) AND
Spatial-temporal dynamics	(spatial* OR temporal* OR spatiotemporal*)

Web of Science – excluded document types: data set, meeting, review article

Scopus – excluded document types: review

Language limited to: English or other

◂**Fig. 1** The PRISMA 2020 flow diagram describing each stage of the literature search and screening process adapted from Page et al. (2021). The search strategy shows the rationale for the inclusion of keywords in the search string applied in this systematic literature review. The asterisk (*) at the end of the keyword broadens the search by representing any group of characters. This allows for capturing, for example, the plural forms of the keywords (http://www.prisma-statement.org/References)

Methods

Key concepts and definitions

We define the key concepts used in this study to establish conceptual clarity. By *nutrient connectivity*, we refer to the flows of nutrients in space and time that connect food webs, habitats, and ecosystems. A *connection type* defines which realms (i.e., land, air, sea, sediment) are connected by nutrients. A *nutrient pathway* is a specific type of connection process, such as atmospheric deposition or seabird-vectored nutrients. A *nutrient flow* is the physical movement of nutrients in space and time. The flow rate can be quantified with units such as m^3/s or µg/h. By definition, a nutrient flow occurs between a source system and a recipient system. A *nutrient source* is the location from which a nutrient flow originates. For example, a sewage outfall is an anthropogenic nutrient source. Nutrient connectivity between two entities, such as a seagrass meadow and a coral reef, can consist of multiple nutrient pathways and may be unidirectional or reciprocal (Sitters et al. 2015).

To understand the spatial–temporal dynamics of nutrient connectivity, it is essential to study spatial and temporal patterns (Risser 1990). Landscape ecology focuses on pattern-process relationships by quantifying spatial and temporal patterns at a range of scales and investigating their ecological consequences (Turner 1989; Wiens 2002). Although a relatively young science, landscape ecology has made important contributions to our understanding and management of the linkages between nutrient pathways and landscape patterns in river catchments (Likens and Bormann 1974; Hunsaker and Levine 1995; Erős and Lowe 2019; Torgersen et al. 2021). Here, we define key concepts applied in landscape ecology. A *spatial (temporal) pattern* refers to a structural feature of the landscape or seascape or a spatial (temporal) distribution (Turner 1989; Wedding et al. 2011). Landscape and seascape spatial patterns can be quantified using *spatial pattern metrics* that measure the *composition* or *configuration* of the structural features studied (Wedding et al. 2011; Pittman et al. 2021). Composition metrics quantify the type, number, and proportion of the landscape and seascape structural features. Configuration metrics quantify the spatial arrangement of patches and mosaics, such as the juxtaposition of different habitat patches, fractal dimension, patch isolation or contagion (Fahrig et al. 2011; Turner and Gardner 2015), and spatial gradients of structure, such as surface morphometry (Lausch et al. 2015; Kedron and Frazier 2019). Importantly, the observation and measurement of the pattern depends on *scale*, i.e., the spatial or temporal dimension of the study, determined by both *resolution* and *extent*. *Resolution* is the precision of measurement (or *grain*), while *extent* refers to the area and duration of the study (Wiens 1989; Turner and Gardner 2015). Finally, *context* describes the social-ecological surroundings of a focal area in space and time (Fahrig et al. 2011; Turner and Gardner 2015).

Systematic literature review

We conducted a systematic literature review of coastal nutrient connectivity studies in tropical and subtropical coastal environments over the past decade (01/01/2012–29/08/2022). We followed the guidelines of the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) extension in ecology and evolutionary biology (O'Dea et al. 2021). The literature search was conducted on the Web of Science and Scopus on 29/08/2022. All the databases available on these platforms were included in the search. The steps of the literature search and screening strategy are provided in the PRISMA 2020 flow diagram (Fig. 1).

The list of studies included in the review and the justifications for the exclusion of each article are provided in Appendix A (Tables A1, A2). The reporting items only relevant for quantitative meta-analyses were excluded (Appendix A, Table A3). A list of data items recorded from each study is provided in Appendix A, Table A4.

To address Research Question 3 "How prevalent is the use of integrative approaches, such as landscape ecology or integrated land-sea frameworks?", the keywords used were: "integrated land-sea", "ridge-to-reef", "summit-to-sea", and "catchment-to-sea", spelled with or without hyphens. Additionally, we searched the studies for "landscape" or "seascape" ecology and the associated key concepts (see section "Key concepts and definitions").

Limitations

Although we focus on recent studies, we recognize that a large body of literature has evolved since the pioneering studies on coastal nutrient connectivity in the mid-twentieth century (Hutchinson 1948; Odum 1953, 1968). Our interest in recent scientific practice meant that we designed the search strategy to capture only studies published in the last ten years that examined (1) nutrients, (2) connectivity, (3) tropical and subtropical coastal marine ecosystems, and (4) spatial–temporal dynamics. Studies that could be relevant for coastal nutrient connectivity were excluded if they failed to explicitly mention relevant search terms in the abstract, keywords, or title. For example, studies that mapped the distribution of sediments or organic matter in coastal environments were not retrieved if they did not refer to nutrients and connectivity in the framing of their study. This might partly explain the low number of remote sensing studies captured in this review. Similarly, we examined the prevalence of integrative approaches by searching for concepts that we considered to be well-established in the study of land-sea connections in tropical and subtropical environments, such as "integrated land-sea" (Álvarez-Romero et al. 2011) and "ridge-to-reef" (Carlson et al. 2019) (see section "Systematic literature review"). We acknowledge that this search may omit some studies that do not refer to this established terminology of land-sea studies. To partially address this limitation, we also quantified the number of studies that sampled both marine and terrestrial environments. It should also be noted that the literature review was limited to peer-reviewed journal articles in English, thereby excluding gray literature and articles published in other languages.

Results

Nutrient pathways and coastal habitat types

The majority of studies examined unidirectional nutrient pathways from land or oceanic sources to a single focal marine coastal habitat (Fig. 2). Seventy-eight percent of the reviewed studies focused on one of the three marine coastal habitat types (coral reefs, mangroves, and seagrasses), 15% included two habitat types, and 7% included three habitat types (Fig. 2A). Coral reefs were the most studied single habitat type (49%), followed by mangroves (29%) and seagrass meadows (1%).

Most studies (62%) focused on a single focal nutrient pathway (Fig. 2B). Land-sea runoff and submarine groundwater discharge received the most research attention (62 and 29%, respectively). A third of studies (33%) focused on anthropogenic nutrient sources, and 28% examined nutrient flows from non-anthropogenic sources. The remainder (39%) did not explicitly distinguish between anthropogenic and other sources of nutrients. Eighty-one percent of the studies that assessed nutrient flows from non-anthropogenic sources were focused on oceanic sources of nutrients, while the rest (19%) studied animal-derived nutrients.

Conceptual frameworks

Amongst studies focused on connections between land and sea, 12% referred to integrative approaches for coastal studies, such as the "ridge-to-reef" (Delevaux et al. 2018, 2019; Amato et al. 2020; Shuler and Comeros-Raynal 2020; Shuler et al. 2020) or the "integrated land-sea" frameworks (Rodgers et al. 2012; Comeros-Raynal et al. 2021; Sakamaki et al. 2022). Additionally, two studies referred to a "catchment-to-sea" approach (Quak et al. 2016; Comeros-Raynal et al. 2021).

