Coral Reefs
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REPORT

Exploring benthic habitat assessments on coral reefs: a comparison of direct field measurements versus remote sensing

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Abstract Coral reefs are spatially variable ecosystems that form biogenic structures ranging in size from 10 to 1000s of meters. Their changes in response to anthropogenic stress are occurring across increasingly broad scales, yet our ability to detect, understand and respond to these changes at relevant scales is limited. Traditional in-water observation-based coral reef ecology and remote sensing-based methods both offer valuable insights into benthic change, but their relative scalability and use to-date must be understood to inform optimal future research approaches. We conducted a systematic literature review comparing the approaches used to quantify benthic habitat, through traditional in-water ecological studies and remote sensing studies, with respect to: (a) their geographic distribution, (b) reef zone selection, and c) their focal questions. Among the 199 studies reviewed, traditional ecological studies primarily concentrated on community composition (89%), using high-detail direct measurements, especially from the reef slope (80%). By contrast, remote sensing studies provided spatially explicit datasets at coarser spatial and thematic resolutions, with a predominant focus on benthic mapping (72%) across entire reef systems. Only 3% of studies integrated both approaches, combining comprehensive in-situ observations with broad-scale remote sensing. As anthropogenic stressors continue to increase in scale, bridging these scientific disciplines offers a promising way to upscale observations to entire reef-scape scales. We identify steps to harness the strengths of both fields and integrate multiple tools at various levels of resolution and scale. Such bridging approaches offer a way forward in understanding and managing coral reef functioning in the Anthropocene.

Keywords Coral reefs · Coral reef ecology · Ecological monitoring · Remote sensing · Review

Introduction

Ecosystems, both terrestrial and marine, share a degree of hierarchical organization with sublevels operating at distinct temporal and spatial scales, collectively contributing to larger systems (O'Neill et al. 1989). Consequently, each subsystem exhibits varying spatio-temporal heterogeneity and patchy distributions, forming the foundation for ecosystem structure and functioning (O'Neill et al. 1989; Azovsky 2000; Wu 2004). These fundamental characteristics, also found in coral reefs, create scale multiplicity in spatial patterns and ecological processes (O'Neill et al. 1989; Levin 1992). Such that, at smaller scales, ecosystems may be dominated by intricate processes or behaviors of individuals, but their influence becomes negligible at intermediate or broad scales, where environmental, evolutionary, or geomorphological processes shape ecosystems (Wiens 1989; Holling 1992). Therefore, understanding ecosystem structure and functioning necessitates studying ecological phenomena at scales most relevant to the underlying processes. Detecting patterns relies on two scale components: resolution and extent. Extent refers to the overall study area coverage, while resolution describes the size of individual observation units

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(Wiens 1989; Wu and Li 2006). Combining extent and resolution sets the upper and lower dimensional boundaries of a study, much like the size and mesh of a sieve (Wiens 1989).

In coral reef ecology, it is crucial to address processes across various scales, which can be categorized into three dimensions: spatial, temporal, and thematic (Wu and Li 2006; Lecours et al. 2015). The spatial dimension encompasses the spatial resolution (i.e., level of detail measured) and geographic extent of an object, area, or process. Temporal resolution refers to the frequency of data collection, while temporal extent describes the period of data collection. Thematic scale, refers to the number of classes identified within a chosen domain/s, mainly concerning taxonomic resolution and the level of organization that can be resolved in datasets (Wu and Li 2006; Lecours et al. 2015). As coral reefs face increasing threats, it is becoming more important for research and conservation responses to address changes at broader spatial and temporal scales and in relevant thematic classes. However, there exists a mismatch between the geographic extent of reef stressors (e.g., marine heatwaves which lead to bleaching events) and the extent of scientific investigation, monitoring, and management responses. These challenges must be addressed if coral reef ecosystems are to be effectively managed and conserved into the future (Hughes et al. 2017; Bellwood et al. 2019a).

Coral reefs provide crucial functions and ecosystem services, such as coastal protection, fisheries, and tourism (Moberg and Folke 1999; Woodhead et al. 2019). The protection of functionally important groups within coral reef ecosystems is vital for ensuring the continual delivery of these services (Bellwood et al. 2019b; Brandl et al. 2019). However, identifying contributors to ecosystem functioning is challenging, and their identities may change in response to climate change (Bellwood et al. 2019b; Wolfe et al. 2021; Streit and Bellwood 2022). Moreover, coral reefs are dynamic environments where interactions among reef organisms and other ecosystem components occur at various scales and hierarchies (Hatcher 1997; Dietzel et al. 2021; Wolfe et al. 2023). Due to their heterogenous nature, spatial variability, and distribution in clumped patches ranging from 10 to 1000 s of meters in extent (Hopley et al. 2007), changes in coral reefs systems are not distributed homogeneously (Morais et al. 2021; Tebbett et al. 2023a). As a result, most coral reef functions are scale dependent. For instance, the rate and extent of vital functions provided by coral reef fishes, such as herbivory or bioerosion, are often estimated by assuming that fish presence equals function delivery (Bellwood et al. 2003; Graham et al. 2018; Perry et al. 2022). However, the implicit assumption of homogeneity of function across the reef is increasingly being questioned (Streit et al. 2019; Tebbett and Bellwood 2020), particularly in the face of the escalating scale of reef disturbance. These presence-function and scale mismatches present challenges when managing and conserving reef systems in the Anthropocene (Bellwood et al. 2019a; Brandl et al. 2019).

In coral reef research, benthic metrics like habitat cover, complexity, and diversity are used for evaluating and monitoring reef health and structure. They are commonly assessed using measures such as coral cover, benthic cover, and rugosity (Bellwood et al. 2004; Bruno and Selig 2007; Graham and Nash 2013). Coral cover indicates the percentage of the seafloor occupied by live coral, while benthic cover evaluates the proportion of different substratum types, including coral, algae, sand, and rubble (Bruno and Selig 2007). Rugosity provides a three-dimensional complexity estimate, helping to understand habitat diversity and potential habitat availability for various other reef inhabitants (Graham and Nash 2013; Ferrari et al. 2018). Assessing these metrics has traditionally involved in-water field surveys by skilled scuba divers. However, these labor-intensive surveys are often limited to specific taxa and specific study areas, representing only a small portion of the entire reef ecosystem (Bellwood et al. 2020; Tebbett et al. 2023a). As a result, findings from localized surveys may not fully capture broader patterns and variation at wider spatial scales. Valuable methods and techniques involving the use of remote sensing technologies, both above and below the water, have been emerging over recent decades with the aim of overcoming these challenges.

Ecology and remote sensing constitute pivotal domains within coral reef research, both characterized by scale awareness and dependence. Their shared objective is to appraise benthic transformations in coral reef systems to improve knowledge and ensure sustainability. While in-situ ecological studies are increasingly addressing coral reef functioning, recent papers have highlighted the constraints placed on our understanding because of the limited spatial extent of study efforts, across both reefs and habitats, as well as the immense associated costs, which constrain our ability to describe dynamic phenomena and processes at broad spatial scales (Hedley et al. 2016; Estes et al. 2018; Bellwood et al. 2020; Kench et al. 2022; Tebbett et al. 2023a). However, the rapid development of in-water remote sensing techniques to derive 3D structural assessments, at unprecedentedly high resolution and across relatively large areas (1ms -100ms), holds the potential to significantly enhance our capacity to monitor these ecosystems (Ferrari et al. 2016, 2022; Calders et al. 2020). While, recent advances in aerial and satellite remote sensing technologies offer a promising avenue to upscale the extent of in-situ observations to the reef-scale, of kilometer/hundreds of kilometers, optimizing the efficiency of such studies (Hamylton 2017; Dornelas et al. 2019; D'Urban Jackson et al. 2020) (Figs. 1 and 2). Nevertheless, the potential for scale-dependency raises the question: How can the methods used in traditional coral reef ecology be optimized to accurately assess biological

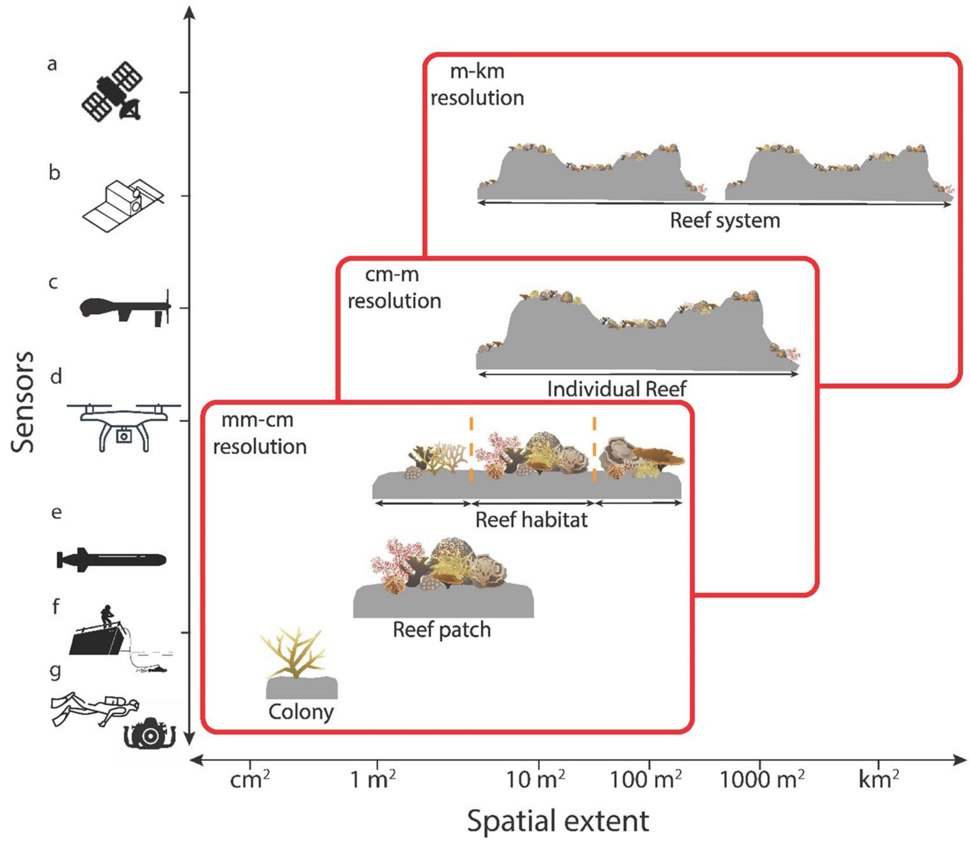

Fig. 1 Differences in spatial extent and resolution among technologies and approaches employed in coral reef ecosystem research. Specifically, differences among satellite and aerial remote sensing platforms (i.e., **a** satellite, **b** aeroplane, **c** unoccupied aerial vehicles, and **d** drones); and in-water remote sensing platforms, including **e** autonomous underwater vehicles, **f** underwater drones, and **g** diver-operated camera systems. Figure adapted from Harris et al. (2023) based on the original schematic in Joyce (2004)

and ecological processes affected by stressors operating at ever-increasing scales? To address this question, this study looked at the relative contribution of two fields (traditional in-situ coral reef ecology and remote sensing), that both assess benthic habitats. This was achieved by conducting a systematic review of relevant literature to compare these two fields of coral reef research and their inherent approaches, in terms of: 1) the geographic distribution of study sites; 2) their inherent approaches; 3) the habitats examined, and 4) their focal questions. Following this evaluation, we outline potential opportunities to create a bridge between these two fields to better address the challenges of scale. Ultimately, by addressing these aims, this study will help identify positive paths toward harnessing the valuable contributions of the two fields, traditional in-water coral reef ecology or remote sensing, in a world that will have to upscale rapidly to meet challenges in the Anthropocene.

Methods

Systematic review

To address our aims, we surveyed the international journal *Coral Reefs,* one of the world's primary journals for coral reef studies, as a representative sample of coral reef research, similar to the approach of Bellwood et al. (2020). We specifically selected the journal *Coral Reefs* due to its comprehensive coverage of research in the coral reef domain globally. It serves as an ideal choice for our study, with the sole inclusion criterion being scientific quality, provided the papers pertain to coral reefs. Importantly, this journal has no geographical or methodological constraints; including papers from diverse locations and employing various approaches. To ensure we sampled a representative range of relevant remote sensing studies, we surveyed the journals *Frontiers in Marine Science*, *PLoS One*, *Remote Sensing*, and *Remote Sensing of Environment* as representative journals for remote sensing-based studies on reefs. We used multiple journals as there were fewer relevant articles available when compared to *Coral Reefs*. We acknowledge the potential omission of some studies through this approach, however the attained sample size was robust and representative of the broader body of scientific coral reef literature (cf. Brandl et al. 2019; Sambrook et al. 2019; Bellwood et al. 2020; Crisp et al. 2022).