One study explicitly employed the landscape ecology framework (Rodgers et al. 2012). Rodgers et al. (2012) quantified spatial patterns of coastal landcover and land use and modeled the relationship between a watershed health index and coral reef health. Additionally, some studies applied key concepts or metrics associated with landscape ecology (e.g. spatial pattern, context, and configuration—see section "Key concepts and definitions"), without explicitly situating their study in the wider landscape ecology conceptual framework and scientific literature. Seventy-six percent of studies considered spatial patterns, for example by discussing the spatial distribution or identifying a spatial gradient of nutrient concentrations. However, as many as 16 of these studies did not use

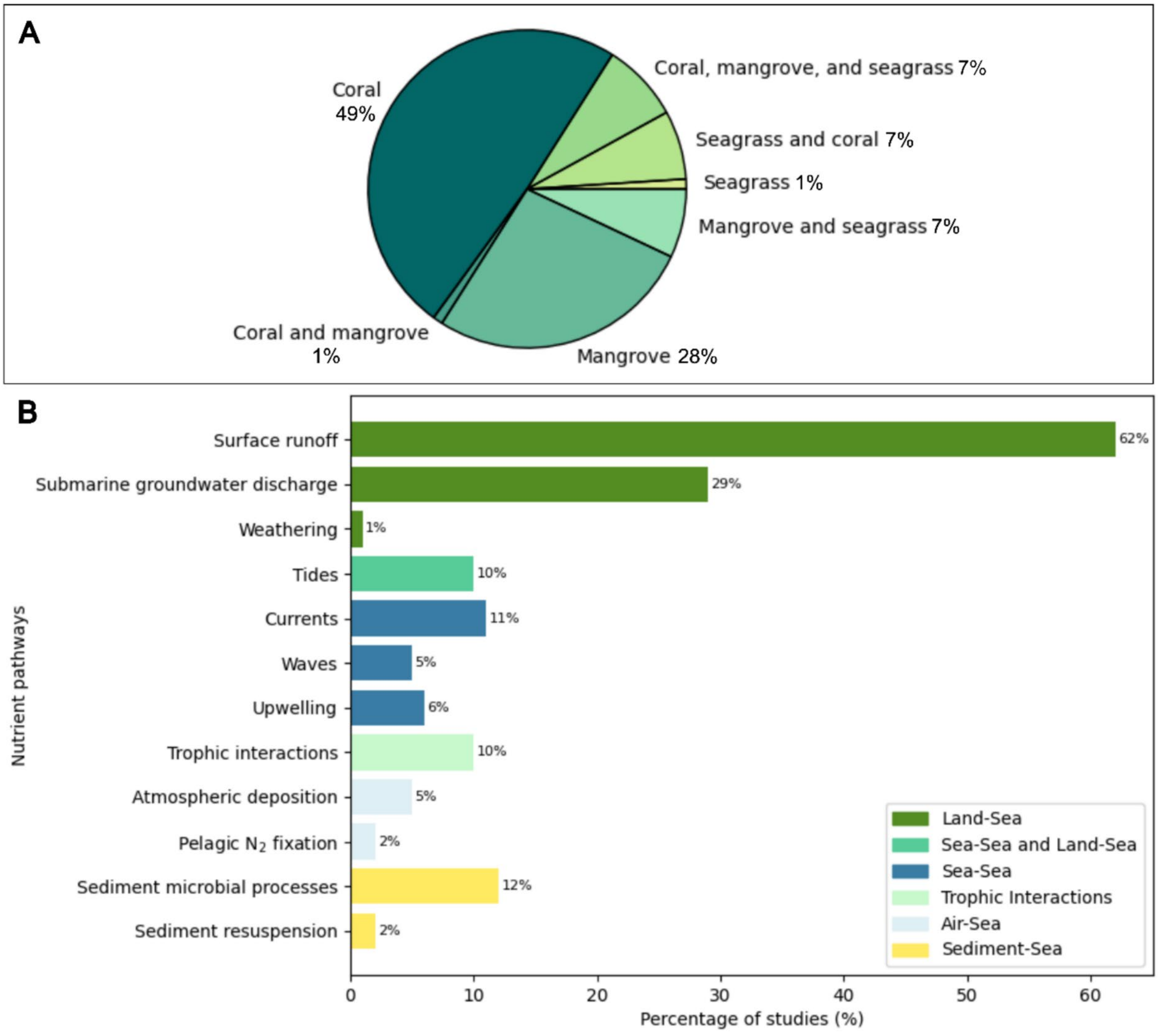


Fig. 2 The proportion of studies that focused on **A** one or more coastal habitat types (coral, mangrove, and seagrass) and **B** different nutrient pathways. As a single study could investigate multiple nutrient pathways, the sum of the percentages is more than 100%. Nutrient pathways of the same connection type are shown in the same color

the concept of "spatial pattern" explicitly, indicating a limited take up of landscape ecology ideas within the coastal nutrient connectivity literature. Several studies quantified spatial patterns using landscape ecology spatial metrics such as "bottom roughness" (Amador et al. 2020), "habitat complexity" (Delevaux et al. 2018), "percent benthic cover" (Li et al. 2015; Yoshioka et al. 2016; Comeros-Raynal et al. 2021), without referring to landscape ecology as a conceptual framework. A small number of studies implicitly discussed the importance of landscape and seascape context and configuration (e.g. Quak et al. 2016; Signa et al. 2017; Delevaux et al. 2018; Cantarero et al. 2019). One study used the concept "configuration" (Comeros-Raynal et al. 2021) and none used the concept "context" in the spatially explicit sense defined in landscape ecology.

Scale

Spatial and temporal scales were frequently inadequately quantified and reported. In many cases, spatial resolution and extent had to be approximated from maps. Half of all studies provided a rationale for choosing the spatial or temporal scale(s). Where a rationale was provided, almost half of such justifications concerned temporal scale. For example, a common justification for the choice of temporal scale was the importance of capturing tidal and seasonal variability or short-term rainfall events (e.g. Smith et al. 2016; Tait et al. 2017; Wadnerkar et al. 2019).

Amongst studies that collected spatial data (67 of 77), 41% provided information on spatial resolution. The most reported spatial resolutions were between 100 m and 1,000 m (12 studies) (Fig. 3). For studies that collected discrete samples at multiple sites over the study area, spatial resolution was defined based on the distance between sample sites. For example, the spatial resolution of a study with twenty equally spaced sample sites within a study area of 50 × 40 m (2 km^2) would be 10 m. Nine percent of the reviewed studies collected data at multiple spatial resolutions. In terms of spatial extent, the majority (64%) of studies were "local" (defined here as < 50 km^2), while 27% were "regional" (defined here as > 50–10,000 km^2). The remaining 9% of the reviewed studies covered study extents larger than 10,000 km^2.

Nineteen studies could not be assessed for their temporal resolution because they did not collect temporal data or because the authors did not report the resolution. Similarly, six studies could not be assessed for their temporal extent. Almost a third of the studies relied on a single field mission, while one-quarter of the studies conducted two to four field missions in a single year. Consequently, more than 50% of studies did not consider year-to-year variability in nutrient