Studies were downloaded in August 2023 from two databases: 'Scopus' and 'Web of Science'. To facilitate direct comparisons, we included search terms that were broadly overlapping between the two fields (see below). Furthermore, we selected a time slice that ensured both fields had a high chance of appearance and influence, i.e.,

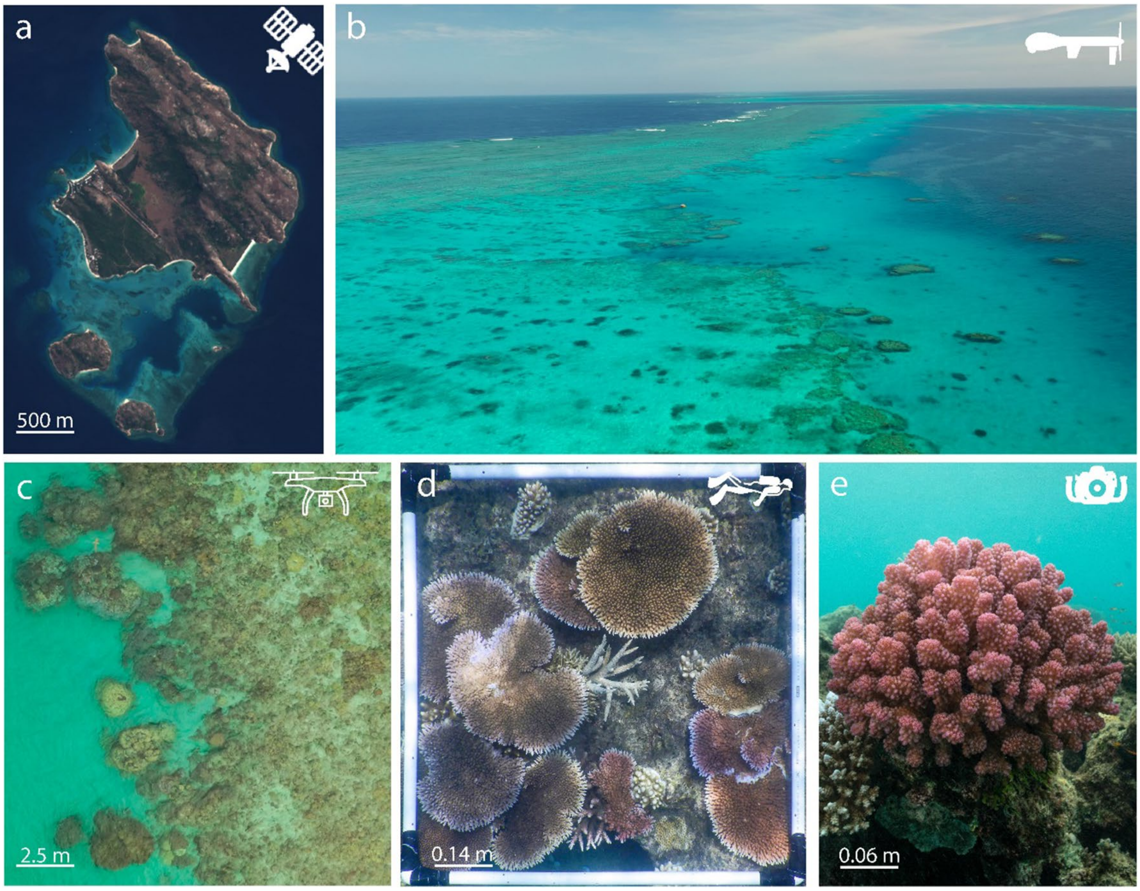

Fig. 2 Examples of the imaging and resolution capabilities of different coral reef remote sensing techniques at Lizard Island Reef in the northern Great Barrier Reef. **a** Satellite imagery (Sentinel-2A imagery. GSD = 10m Courtesy of European Space Agency—ESA), **b** unoccupied aerial vehicles and non-consumer grade drones (UAVs) (GSD ~ 10cm, but cover larger extents), **c** consumer-grade drones (GSD ~ 2cm, cover much smaller extents), **d** and **e** high resolution in-water photography (GSD ~ 5mm)

between 2012 and 2021, inclusive. For the four representative remote sensing journals, the respective search terms were: [Topic sentence (TS) = coral* OR "Coral reef"] AND [TS = Satellite OR UAV OR drone* OR algorithm OR "airborne sensor" OR structure-from-motion OR s-f-m OR "structure from motion" OR photogrammetry OR photomosaic* OR "photo mosaic" OR camera OR "photo-mosaic" OR "remote sensing" OR multispectral OR "imagery" OR "3D" OR "3D mapping" OR "3D modeling" OR "terrain reconstruction" OR "orthomosaic" OR "Large area imaging"]. Hyperspectral sensors hold great promise and are gaining importance in assessing benthic changes on coral reefs by offering imagery data across numerous narrow bands, possibly improving the thematic resolution of outputs (Bajjouk et al. 2019; Dierssen et al. 2021). However, we did not include "hyperspectral" as a search term in this review because, at present, these sensors and the platforms on which they operate, have lower operational efficiency and are not yet as widely available and adopted compared to the majority of methods covered. When a study using hyperspectral imagery was encountered in the review (e.g., Joyce et al. 2013) it was included (N = 11).

For the Journal *Coral Reefs*, the topic sentence was surveyed for: [benth* OR bathym* OR complexity OR cover OR rugosity OR map*]. Both searches were limited to full articles. After removing duplicates, the initial pool consisted of 747 studies. Among these, 359 were categorized as traditional in-water coral reef ecology (i.e., appearing in *Coral Reefs*), and 363 were classified as remote sensing (i.e., found in the four remote sensing journals). The search in *Coral Reefs* also yielded 25 studies that primarily used remote sensing methods to raise their final metrics (e.g., Doo et al. 2017; Newnham et al. 2020). Consequently, these were included in the remote sensing category, resulting in a total of 388 studies.

To ensure a meaningful comparison between the two fields we adopted a filtering protocol to select studies that were broadly comparable. We filtered the initial pool to identify suitable studies from the two fields by specifically looking for studies that assessed a benthic component on coral reefs and were concerned with in-situ measurements by screening the Abstract and Methods. To be included, remote sensing publications had to be undertaken on tropical coral reef systems, involve a benthic component (e.g., studies focusing on water quality were excluded), and had to address an ecological aspect of coral reefs, i.e., they must be concerned with metrics and processes (functions) that contribute to the movement or storage of energy or material on coral reefs. Review-style studies or studies in deep-sea or cold-water environments were excluded. Similarly, ecological papers had to be conducted on tropical reefs, in less than 20 m depth, and be non-experimental (i.e., studies employing terra cotta tiles or collecting specimens for lab experiments were excluded). This screening process resulted in the retention of 111 remote sensing studies and 88 traditional in-water coral reef ecology studies for analysis (see Table S1).

These remaining 199 papers were thoroughly reviewed and for each we recorded: 1) the category of the study (i.e., traditional coral reef ecology or remote sensing), 2) focal question(s) addressed, 3) organisms/parameters investigated, 4) method/approach employed, 5) geographic region(s) each study was conducted in, 6) geomorphic zone(s) surveyed, 7) whether study sites were identified in a reproducible way (i.e., with geographic co-ordinates or shown on a map), and 8) sensor platform(s), 9) spatial resolution, and 10) whether in-water field verification of broad spatial scale remote sensing was undertaken. These variables were chosen to allow for effective and insightful cross-domain comparison (see Table S2 for additional justification). Reporting the "spatial extent" of studies was exceptionally rare, leading us to rely on the geomorphic zone/s of operation as a proxy. Due to the wide range of papers addressing various themes at a range of scales, classifying thematic resolution (e.g., taxonomic resolution or number of benthic classes) consistently and meaningfully proved nearly impossible, necessitating the use of the broader "focal question" category as a substitute. The resulting data were then quantitatively explored to identify the potential overlap and divergences between ecological and remote sensing literature on coral reef systems.

Categorizing studies

Initially, we categorized all studies based on their approach or the type of data they generate. For simplicity and illustrative clarity, we classified studies into two categories: direct ecological observations, primarily utilizing or generating localized in situ data (termed traditional coral reef ecology or CR), and remote sensing (RS), primarily involving the use or creation of spatially explicit map-based data. The focal question(s) addressed in each study were identified and divided into the following categories: benthic mapping, bathymetry, carbonate budget, bleaching detection, disease impact, bioturbation, organism ecology, climate change, or community composition. Benthic mapping was defined as studies concerned with dividing different substrata into respective groups and spatially mapping their location, often producing spatially explicit datasets across large extents (e.g., identifying the benthic communities across the Capricorn Bunker; Hamylton et al. 2017). In contrast, community composition studies assessed and categorized an ecosystem component into high-detail taxonomic categories, quantifying their presence and abundance often in form of localized point based assessments (e.g., assessing spatial and temporal patterns in hard coral cover; Roelfsema et al. 2021a). When studies addressed multiple focal questions, each of these instances was treated as distinct observations in the dataset. Thus the number of focal questions identified is greater than the number of papers assessed.

Categorizing methods used

We categorized the approaches used in the studies into four main groups: direct quantification, sensor-based, linked studies, and upscaled linked studies. Direct quantification studies involved counting organisms present (e.g., Perry and Morgan 2017). Sensor-based studies utilized various sensors such as satellites or cameras, primarily for mapping or three-dimensional imaging of the benthic environment (e.g., Ferrari et al. 2016). Linked studies combined direct quantification and sensor-based approaches, linking in-situ observations and remote sensing approaches to infer stronger relationships between multiple metrics, such as assessing how coral colony complexity affects fish distributions (e.g., Oakley-Cogan et al. 2020). Upscaled linked studies introduced an additional aspect of aerial remote sensing and ground-truthing to extend ecological observations to entire reef-scape scales such as measuring the biomass of foraminifera in different reef zones and upscaling that to the reef scape scale using classified satellite imagery (e.g., Doo et al. 2017).

Categorizing geographic regions and habitat assessed

To assess how studies from the different fields (CR and RS) were distributed globally and determine if number of studies in a region was related to the area of reef present, we categorized the geographic region/s of each study based on the size of reef areas mapped by the Allen Coral Atlas (2022). For instance, studies conducted in the Great Barrier Reef (GBR) were assigned to the corresponding geographic region "Great Barrier Reef and Torres Strait" mapped area in the Allen Coral Atlas. In cases where a study covered multiple mapped areas, it was classified as surveying 'multiple' reef areas. To calculate the area of reef present in the studied regions the reef areas were extracted from the Allen Coral

Atlas in early November 2022 and included the reef's benthic classes such as Coral/Algae, Microalgal Mats, Rock, and Rubble. We excluded Sand and Seagrass as benthic classes to maintain a focus on biogenic reef framework building structures and to prevent an overrepresentation of mapped reef areas, especially in cases with extensive sand banks and seagrass habitats, particularly within the Caribbean context. Data were handled and visualized using ArcGIS Pro (version 2.9) and R (R Core Team 2022), using the *'tidyverse'* package (Wickham et al. 2019).

To assess which coral reef habitats were studied we categorized the habitats investigated within each study into their corresponding geomorphic zones. Our analysis included only those geomorphic zones that were consistently identified, namely back reef, lagoon, reef crest, reef flat, and reef slope/fore reef (as defined in Kennedy et al. 2021). If studies encompassed multiple geomorphic zones, each zone was treated as a separate allocation. Studies that assessed or mapped entire reef-scapes were categorized as 'Entire reef'. To determine the distribution of studies across different zones in relation to the proportional reef area each zone represents, we calculated the average area of each geomorphic zone across all reefs in the Great Barrier Reef and Torres Strait mapped region (Allen Coral Atlas 2022) and derived the relative proportions. It is important to emphasize that our study did not specifically center on this particular region and we recognize that it may not be representative of reef proportions in all other regions globally. We chose this region to represent the proportional reef area of geomorphic zones because it has received the most extensive scientific attention (Fig. 3A), making it likely to provide the most reasonable geomorphic zone area estimates due to the substantial mapping efforts (Kennedy et al. 2021; Roelfsema et al. 2021b).

Results

A broad and variable geographic spread of studies was identified (Fig. 3A) with most studies coming from the Great Barrier Reef (GBR) (36 in total, 18% of all studies) with a relatively equal split between traditional in-water ecology and remote sensing (Fig. 3B). Some regions were dominated by remote sensing studies, for example the SW Pacific, Hawaiian Islands and the Central South Pacific (over 70% of studies) with a paucity of traditional ecological studies (N = 9). There was no obvious relationship between the number of studies conducted in a region and its mapped reef area (Fig. 3B, Figure S1). For instance, the South-east Asian Archipelago, which had the largest mapped reef area, had only six studies included in the review (Fig. 3B). In contrast, the Hawaiian Islands, with a relatively small reef extent, contributed 17 studies, almost 90% of which were remote sensing studies (Fig. 3B). Notably, barely any traditional coral reef ecology studies surveyed more than two regions (N = 2), while remote sensing studies frequently covered multiple regions (N = 13) (Fig. 3B, number 28 – "Multiple").

Traditional in-water coral reef ecology studies addressed a wide range of focal questions, but primarily focused on community composition of the benthos, involving a taxonomic level of identification (Fig. 4A). In contrast, most remote sensing studies (72%) were concerned predominantly with benthic mapping, i.e., the classification of substrata into distinctive groups based on spectral signatures, and/or quantifying bathymetry (18%) (Fig. 4A). Numerous studies (18%, N = 20) using in-water remote sensing technologies were bridging this gap in focal questions, increasingly investigating community composition with a taxonomic level of identification similar to that of ecological studies (Fig. 4A, Figure S2). Unsurprisingly, remote sensing studies predominantly (86%) employed primarily sensor-based approaches ranging from satellite imagery to unoccupied aerial vehicles (UAVs) or underwater photogrammetry approaches (Fig. 4B). These approaches were mainly passive, gaining data and producing metrics through imagery processing. In-situ field surveys mostly employed methods that directly quantify or count the presence of organisms (95%) (Fig. 4B). Only 7% (N = 14) of studies used a linked approach combining direct quantification (e.g., counting fish) with, mostly, in-water sensor-based techniques (e.g., photogrammetry), allowing for a more nuanced understanding of processes and higher-order metrics, such as rugosity (e.g., Oakley-Cogan et al. 2020). Notably, only 3% (N = 6) of studies combined multiple approaches (i.e., in water counts, drone imagery and satellite imagery) to upscale observations to an entire reef-scape (Fig. 4B) (e.g., Doo et al. 2017).