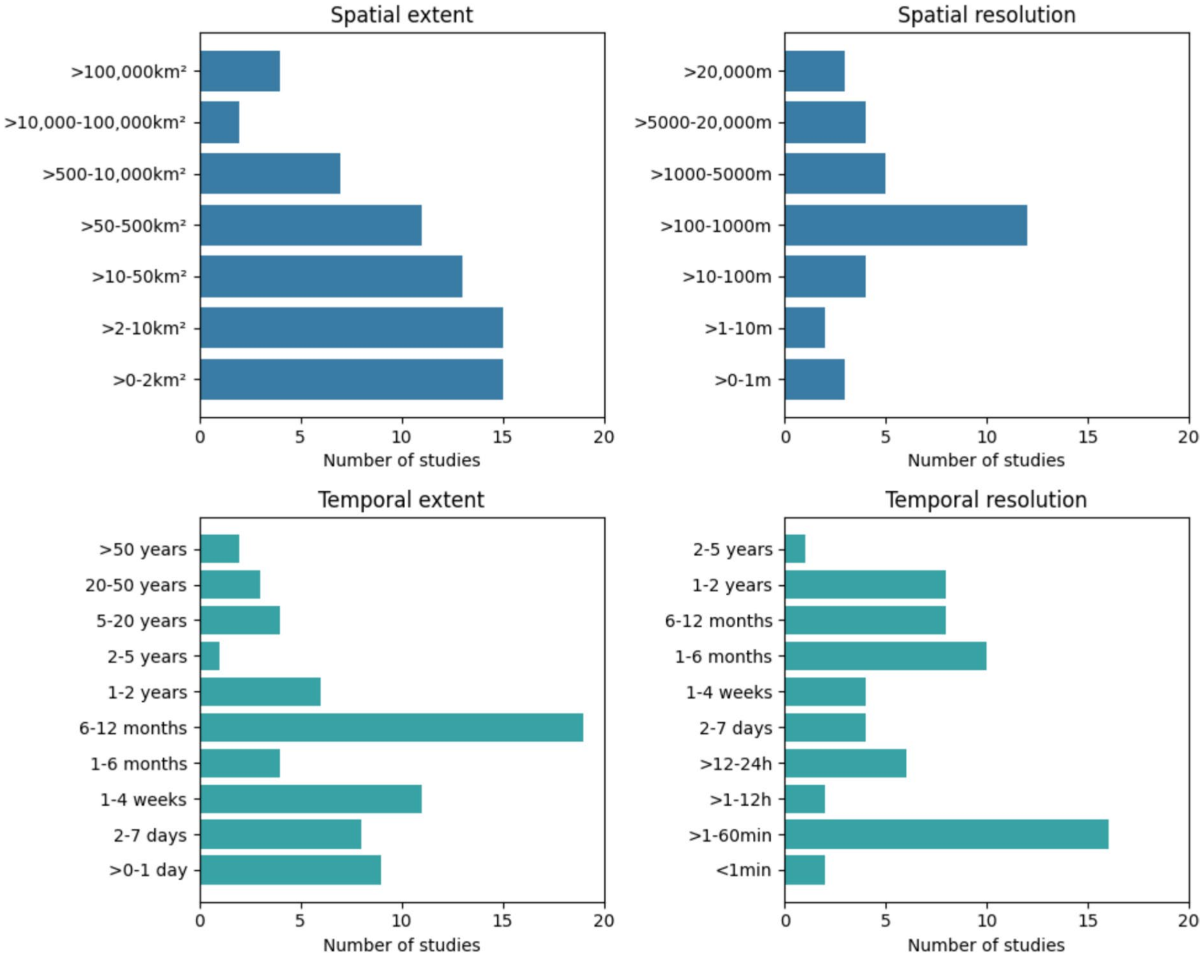


Fig. 3 The number of studies in the reviewed literature that collected data at the specified spatial/temporal extents and resolutions

flows, and almost one third did not capture seasonal variability. Twelve percent of studies collected data at multiple temporal scales.

A trade-off between spatial and temporal resolutions was apparent, as the studies that relied on only one sample site tended to justify this by the need to collect high-resolution temporal data (Gleeson et al. 2013; Kaiser et al. 2015; Starke et al. 2020; Reithmaier et al. 2021; Terada 2022). Similarly, there was a trade-off between resolution and extent. For example, studies with very high temporal resolutions (< 1 h) tended to have a limited temporal extent (1–7 days), and vice versa.

Methods

Most studies focused on mapping nutrient flows through in-situ sampling at point locations (Fig. 4). Not counting coastal groundwater, rainwater, and mangrove samples, only one study sampled both marine and terrestrial environments (Quak et al. 2016). Few studies used field experiments, social-economic data, local knowledge, remotely-sensed data, or machine learning (Fig. 4).

Stable isotope analysis was the most prevalent method for identifying the source of nutrients (anthropogenic vs non-anthropogenic). For example, several studies used the elevated ratio of the nitrogen isotope N15:N14 (δ15N) as an indicator of nutrient flows from wastewater discharge (Richardson et al. 2017; Amato et al. 2020; Fong et al. 2020; Sanchez et al. 2020), aquaculture (Li et al. 2015), and runoff from agricultural lands (Sakamaki et al. 2022). In addition to δ15N, some studies analyzed the carbon isotope δ13C to distinguish between terrestrial and oceanic nutrient sources (Perez et al. 2020; Sakamaki et al. 2022). Additionally, radon and radium isotopes were used to estimate submarine groundwater discharge (e.g. Gleeson et al. 2013; Smith et al. 2016; Richardson et al. 2017; Amato et al. 2020; Shuler et al. 2020). In addition to stable isotope analysis, spatial and/or temporal co-occurrence of likely nutrient sources and increased nutrient concentrations were commonly used as evidence of a causal connection. For example, Limates et al. (2016) mapped the spatial and temporal co-occurrence of poor water quality, mangroves, seagrass meadows, septic systems, storms, and tourist arrivals to determine the sources of coastal water pollution and nutrient loading in the Philippines.

Ecological impacts and management

Twenty-one percent of studies discussed the effects of climate change on nutrient connectivity. Most of these studies only briefly mentioned potential impacts, and none included “climate change” in their title. Twenty percent of studies assessed the ecological impacts of nutrient connectivity, including effects on coral trophic strategy and growth, coral-to-macroalgae regime shifts, phytoplankton production, and fish density (Table B1, Appendix B). Most (73%) of these studies assessed the ecological impacts of anthropogenic nutrient sources and terrestrial runoff. Fifty-one percent of studies briefly mentioned the potential implications of their results for management applications, and 7% included management as a research focus and provided specific recommendations for managers. The ecological impacts and guidance for management identified in the reviewed studies are provided in Appendix B (Tables B1 and B2).

Discussion

The importance of land-to-sea nutrient flows for nearshore marine ecosystems has long been recognized (Odum 1968; Fabricius 2005). A large body of research has provided insights into the dynamics of nutrient flows in different coastal environments, from tide-driven mangrove estuaries (Gleeson et al. 2013; Smith et al. 2016) to wave-driven coral reef environments (Huang et al. 2012; Adam et al. 2020). The causal links between watershed land use change, increased nutrient loading to coastal waters, and decreased water quality are well-established (Fabricius 2005; Oliver et al. 2011; Kagalou et al. 2012). Building on this previous work, this systematic literature review advances research on coastal nutrient connectivity by identifying 15 research needs that must be addressed to better integrate nutrient flows into coastal management strategies and spatial planning (Table 1). Following a brief discussion of the key findings of the literature review, we present a novel integrated approach for coastal nutrient connectivity studies that we call nutrientscape ecology, aimed at supporting future studies that address the identified research needs. We recognize that related science may have occurred before our decadal review period,

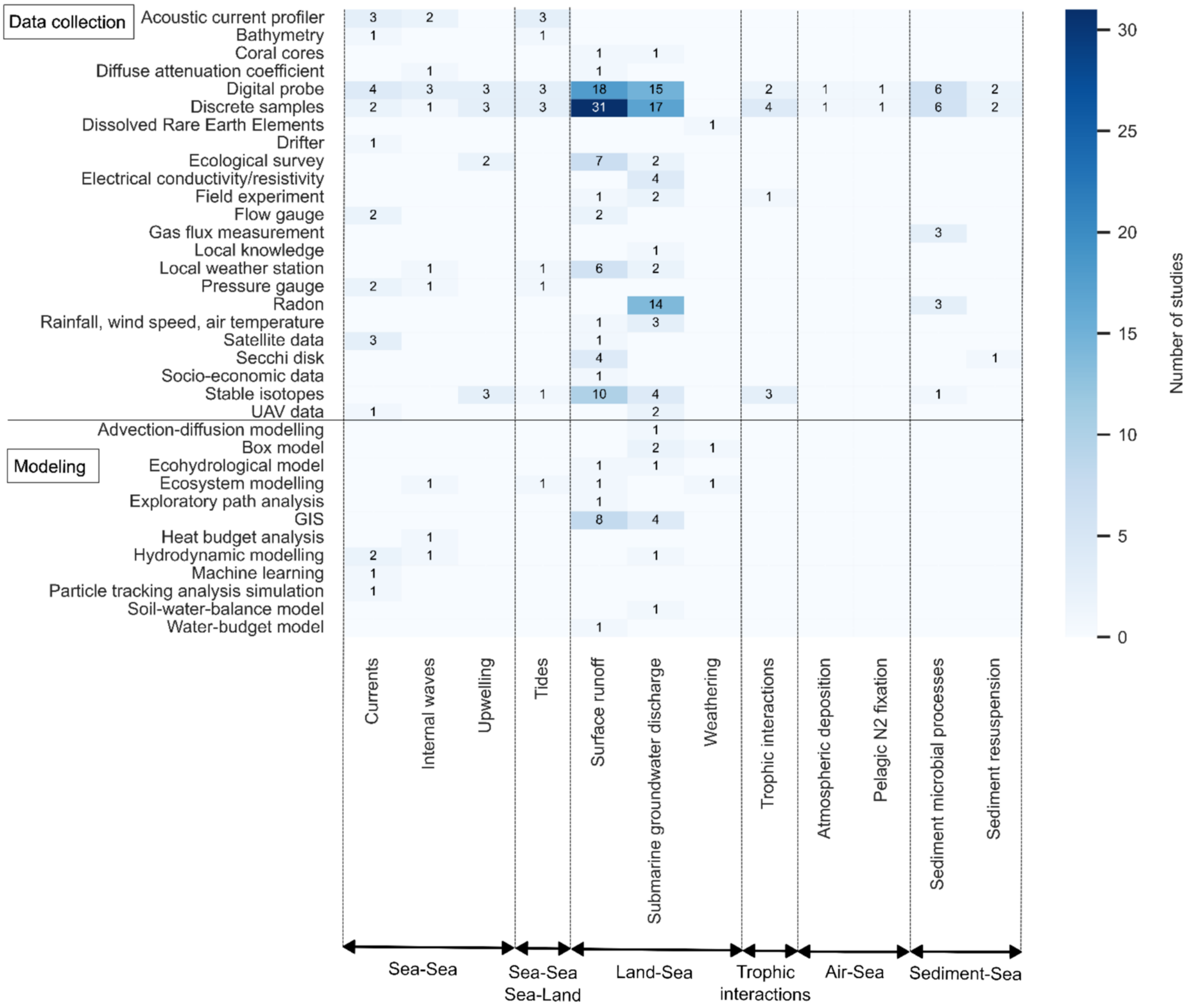


Fig. 4 Data collection and modeling methods applied to the study of different nutrient pathways in the reviewed literature. The value in each cell indicates how many studies applied a specific method (listed on the y-axis) to the study of a specific nutrient pathway (listed on the x-axis). The different nutrient pathways are grouped together according to their corresponding connection type. Animal-vectored nutrient pathways are included here as a separate category, as animals may connect different realms depending on the species in question

however, our focus was on the most recent state of practice in studying coastal nutrient connectivity.