Most (73%) remote sensing studies accurately reported the location of their study sites in a manner that allowed for reproducibility (i.e., giving coordinates). Just over half (58%) of traditional coral reef ecology studies did likewise (Figure S3). Overall, 45% (N = 40) and 33% (N = 37) of traditional coral reef ecology and remote sensing studies, respectively, did not specify which geomorphic zone (i.e., back reef, lagoon, reef crest, reef flat, and reef slope/fore reef) their study was conducted on. Of those studies that did specify, geomorphic zones examined by each field contrasted markedly (Fig. 5). The reef slope was the most surveyed habitat (80%) in traditional ecological studies (N = 37), while most remote sensing studies (N = 50) covered entire reef systems (68%) (Fig. 5). Notably, the reef flat, which often accounts for the largest proportion of a reef by area (Yamano et al. 2001; Lutzenkirchen et al. 2023), received relatively little attention by traditional coral reef ecology, with only 30% of studies specifically mentioning this habitat (Fig. 5). While only 14% of remote sensing studies explicitly mention this geomorphic zone,

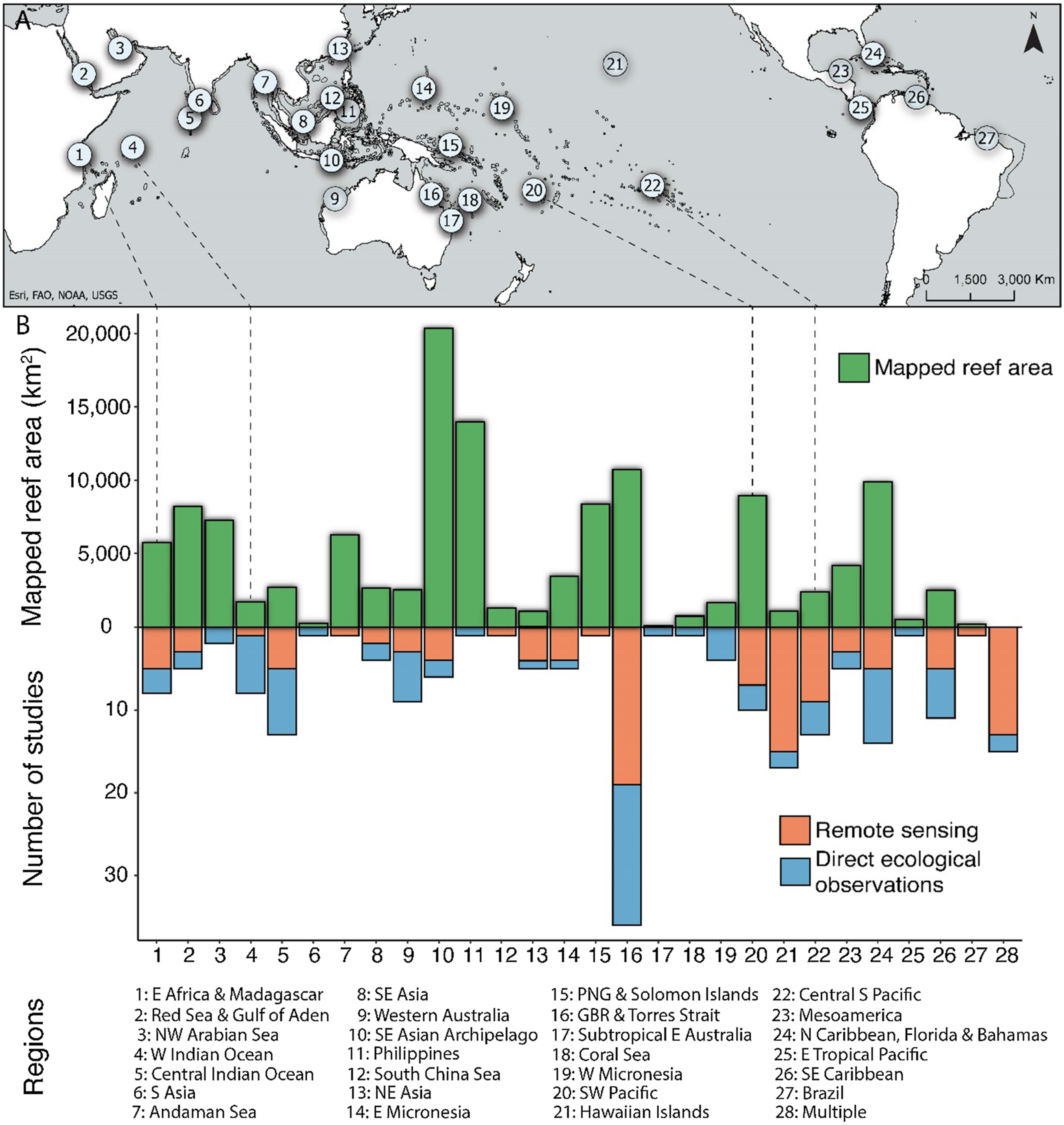

Fig. 3 **A** Map showing the locations of the major reef regions (Allen Coral Atlas 2022). **B** Graph comparing the mapped reef area (km^2) (presenting the mapped area of the benthic classes Coral/Algae, Rock, and Rubble; sourced from Allen Coral Atlas 2022) of each region) to the number of studies included in this analysis from each field. The numbers and corresponding name of each major region labeled on the map are displayed at the bottom

it would be encompassed within the 81% of studies operating across entire reef systems (Fig. 5). In contrast, the smallest of all geomorphic zones on reefs by area, the reef crest (at 3% area), was barely assessed by remote sensing studies (1%) but received moderate attention by coral reef ecologists (26%) (Fig. 5). There were also temporal scale constraints, with most studies being single, one-off studies (62%). Only 38% of all studies from either field included multiple years.