The literature review revealed that many studies focused only on a single nutrient pathway. This tendency is likely due to the specialization of researchers in particular pathways and associated methods and the limited time and resources to carry out fieldwork. However, nutrient pathways do not occur in isolation. Instead, we propose that the coastal nutrientscape is formed through the interactions of multiple nutrient pathways that operate in complex ways over time across a geographical space (Leichter et al. 2012; Shantz et al. 2015; Graham et al. 2018; Adam et al. 2020). For example, Ziegler et al. (2019) showed that while tides can directly act as physical vectors of nutrients, tides can also interact with animal-mediated nutrient pathways through their impact on food web dynamics. Additionally, the relatively small number of cross-habitat nutrient studies in coastal ecosystems highlights a significant knowledge gap and also presents future opportunities to address our limited ecological understanding of interconnected coastal

Table 1 Future research needs in nutrient connectivity studies in tropical and subtropical coastal environments

Research needs	
Nutrient pathways and coastal habitat types	
1	Investigating the interactions between multiple nutrient pathways rather than focusing on a single pathway
2	Studying nutrient flows and their ecological impacts across terrestrial and marine environments and multiple coastal habitat types
3	Advancing the understanding of the different nutrient sources (anthropogenic and non-anthropogenic) contributing to the observed patterns of nutrient flows and hotspots
4	Studying the dynamics and ecological significance of animal-vectored nutrient pathways
Scale	
5	Developing an understanding of how the spatial–temporal patterns and ecological impacts of nutrient connectivity change across scales
6	Collecting long-term datasets to differentiate between long-term trends and short-term variability
Conceptual frameworks and methods	
7	Developing and applying a conceptual framework that supports whole-system research and cross-disciplinary study of coastal nutrient connectivity
8	Recognizing the importance of local knowledge and collaboration
9	Leveraging the potential of new technologies, such as networks of field-deployed instruments, remote sensing, and machine learning
10	Developing predictive science and quantifying spatial linkages between landscape and seascape patterns and nutrient flows
Human impacts and management	
11	Examining the cumulative impact of nutrient flows and multiple stressors on the ecosystem
12	Advancing our understanding of the potentially contrasting ecological impacts of nutrients from different sources
13	Investigating the impacts of climate change on coastal nutrient connectivity
14	Investigating the feedback loops between the social-economic and ecological systems (social-ecological systems interactions)
15	Conducting research that specifically aims to inform local environmental management and restoration in practice

seascapes (Olds et al. 2018). Prioritizing a single habitat type for conservation action may reduce the success of conservation investments such as restoration and threat mitigation (McAfee et al. 2022; Vozzo et al. 2023).

Different nutrient pathways operate across different spatial and temporal scales (Shantz and Burkepile 2014). Studies conducted at inadequate spatial–temporal scales will provide narrow, oversimplified and potentially misleading results (point samples, snapshots) that do not adequately capture the ecosystem reality (see e.g. Shuler and Comeros-Raynal 2020). For example, Delevaux et al. (2019) found that their results were consistent with a previous regional-scale study that did not account for within-watershed spatial heterogeneity. However, quantifying finer scale (within-watershed, 60 × 60 m) spatial patterns revealed ecologically meaningful insights that supported different recommendations for local management (Delevaux et al. 2019). Such careful consideration of scale was largely lacking in most reviewed studies. We encourage explicit quantitative reporting of the study scale and data resolutions to allow a scale-dependent operational understanding of the different nutrient pathways under study. Trade-offs between resolution and extent may be inevitable due to a range of practical limitations, such as limited funding and resources. Our proposed nutrientscape framework both encourages funders to consider the “more than the sum of the parts” knowledge benefits of a whole-system approach and also the potential for bringing together different studies across scales resulting in economies of scale. We recognize that no single discipline can address the whole-system knowledge gap and call for more transdisciplinary working (e.g. between biogeochemists, ecologists, hydrologists, social scientists, and management practitioners) in the design and implementation of research projects.

In addition to explicit consideration of scale and scaling, working within a clearly defined conceptual framework will help advance coastal nutrient connectivity research. The conceptual understanding of the coastal environment affects what research questions are being asked, and what methods are being used. For instance, in local knowledge systems across the Pacific Islands, land and sea are traditionally not understood as separate but as fundamentally interconnected (Hickey 2007; Poepoe et al. 2007). This conceptual understanding of a land-sea continuum rather than a binary classification was reflected in the management practices. For example, Hawai'ians traditionally divided high islands into zones known as *ahupua'a* that generally extended from the mountain into the sea (Smith and Pai 1992). This system allowed for the balanced management of the different terrestrial and marine resources along a so-called 'ridge-to-reef continuum' (Smith and Pai 1992; Minerbi 1999; Wilmot et al. 2022). In contrast, Western environmental research and management is conventionally siloed into studies of landscapes and studies of seascapes that are typically conducted by distinct and separate disciplines and managed by different institutional units (Stoms et al. 2005; Álvarez-Romero et al. 2011; Collin et al. 2013, 2021).

Although conceptual frameworks to support integrated land-sea management in the coastal zone have been proposed (Beger et al. 2010; Álvarez-Romero et al. 2011; Makino et al. 2013), the primary focus has been on risk management from land-based sources of pollution impacting aquatic ecosystems (Álvarez-Romero et al. 2011; Carlson et al. 2019). Furthermore, these frameworks place little emphasis on the role of landscape ecology and systems science where spatial pattern metrics, scale, and scaling relationships provide additional insights into the fundamental role of landscape and seascape structure and function and enable scenario modeling and spatial prediction to unobserved regions (Wu 2004; Frazier 2023). Here, we propose a new framework that builds on previous calls for integrated land-sea studies, specifically focusing on a whole-system, spatially explicit, and cross-disciplinary approach to study nutrient connectivity.

A shared conceptual framework for coastal nutrient connectivity studies could support a broader application of a spatially explicit social-ecological systems approach and facilitate cross-disciplinary collaborations. Furthermore, building a coordinated evidence base would support greater comparability of results between studies and help identify and prioritize knowledge gaps within the research field (Fausch et al. 2002; Ostrom 2009; Dunham et al. 2018; Pittman et al. 2018).

Nutrientscape ecology

To support research efforts that address the 15 research needs identified (Table 1), we present here a new framework for nutrient connectivity studies that we term "nutrientscape ecology" (Fig. 5). Nutrientscape ecology integrates social-ecological systems thinking with the spatial pattern-focused concepts and analytical tools of landscape ecology. We propose that the integrated, multiscale, and spatially explicit study of the coastal nutrientscape—nutrientscape ecology—could help inform the management of nutrient connectivity and thereby contribute to local efforts to manage human impacts and increase the resilience of tropical coastal environments to climate change. Indeed, due to the fundamental role of nutrient flows in determining coastal ecosystem dynamics, the management of nutrient connectivity ought to be a high priority in coastal conservation and restoration efforts (Howarth et al. 2005; Seitzinger et al. 2010). A key goal of our proposed nutrientscape ecology framework is to support solution-focused research that is informative and useful for local managers and stakeholders and helps bridge the science-policy gap.

Nutrientscape ecology: theoretical foundations

We propose that leveraging Social-Ecological Systems (SES) thinking would benefit and increase the policy impact of coastal nutrient connectivity research in several ways. First, rather than studying parts of the system in isolation, the aim of SES thinking is to

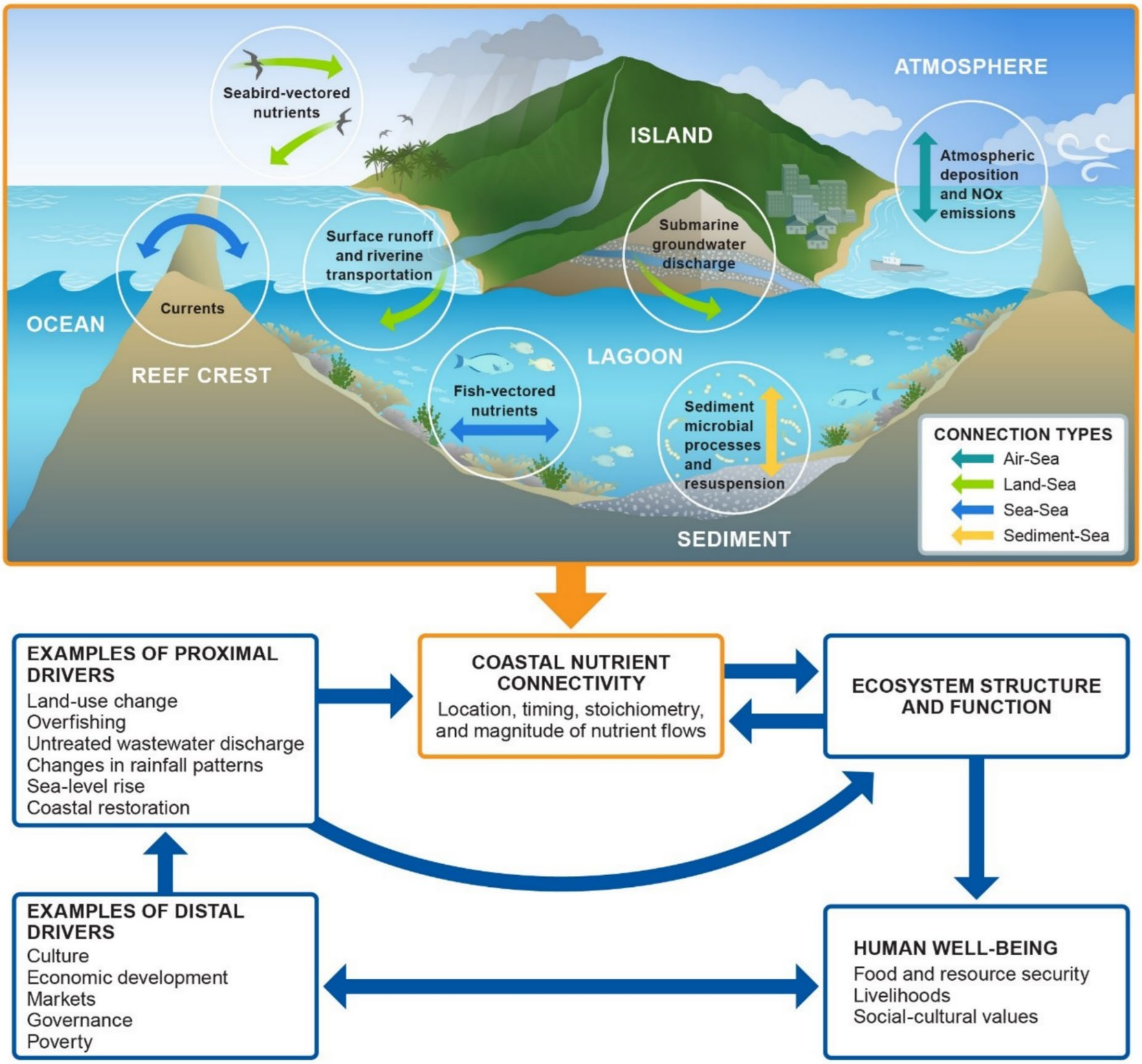


Fig. 5 Nutrientscape ecology: the integrated, spatially explicit, and multiscale framework for studying coastal nutrient connectivity. Social-ecological systems analysis can help us understand how distal and proximal anthropogenic drivers act together to alter coastal nutrient connectivity, and how the resulting ecological changes impact human well-being. The analytical and conceptual tools of landscape ecology enable the spatial study of pattern-process relationships associated with different coastal nutrient pathways at a range of scales: for example, from the whole island to individual habitat patches and from decadal trends to diurnal cycles

understand how system components interact to form the complex whole (Odum 1977; Ostrom 2009; Pittman et al. 2018). Thus, SES encourages the examination of the interlinkages between multiple habitat types and different nutrient pathways including linkages to human well-being and human impacts. Additionally, from a SES perspective, changes in nutrient connectivity are considered in the context of other drivers of change, such as climate change (Ban et al. 2014; Zaneveld et al. 2016; Donovan et al. 2020).

Second, taking a whole-system perspective and studying multiple nutrient pathways requires cross-disciplinary collaboration. However, when experts from different disciplines rely on different epistemologies, it may take considerable time and effort to build a shared understanding of the research problem statement and potential solutions. Consequently, an advance in nutrientscape ecology requires a shift in mindset from specialized single disciplinary and reductionist research into collaborative, cross-disciplinary and holistic approaches (Odum 1977; Voigt 2011; Pittman et al. 2018). The SES approach was developed as a unifying framework that facilitates the integration of the different research approaches and methods used in different disciplines to study a complex system (Ostrom 2009). Hence, SES could expedite the cross-disciplinary collaborations required for studying multiple nutrient pathways and habitat types.

Third, through its focus on interactions between components of a system, the SES approach allows for identifying feedback loops within and between the social-economic and ecological systems (Scheffer et al. 2001; Folke et al. 2005; Levin et al. 2013; Leslie et al. 2015). For example, diminishing fish stocks may lead to increased fishing effort by fishers that do not have access to an alternative livelihood. This, in turn, can result in an even greater reduction of the fish stocks (Cinner et al. 2009; Nyström et al. 2012). Overfishing can disrupt fish-vectored nutrient pathways (Layman et al. 2011) and risk deteriorating the food and nutritional security of coastal populations that depend on fish-derived micronutrients in their diet (Maire et al. 2021). Identifying and understanding feedback loops is critical for the success of environmental management strategies, both to avoid unintended consequences of management interventions and to find effective levers to increase systemic resilience to disturbances (Hughes et al. 2017). Positive feedback loops could also be harnessed to amplify the impacts of a management action (Farmer et al. 2019; Riechers et al. 2021).

Despite theoretical and methodological advancements in SES research, few studies have implemented a spatially explicit approach (Pittman et al. 2018). Yet, understanding spatial patterns is often key for understanding system dynamics (Polis et al. 1997; Loreau et al. 2003; Jenerette and Wu 2004; Bailey 2010). Spatial information is also essential for environmental management and spatial planning (Van Kouwen et al. 2007; Caldow et al. 2015). To bridge the conceptual analysis of complex systems and driver-impact-relationships with the spatial study of real ecosystems, the analytical tools of landscape ecology can be leveraged (Virah-Sawmy et al. 2009). We propose that integration of landscape ecology and SES will form a solid foundation for the whole-system science of coastal nutrient connectivity.

To support the operationalization of nutrientscape ecology, we provide a set of recommended questions to consider during the formulation of a research project (Table 2). Then, we discuss analytical tools from landscape ecology and SES and explore novel technologies that could be leveraged to develop nutrientscape ecology as a multiscale, integrated, and spatially explicit science.

Nutrientscape ecology: analytical tools

Multiscale analysis

Understanding scale is a core component of landscape ecology research (Turner 1989; Wiens 2002), and the first key recommendation for any study in nutrientscape ecology is quantitatively reporting and justifying the spatial and temporal extent(s) and resolution(s) of the study. Avoiding ambiguous and inappropriate scale selection will address a key knowledge gap identified in this review. The second recommendation is to employ a multiscale approach to better understand how nutrient pathways operate and interact across scales and avoid limitations with scale-dependent results. For example, biogeochemical processes that impact the composition (i.e., stoichiometry) of a nutrient flow can occur at the level of individual organisms, ecosystems, and landscapes-seascapes (Cherif et al. 2017; Van de Waal et al. 2018; Fonseca et al. 2022). A multiscale nutrientscape ecology framework is enabled by integration of new and increasingly cost-effective data from drones, satellites, and in-situ sensor networks that would increase the study's spatial and temporal resolution and extent (Thomson et al. 2021; Besson et al. 2022).