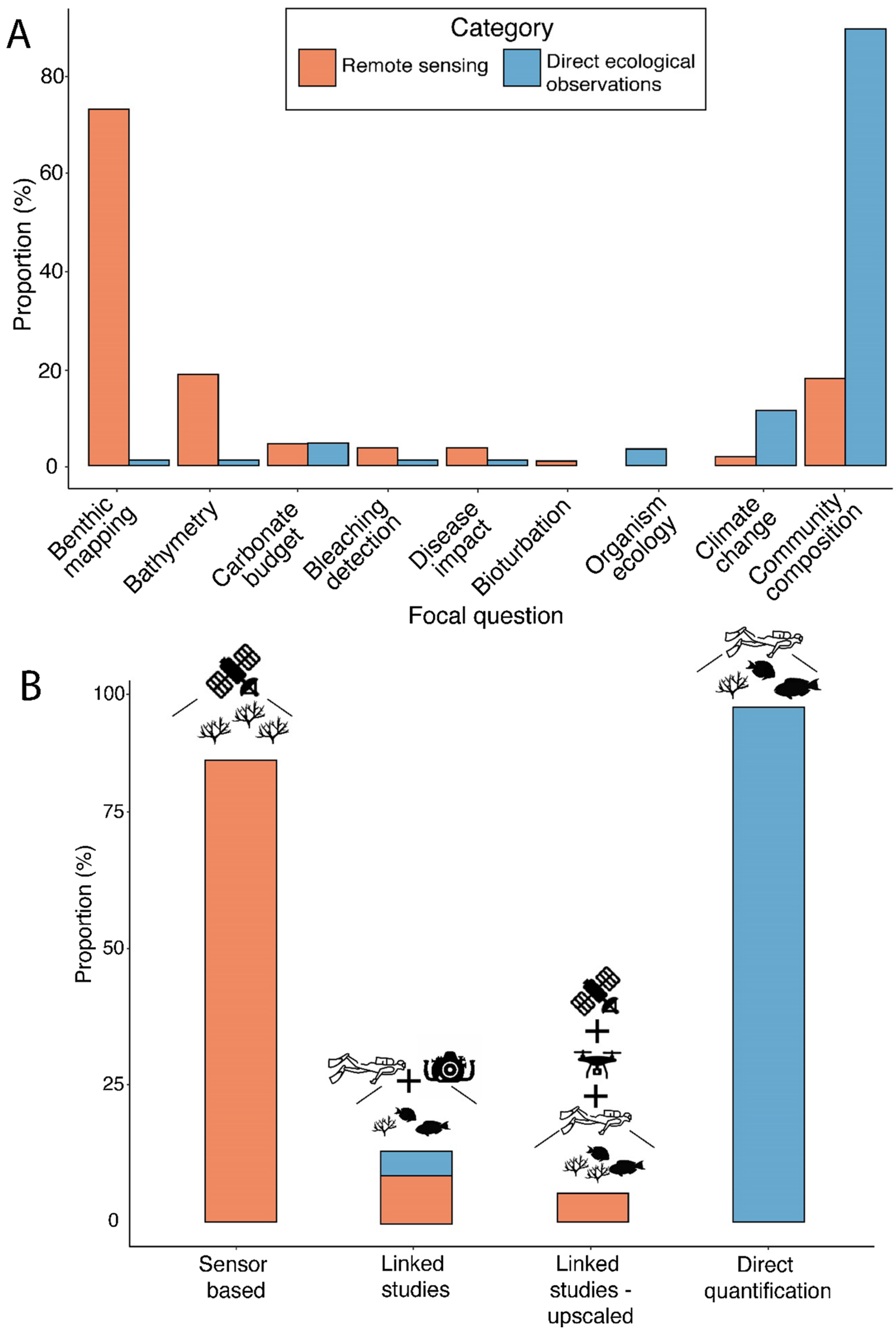

Fig. 4 **A** Proportion (%) of focal questions answered by traditional coral reef ecology studies (blue) (N = 100) and remote sensing studies (orange) (N = 139). **B** Relative proportion (%) of methodological approaches employed by traditional coral reef ecology studies (blue) (N = 88) and remote sensing studies (orange) (N = 112). Note, when studies addressed multiple focal questions, each of these instances was treated as distinct observations in the dataset

Discussion

Unsurprisingly, despite their shared focus on the reef benthos, we found that traditional coral reef ecology and remote sensing studies generally use different approaches and address distinct questions. Integration between the two fields is increasing but to-date there are relatively few studies using a linked approach, that combines in-water and aerial sensor-based methods, to upscale ecological observations to the reef-scape level. While not all coral reef ecosystem functions occur at the reef scale (i.e., across multiple reef habitats), negating the need for wholesale upscaling, this lack of integration to-date shows that our understanding of coral reef systems and their functioning is not easily translatable to larger scales. This is concerning, as threats to these systems are steadily increasing in magnitude. Below, we discuss

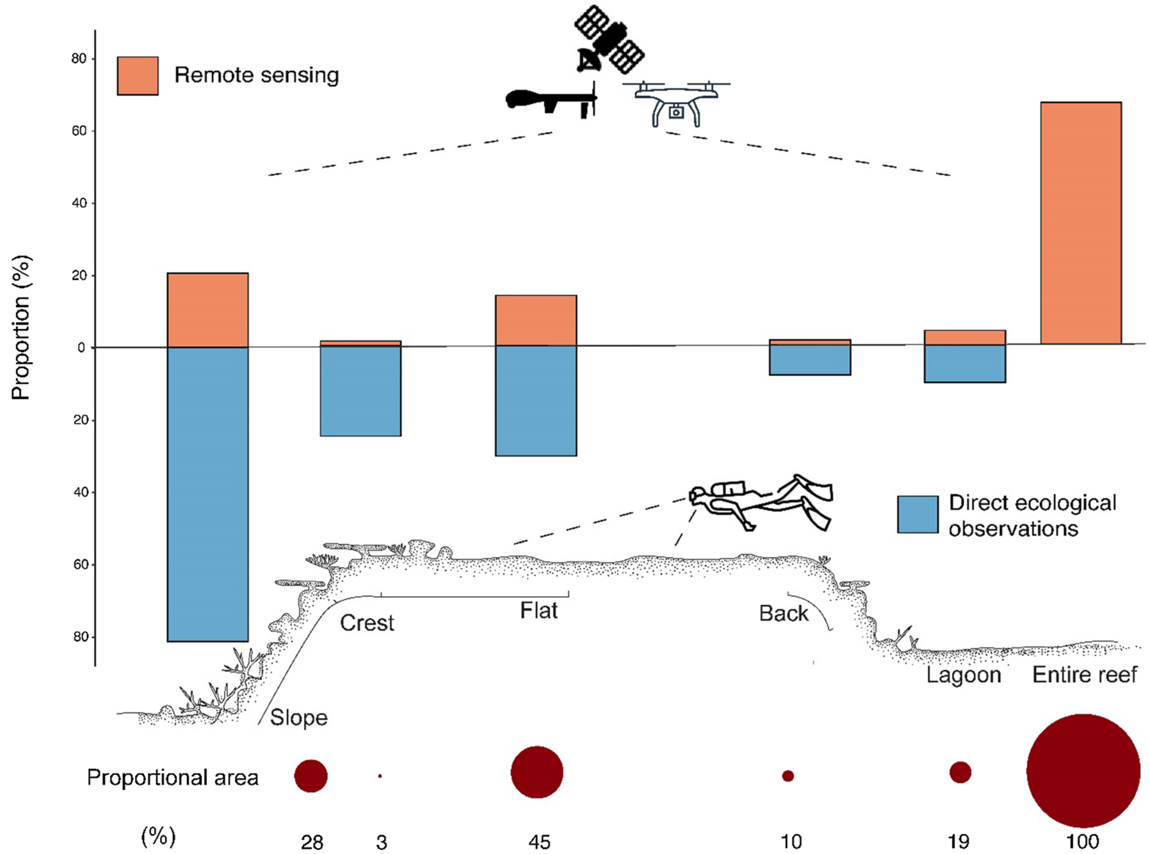

Fig. 5 Comparing the proportion of studies that allocated specific geomorphic coral reef zones as their area of operation from the fields of traditional coral reef ecology (blue) (N = 48, 45%) and remote sensing (orange) (N = 75, 33%). The size of red circles represents the average proportional area (%) of each reef habitat based on the average mapped area of those zones for all reefs of the GBR and Torres Strait as mapped by the Allen Coral Atlas (2022)

the limitations of each field and outline a joint approach for future research and development that could enhance the utility of both fields and provide a basis for positive synergies.

Traditional coral reef ecology

We found that studies in traditional coral reef ecology predominantly employed methods that aim to directly quantify organisms on a very fine taxonomic scale, i.e., genus and species. Such detailed in-situ assessments are valuable to get a high-resolution picture and to make inferences that may help to identify causal relationships and responses to threats (Hughes et al. 2017; Bellwood et al. 2019a). High-detail data enable us to predict the future impact of disturbances on ecosystem functioning in a causal and robust manner, especially at the community and population scale.

However, the greatest problem in upscaling these high-resolution observations is that the delivery of functions by coral reef organisms is not homogenously spread across reef scapes (Streit et al. 2019; Tebbett and Bellwood 2020), emphasizing that there is not one unifying scale at which to measure all processes (Holling 1992; Levin 1992; Wu 2004). For example, detritivory delivered by *Ctenochaetus striatus*, a reef surgeonfish, was shown to occur over less than 28% of the entire reef-scape (Tebbett and Bellwood 2020). Thus, *where* we measure shapes *what* we understand. While certain ecosystem functions may occur at smaller scales and provide insights into broader patterns, measuring in high detail everywhere is impossible. Despite coral reef ecologists' substantial effort to broaden their observations' scope and scale, this review identified that study effort is unevenly distributed both at the reef-scape scale and at global levels. Consequently, as researchers, we need to acknowledge that the scale of our research ultimately constrains the scale of our understanding and predictions.

For example, traditional coral reef ecology studies primarily target the reef slope, a structurally complex habitat, which often supports the highest fish densities and coral cover (Wismer et al. 2009; Oakley-Cogan et al. 2020). While covering less than a third of the total reef area (when measured above 20m depth), the reef slope was the focus of 80% of all traditional coral reef ecology studies that specified a habitat. However, relying on a single site or geomorphic zone to represent an entire reef overlooks critical within-reef variability. A long-term study on Heron Island on the GBR spanning 16 years across 31 sites, including 567 subsites, revealed significant variation at multiple scales, spanning from the entire reef-scale to smaller subsite divisions (Roelfsema et al. 2021a). Accordingly, recent papers have highlighted the constraints placed on our understanding of coral reef functioning by the limited spatial and temporal distribution of study effort, which often focuses on only a limited subset of available shallow reef habitats (Rocha et al. 2018; Bellwood et al. 2020; Collins et al. 2022; Kench et al. 2022; Tebbett et al. 2023a). For instance, we found that the reef flat, which may play a significant role in reef functioning, and is typically the largest reef habitat in terms of area (Bellwood et al. 2018), is often underrepresented in traditional coral reef ecology studies (Bellwood et al. 2020; Tebbett et al. 2023a). In a recent global assessment of coral reef benthic composition change based on 24,000 observations over 22 years, Tebbett et al. (2023a) found that only 7% of the data were derived from reef flat observations. Likewise, less than a quarter of all reef ecology studies included our analysis investigated the reef flat.

Beyond such biases, or selective focus on specific reef habitats, we distinguished regional hotspots of research effort on a global scale. Most coral reef ecology studies took place in a few well-established research areas with existing infrastructure (i.e., research stations), that facilitate effective sampling. These infrastructure patterns may drive local overrepresentation and possibly ecological bias – not because of ecological factors but ease of access (Hedley et al. 2016). In addition, published papers may be biased toward countries and organizations with resources to support publication, potentially overlooking research conducted in nations with more limited financial means. Few ecological studies were able to survey entire reef systems regionally or multiple regions on a global scale.

In sum, these results indicate that traditional coral reef ecology studies are valuable but somewhat limited in their extent and ability to be upscaled, as observations of organisms and their environments are often spatially sparse. They are frequently conducted at scales (spatial, temporal, or thematic) that are chosen subjectively and often dictated by practical factors such as access, time or costs, rather than by the ecosystem processes investigated. These challenges may lead to a considerable mismatch (of an estimated 5.6 orders of magnitude; Estes et al. 2018) between the scales at which ecologists conduct research and the areas their observations are supposed to represent (Wheatley and Johnson 2009; Lecours et al. 2015; Estes et al. 2018). Ecologists acknowledge the disparity between collected samples and the resulting inferences drawn from them. To address this disparity, statistical techniques are frequently employed (e.g., Brown et al. 2021; Castro-Sanguino et al. 2021; Edgar et al. 2023). Nonetheless, the efficacy of a model and its transferability heavily depend on the quality of the underlying data it relies upon (Yates et al. 2018). The potential for substantial enhancement in model performance lies in the improved spatial representation of data. Such enhancement becomes even more crucial when considering the inherent spatial heterogeneity, patchiness, and hierarchical structure within ecosystems. Changes in scale can unveil different drivers of patterns and processes (Wiens 1989; Holling 1992; Levin 1992; Wu and Li 2006). Consequently, the presumption that observations made in a single reef habitat can aptly represent an entire reef-scape can introduce scale-related artifacts. These mismatches between ecological, observational, and analytical scale, ultimately hinder the detection of causal relationships in macroecological patterns (Wheatley and Johnson 2009; Lecours et al. 2015) and the formation of effective management responses (Bellwood et al. 2019a).

If unidentified, such scale artifacts can become widespread and lead to fundamental ecological misinterpretations. We found that most (95%) traditional ecological studies used direct observation techniques which are labor intensive to collect and analyze, while also being limited to restricted spatial and temporal scales. These limitations are likely to cause mismatches among scales. For instance, recently, discrepancies across both temporal and spatial scales have been found to drive the identified occurrence of coral reef phase shifts (Crisp 2022; Crisp et al. 2022). As a result, the reporting of phase shifts in the coral reef literature may have been overrepresented because most studies detecting phase shift occurrences did not persist long enough to capture reverses (i.e., bidirectional change), thus interpreting short-lived blooms as shifts (Crisp et al. 2022). Spatially, the detectability of phase shifts was highly dependent on the scale of sampling, with a decrease in apparent phase shifts as spatial scale increased (Crisp 2022).

Remote sensing

Remote sensing approaches may help to address the problem of scale in ecological coral reef studies (Hedley et al. 2016; Kutser et al. 2020). Unlike traditional in-situ studies, our results show that remote sensing studies can assess entire reef systems, even in remote locations, and can encompass multiple geographic regions globally. Over 60% of remote sensing studies in this review assessed entire reef-scapes, rather than specific reef habitats. This offers the opportunity to evaluate benthic changes across diverse spatial, temporal, and thematic scales (Lecours et al. 2015; Hedley et al. 2016; D'Urban Jackson et al. 2020).