Furthermore, a better understanding of long-term environmental change could be achieved through local knowledge and funding to enable location-specific long-term research programs such as the US National Science Foundation's Long-Term Ecosystem Research (LTER). Important advances in watershed nutrient dynamics and connectivity have resulted from the LTER programs at Hubbard Brook Experimental Forest (New Hampshire) since the 1960s (Likens and Bormann 1974), Moorea Coral Reef LTER (Adam et al. 2020), and Florida Coastal Everglades

Table 2 Questions and examples to consider before starting a nutrientscape ecology study. Funding considerations, although crucial, are not included here. To successfully carry out the project, the types of expertise required – across different disciplines – should be thoughtfully considered

Social-ecological systems	1. Identify components of the social-ecological system and their interactions	
	1.1 Consider potential nonlinearities in the interactions	Nutrients may have a positive fertilizing effect until a threshold is breached, after which the effect becomes negative (Stockbridge et al. 2020)
	1.2 What are the proximal and distal drivers of change?	Increased terrestrial nutrient loading to coastal waters may be associated with land use change (proximal driver) driven by economic development (distal driver) (Ramos-Scharrón et al. 2015)
	1.3 What are the relevant temporal scales, and are there trends or periodicities that should be considered?	Riverine transport of nutrients from land to sea may be impacted by long-term climate periodicities, such as El Niño and the Pacific Decadal Oscillation (Slater et al. 2019)
Landscape ecology	2. Develop a spatial understanding of the system	
	2.1 Is the consideration of spatial heterogeneity important for the research question at hand?	The influence of land cover spatial heterogeneity on nutrient connectivity depends on the relative abundance of different land cover types (Gergel 2005)
	2.2 Does the nutrient flow undergo stoichiometric transformations as it moves through space or through the food web?	Benthic consumers may alter the stoichiometry of dissolved nutrient pools that are subsequently used by algae (Cross et al. 2005)
	2.3 How do the interactions between system components occur spatially?	Fish movement patterns determine the spatial distribution of fish-derived nutrients, creating nutrient hotspots within the coral reef environment (Shantz and Burkepile 2014)
	2.4 What are the relevant spatial scales, and are local spatial interactions generating emergent phenomena at broader spatial scales?	Jenerette and Wu (2004) observed nitrogen limitation at a local scale but not at broader spatial scales. In other words, they found nitrogen limitation to be scale dependent

LTER (Armitage et al. 2011). Much of this research has been influenced by landscape ecology and systems thinking and we encourage the continued cross-pollination of ideas and transferable technologies from these disciplines to advance our understanding of the nutrientscape.

Integrated analysis

By “integrated nutrientscape ecology”, we mean taking a whole-system perspective on the coastal nutrientscape: studying land and sea, the social and the ecological, multiple habitats, and multiple nutrient pathways and their interactions. Systems mapping can be used to identify the system’s key components, their interactions and possible feedback loops, and proximal and distal drivers of change. This literature review revealed that many studies do not identify the proximal sources of nutrients (e.g. wastewater discharge), and even fewer studies identified the underlying social, political, or economic drivers (e.g. increase in unsustainable tourism). The systems map shown in Fig. 6 illustrates that climate change is expected to directly and indirectly affect many system components, highlighting the urgent need to address the knowledge gap about climate change impacts identified in this literature review.

Another tool for analyzing SES is the drivers–pressures–state–impact–responses (DPSIR) framework (EEA 1999). This framework has been widely used to communicate chains of cause–effect relationships in coastal and marine environmental policy (Atkins et al. 2011a, 2011b; Gari et al. 2015; Patrício et al. 2016). In particular, DPSIR has often been applied to link drivers of land-based nutrient loading to eutrophication in coastal waters (Karageorgis et al. 2005; Pirrone et al. 2005; Pinto et al. 2013). Compared to a systems map, a disadvantage of this framework is

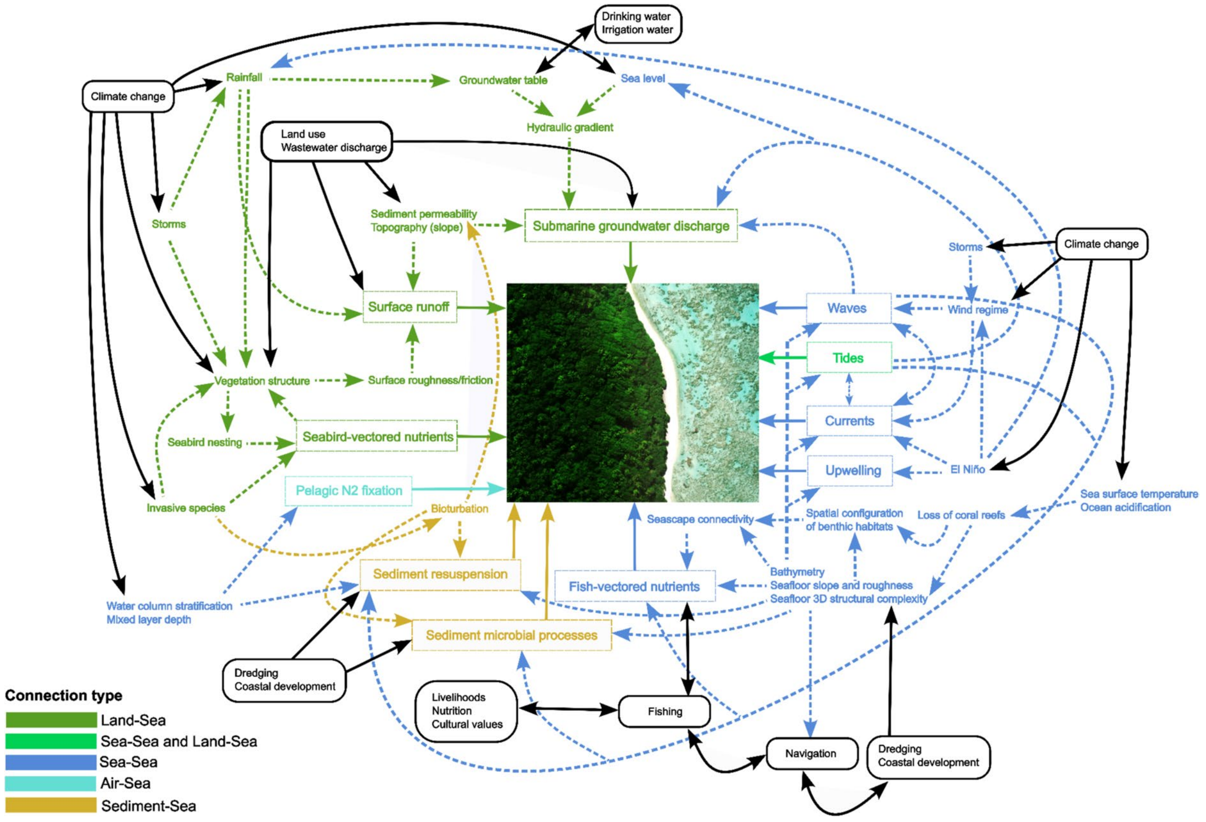


Fig. 6 Systems map of the coastal nutrientscape. The key nutrient pathways are shown in dashed-lined boxes and solid arrows. Impacts and interactions between the different components of the system are shown in dashed arrows. The black boxes and black solid arrows show anthropogenic impacts on the system components

that it proposes linear unidirectional causal chains and fails to capture complex system dynamics and interactions (Rekolainen et al. 2003; Niemeijer and de Groot 2008). Nevertheless, coupled with a whole-system approach, the DPSIR framework can be useful for structuring problems by identifying and communicating the proximal and distal anthropogenic drivers of environmental change (Atkins et al. 2011a; Lewison et al. 2016).

Missing from both the systems map and the DPSIR framework are the spatial and temporal dynamics (Cumming et al. 2017; Agramont et al. 2022). For example, at relatively broad scales (10–100 s km, seasons-years), there can be temporal variation in the circulation patterns of coastal waters caused by the monsoon season or El Niño (Craig et al. 2007; Wang et al. 2019). Similarly, surface runoff is often spatially and temporally focused, for example near agricultural lands during and after a large storm (Adam et al. 2020; Fong et al. 2020).

The whole-system study of coastal nutrientscapes will require integrating data collected across the land-sea continuum including social-economic data. When conducting research in the lands and seas of indigenous peoples, the conceptual framework should support pluralistic knowledge creation and the decolonization of research (Smith 2021; Reynolds and Wheeler 2022). A greater appreciation and application of local knowledge, in written form or through surveys and interviews, could help advance nutrientscape ecology by providing important historical and local contextual information. Participatory mapping can be a useful tool to summarize and visualize local knowledge in a spatially explicit way (Klonner et al. 2021).

Spatial analysis

Developing accurate spatial models of nutrient connectivity is challenging because a nutrient flow is affected by biogeochemical processes taking place at different scales (Turner and Gardner 2015; Smithwick 2021), and the stoichiometry of the flow changes as it moves through space and interacts with the surrounding biotic and abiotic features (Schade et al. 2001; Sitters et al. 2015). Thus, the quantity and composition of a nutrient flow is a function of the local conditions (i.e., the biogeochemical processes occurring within a habitat patch), the composition and configuration of the surrounding environment (e.g. distance to different habitat patches), and the resistance to movement to, and away, from that point (e.g. water flow velocity determined by terrain roughness) (Gergel 2005; Turner and Gardner 2015).

Landscape ecology provides powerful tools for connectivity modeling that leverage the physical attributes of the landscape or seascape (Calabrese and Fagan 2004; Treml and Kool 2017). Terrestrial landscape ecology studies have highlighted the importance of geomorphological metrics such as slope, curvature, and terrain roughness in determining nutrient connectivity (Moore et al. 1991; Chadwick and Asner 2016). For instance, in agricultural lands, soil phosphorus tends to be deposited in flatter, downslope areas where runoff converges and slows due to local curvature (Evans et al. 2016). Quantifying slope, curvature, and terrain roughness is foundational in hydrology (Hendriks 2010) and widely used in seascape ecology studies of fish distribution and movement (Borland et al. 2021). However, the link between these geomorphological metrics and nutrient connectivity in coastal seascapes remains largely unexplored (Hearn et al. 2001), presenting an exciting research avenue for the spatially explicit, predictive study of the coastal nutrientscape.

In addition to geomorphological metrics, spatial pattern metrics that quantify habitat composition and configuration could be leveraged to model and predict the stoichiometric transformation of nutrient flows across geographical space (Sitters et al. 2015; Smithwick 2021). Several studies have leveraged terrestrial composition and configuration metrics to predict riverine water quality and nutrient concentrations (Uuemaa et al. 2005; Wu and Lu 2019). In a pioneering surface-flow simulation study, Gergel (2005) found that the spatial configuration of land cover types is most important in the prediction of nutrient connectivity patterns in watersheds with intermediate relative abundance of different cover types. In an empirical study, Jones et al. (2001) found that while land cover spatial pattern metrics were able to explain 65–86% of the variation in nitrogen loading to streams, the predictive power varied depending on the biophysical characteristics of the watershed (e.g. the relative importance of atmospheric nitrate deposition). The findings of these pioneering studies suggest that developing spatial analysis in nutrientscape ecology could allow establishing heuristics for determining when simple composition metrics are sufficient and when more elaborate configuration metrics would be needed. We advocate building on these terrestrial case studies and developing predictive modeling of nutrient connectivity across land *and* sea.

Nutrientscape ecology: novel technologies

In addition to analytical developments, we identify recent technological advancements to support the operationalization of nutrientscape ecology in practice. We note that technological and theoretical advancements go hand in hand whereby novel approaches for data collection and computational modeling may be used to both inform and test nutrientscape ecology theory. We anticipate that future technological evolution and application of an integrated nutrientscape conceptual framework will enable the formulation of novel research questions and hypotheses.

Data collection

New remote sensing technologies provide unprecedented amounts of environmental data. Multiple satellite constellations now provide daily revisit times, and the spatial and spectral resolutions have been improving at each generation of satellites (Fig. 7). Additionally, drone-based mapping can achieve up to a sub-centimeter scale spatial resolution while also avoiding the issue of persistent cloud cover in many tropical coastal regions (Collin et al. 2018; Bennett et al. 2020). Marine and terrestrial habitat maps derived from satellite and drone data can be used to calculate composition, configuration, and geomorphological metrics, thereby supporting spatially explicit nutrient connectivity modeling (Lepczyk et al. 2021). Furthermore, while nutrients dissolved in water do not have a significant optical signal, their presence can be inferred through a number of proxies detectable from remotely-sensed data (Soto et al. 2009; Wang et al. 2018a). For example, increased nutrient loading can result in elevated phytoplankton biomass in coastal waters (i.e., greener surface waters), which can be detected from remotely-sensed imagery presenting opportunities for spatial indicators of change (Cillero Castro et al. 2020; Cael et al. 2023). Thermal infrared sensors mounted on drones or satellites can be used to map sea surface temperature and thereby identify potential groundwater discharge sites (Oehler et al. 2018; Oberle et al. 2022). Dye tracing experiments that leverage drones allow tracking coastal water flows at very high spatial resolutions (Johansen et al. 2022).

In addition to remote sensing, there is opportunity for developing networks of field-deployed sensors capable of data collection at high temporal resolutions (1 s to 24 h) (Fig. 7B) (Bieroza et al. 2023). Field-deployed sensors can provide detailed time-series data that cannot be obtained from traditional field sampling and subsequent laboratory analyses (Reading et al. 2017). Nutrients such as ammonium, nitrate, and phosphate can be measured using wet-chemistry sensors and ion-selective electrodes (Pellerin et al. 2016). Additionally, optical sensors can be leveraged to estimate a range of key parameters associated with biogeochemical flows, such as turbidity and concentrations of phytoplankton and colored dissolved organic matter (Bieroza et al. 2023). The high-frequency data collection through sensor networks could reveal previously unobserved patterns in the flows and transformation processes of nutrients in space and time (Bieroza et al. 2014, 2023). The data from field-deployed sensor networks can also serve as calibration and validation data for remote sensing models (Lyu et al. 2022). However, the cost of setting up and maintaining a sensor network is still prohibitively high for many individual research groups. Creating a comprehensive sensor network may therefore require a coordinated effort between multiple research groups and universities, as well as collaborations with research institutions that develop new sensor technologies.

The complementary use of field-deployed sensor networks, remote sensing, and traditional field experiments enables the multiscale study of environmental change (Shiklomanov et al. 2019). The integrated application of novel technologies could provide insights into how local and regional alterations might drive changes in global biosphere integrity (Nash et al. 2017). To fully realize the potential of novel technologies in coastal nutrient connectivity research, interdisciplinary collaborations between data scientists, remote sensing experts, ecologists, hydrologists, and biochemists should be encouraged (Shiklomanov et al. 2019; Ward et al. 2020). Innovative ways to combine multiple sources of data need

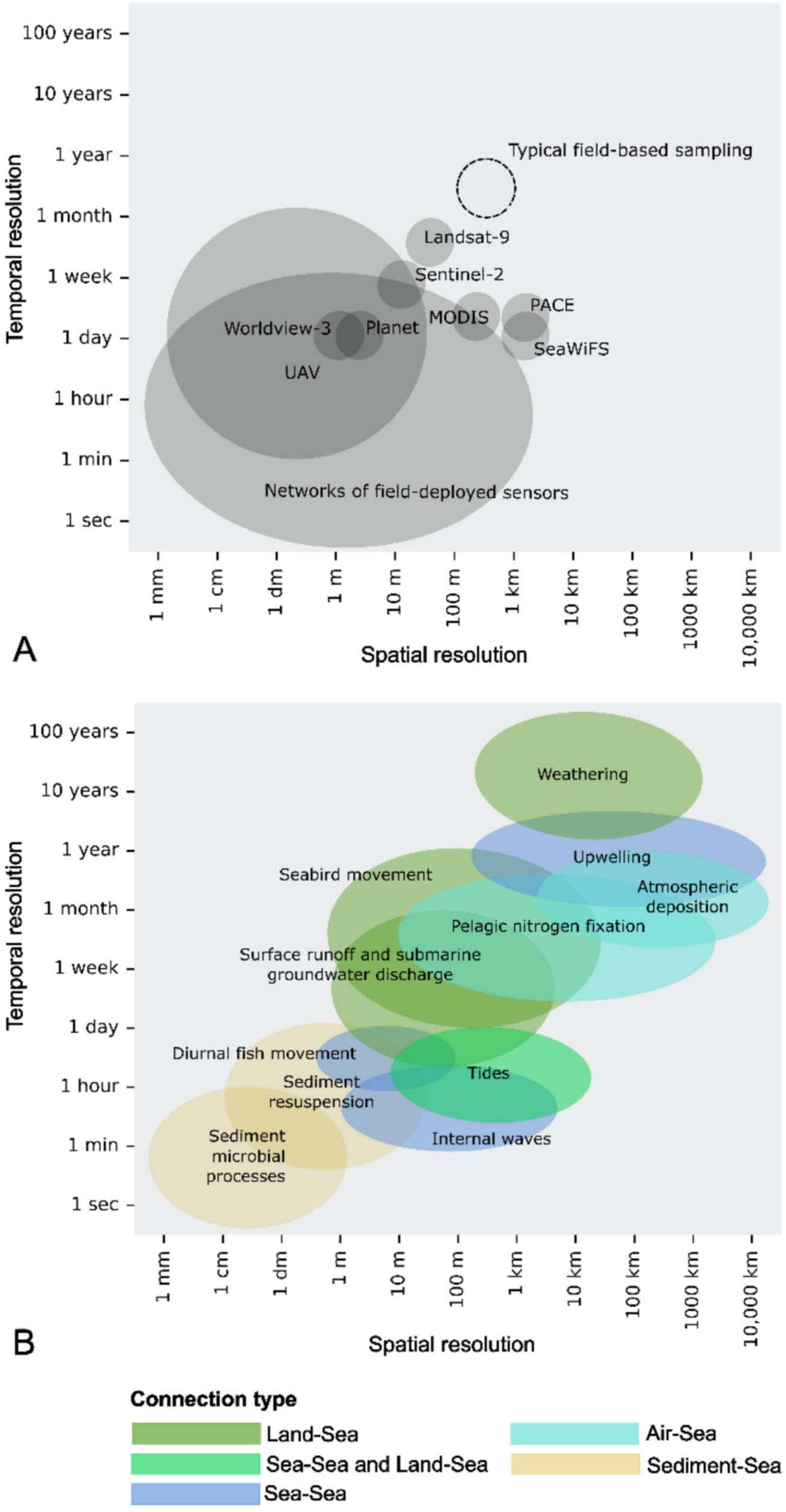


Fig. 7 **A** The temporal and spatial resolutions of remote sensing technologies (satellites and UAVs) and field-deployed instruments. The typical temporal and spatial resolutions of traditional field campaigns are shown with the black dashed-line circle: many field studies collected data every 1–12 months to cover seasonal variability, at a spatial resolution of 100–1000 m. **B** Temporal and spatial resolutions likely to be relevant for studying different coastal nutrient pathways. The selection of the temporal and spatial scale(s) will depend on the specific research questions of the study. Scale information integrated from Dickey (2020), Hedley et al. (2018), and Taniguchi et al. (2019)

to be explored (Trantas et al. 2023). In the following sections, we have summarized two promising modeling approaches for making full use of data from different sources in nutrientscape ecology: digital twins and physics-informed machine learning.

Computational modeling

The large quantities of environmental data provided by remote sensing and in-situ sensor networks is stimulating advances in computational modeling techniques, such as digital twins (Blair 2021; Blair and Henrys 2023). A digital twin is a virtual representation of a physical system (Jones et al. 2020) and provides a spatial template with which to integrate and model diverse cross-scale spatial data (Brocca et al. 2024). Digital twins differ from other computational modeling approaches primarily through their usage of evolving data in real-time so that the states of the virtual and physical systems are synchronized (Jones et al. 2020; Wright and Davidson 2020). In contrast, a traditional computational model describes the behavior of the system according to set processes that do not evolve over time, thereby making the model potentially inaccurate over timescales within which significant alterations in the system and its behavior would occur (Wright and Davidson 2020). Thus, digital twins could support timely environmental management interventions, as the model is built to continuously integrate new information moving towards near-real time models (Moghadam et al. 2020; Trantas et al. 2023). This makes digital twins a promising spatial modeling approach for supporting nutrient connectivity management in highly dynamic coastal environments. However, environmental digital twins research is still nascent, and more work is needed to explore and realize the full potential uses of this modeling approach (Blair and Henrys 2023; Purcell and Neubauer 2023; Purcell et al. 2023).

Another promising new technology to support nutrientscape ecology is physics-informed machine learning (Karniadakis et al. 2021). This novel research field integrates physical rules and domain knowledge with machine learning, providing three key advantages for the predictive modeling of social-ecological systems. First, while purely data-driven machine learning models may achieve good training and validation accuracies, their predictions may still be physically unrealistic (Karniadakis et al. 2021). For example, a model trained on existing environmental data may not be able to accurately extrapolate into the future when environmental and climate conditions change (Kashinath et al. 2021; Zhong et al. 2023). Second, many traditional machine learning models are black boxes—in other words, the model predictions are not explained in a meaningful way (Rudin 2019). Integrating a physics-based understanding into the machine learning model supports the interpretability of the model (Rudin 2019; Kashinath et al. 2021). For example, physical meaning can be incorporated into the intermediary nodes of a neural network, thus enabling an interpretable information flow through the network (Wu et al. 2024). Third, applying purely physics-based models is limited by the requirement of high-quality data, expert knowledge for accurate model parameterization, and a trade-off between computational cost and high spatial resolution (Soriano et al. 2021). A number of pioneering studies have already applied physics-informed machine learning to study issues relevant for coastal nutrientscape ecology, such as groundwater contamination (Soriano et al. 2021), terrestrial runoff (Zhong et al. 2023), surface water flows (Bertels and Willems 2023), sea surface temperature (de Bézenac et al. 2019), and ocean vertical mixing (Zhu et al. 2022). However, similarly to digital twins research, applications of physics-informed machine learning for predictive environmental modeling are only just emerging with great opportunity for further developments and discoveries (Kashinath et al. 2021).

Conclusions

Nutrient flows within and across ecosystems are major drivers of ecosystem structure and functions. These flows operate across multiple scales and are characterized by complex interactions. The condition of the nutrientscape directly and indirectly influences human health and well-being through intimately interconnected social-ecological systems. A key research priority is a better understanding of the local and global human impacts on nutrient flows and the consequences of these flows on the functioning and resilience of coastal social-ecological systems. This study summarized the recent state-of-science in tropical and subtropical coastal nutrient connectivity studies with a systematic literature review. Our results show that research to date has largely focused on unidirectional flows of nutrients, with limited consideration of the reciprocal flows between spatially connected ecosystems. Furthermore, nutrient connectivity studies are typically based on traditional field-based surveys and sampling at a single spatial scale within a narrow temporal window, thereby forming a set of snapshots of the system's patterns and processes. To develop improved resilience-based environmental management and restoration strategies, new research approaches are needed that understand nutrient connectivity from a spatially explicit whole-system perspective. We suggest that great potential exists for a nutrientscape approach to advance and accelerate the scaling up of coastal restoration through site selection, functionally meaningful design of interventions, and effective cross-scale monitoring.

Building on the results of our review, we identified 15 future research needs and presented a novel research approach that we called "nutrientscape ecology". The framework of nutrientscape ecology serves three primary purposes. First, this framework can advance coastal nutrient connectivity research as a multiscale, spatially explicit study of pattern-process relationships across landscapes and seascapes by applying landscape ecology concepts and analytical methods. Second, this work can support the application of systems thinking that goes beyond the study of individual nutrient pathways in isolation and situates the nutrient flows and pathways in the wider context of the coastal social-ecological system. Third, the framework encourages the novel integration of advanced technologies in nutrient connectivity research that are capable of generating insights into nutrient connectivity at scales meaningful to environmental management, conservation, and spatial planning. These technologies include remote sensing, field-deployed sensor networks, machine learning, and digital twins. A likely barrier to the implementation of the nutrientscape ecology framework is securing sufficient funding to conduct multiscale, cross-disciplinary research. Thus, there is a need for novel funding programs that understand the critical importance of nutrient connectivity to coastal social-ecological systems and recognize the benefits of a whole-system approach, cross-disciplinary collaborations, and long-term environmental monitoring.

While this literature review focused on tropical and subtropical coastal environments, the nutrientscape ecology framework can be readily applied to the study of nutrient connectivity in other coastal environments. This work can serve as a foundation to develop a predictive and solution-oriented science of nutrient connectivity that supports local management efforts in the context of mitigating and adapting to accelerated global warming and other environmental changes.

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Declarations

Conflict of interest The authors declare no competing interests.

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