Accordingly, our results show that remote sensing studies have made significant progress in upscaling observations to reef-scape scales by combining approaches and linking methodologies. This progress is driven by advances in medium and high-resolution sensors, such as satellites, and UAVs, as well as in-water photogrammetry studies (Ferrari et al. 2016; Bennett et al. 2020; Roelfsema et al. 2021b; Remmers et al. 2023). The Allen Coral Atlas (2022), a global coral reef mapping project, is an example of recent developments. This project used Planet Dove imagery (3 m pixel resolution) and a 'Reef Cover' classification (Kennedy et al. 2021) to map all coral reef systems on Earth. By using uniformly defined algorithms and classification systems, this is the first to create globally consistent benthic and geomorphic reef classes.

Maps are powerful tools for conveying complex spatial information to diverse audiences (Stieb et al. 2019). While a single map can offer a snapshot of a specific reef or marine community, a series of maps can be an effective monitoring tool to track changes in entire coral reef systems across extended temporal and spatial scales (Hedley et al. 2016; Hamylton 2017). However, only a minority (17%) of the remote sensing studies analyzed in this review employed multiple time steps. Furthermore, to maximize the utility of time-series analyzes, accuracy, i.e., the consistent correct identification of actual features, is key. Ground-truthing fieldwork is commonly used in remote sensing mapping studies to train and validate classification algorithms by conducting georeferenced surveys (Roelfsema and Phinn 2010; Hamylton 2017).

Despite improvements, aerial and satellite remote sensing products are often still limited in their ability to provide an ecological understanding of coral reef systems. Most remote sensing studies are concerned with benthic mapping, but as spatial extents increase, spatial and taxonomic resolution decreases accordingly. Thus, simply mapping broad benthic classes does not measure the ecological status of the benthos (Hedley et al. 2016). Without empirical ecological in-situ data and multiple time steps, they at best, detect changes, not the cause of change, which is key when developing management responses. Furthermore, mapped benthic classes derived through aerial and satellite remote sensing technology are often based on spectral signatures, restricting accurate datasets to shallow reef zones due to the spectral interference of water. Moreover, the spectral similarity of benthic organisms, such as algae and coral, makes it extremely difficult to separate them (Knudby et al. 2010; Kutser et al. 2020). While not specifically assessed in this review, hyperspectral sensors, with their expanding capabilities and the ability to assess a narrower range of spectral bands, hold the potential to enhance discrimination of benthic components (Bajjouk et al. 2019; Dierssen et al. 2021). Beyond spectral limitations, submergence and light attenuation in the water column also pose significant challenges for aerial and satellite remote sensing (Purkis 2018). Despite improvements in sensor capabilities, including global coverage, higher spatial and temporal resolution (Hedley et al. 2016; Kutser et al. 2020), accurately distinguishing spectrally similar substrata in a heterogeneous environment modulated by variable water depth and quality remains a major challenge (Lucas and Goodman 2015; Purkis 2018). Even moderate-spatial and high-spatial resolution sensors are often unable to reliably differentiate benthic groups, such as algae and hard coral. As a result, aerial and satellite remote sensing studies have difficulty detecting the main ecological transformation on coral reef systems (i.e., algae to/from coral; Tebbett et al. 2023a) (cf. Cornet and Joyce 2021). This predicament is reflected in the distribution of focal questions identified herein. While most traditional in-water ecological studies address community composition, possibly elucidating the response of individual species or groups to environmental variables, most remote sensing studies employing aerial sensors are currently limited to mapping broad benthic classes (i.e., coral and/or algae as one class). Consequently, there is a mismatch between aerial and satellite remote sensing data sets, and the eco-physiologically based demands of potential end users (i.e., ecologists and reef managers) (Kutser et al. 2020).

To establish a functional and mechanistic understanding of coral reef systems and their changes, integrating remote sensing studies with empirical ecological in-situ data is essential. This gap is being effectively bridged using relatively new techniques, particularly in-water photogrammetry, which plays a crucial role in expanding quantitative data on structural complexity (Friedman et al. 2012; Figueira et al. 2015; Ferrari et al. 2016; Pygas et al. 2020; Remmers et al. 2023). These techniques actively leverage in-water remote sensing technology to unite ecological observations with advanced tools, promising a more comprehensive and holistic comprehension of intricate ecosystems like coral reefs. However, comparable links at larger extents afforded by aerial and satellite remote sensing, remain elusive.

Future directions

As human-induced stressors continue to reshape ecosystems, coral reefs are particularly vulnerable (Hughes et al. 2017; Bellwood et al. 2019a; Woodhead et al. 2019). To understand and manage these fragile ecosystems in the Anthropocene, we may benefit from novel approaches and the integration of scientific disciplines (Dornelas et al. 2019; Williams et al. 2019). Indeed, as threats escalate in scale, it is essential to establish dynamic relations and to upscale observations by combining multiple tools that vary in scale and resolution (Dornelas et al. 2019).

Below we identify approaches that may enable us to harness the best of both traditional coral reef ecology and remote sensing fields, offering the greatest potential to address the scale mismatch between coral reef research and anthropogenic threats by rapidly upscaling observations and inferences. Shallow reef environments (i.e., reef flats and crests) offer the optimal habitats for these upscaled studies as they impose the fewest limitations for aerial and satellite remote sensing (Hedley et al. 2016; Purkis 2018; Kutser et al. 2020). Furthermore, these habitats are ecologically critical (Kench and Brander 2006; Bellwood et al. 2018), yet are often underrepresented in coral reef ecology studies (Bellwood et al. 2020; Kench et al. 2022; Tebbett et al. 2023a). To understand coral reef ecosystem functioning on regional and global scales, in-situ measurements, which provide the finest detail but present multiple trade-offs and a lack of scalability, need to be linked directly (in space and time) with multiple sensors that are less detailed in resolution but offer effective and continuous large spatial coverage (Fig. 6) (Calders et al. 2020).

For effective cross-scale work, combining ground-truthed remote sensing with high-detail ecological observations in shallow reef settings, like inner and outer reef flats, is crucial. To ensure accurate benthic maps from moderate to high-resolution (< 3m) satellite imagery, georeferenced images could be taken along transects or quadrats, estimating benthic structure and organism abundance in-situ (e.g., Roelfsema et al. 2021b). Several studies have successfully upscaled in-situ ecological measurements via remote-sensed benthic maps (e.g., Doo et al. 2017; Hamylton et al. 2017; Williamson et al. 2021) (Fig. 6). This approach appears to be particularly promising with the possibilities to expand on these concepts, combining the strengths of both fields for ongoing cross-calibration between sensors and upscaling of ecological observations to large reef-scape scales (Fig. 6). These methods involve "small-area-high-resolution" in-situ observations and in-water technologies (< 1cm resolution) across shallow reef sites to provide ecological context and ground-truthing, ensuring accurate delineation of key benthic components and data reliability (Fig. 6A, B), while recent "large-area-lower-resolution" (< 3m) imagery and mapping methods further enhance the reliability of upscaling ecological observations and novel metrics (Fig. 6C).

While combining these approaches will ensure more empirically linked upscaling onto larger reef-wide scales, the utility of each approach may be enhanced by:

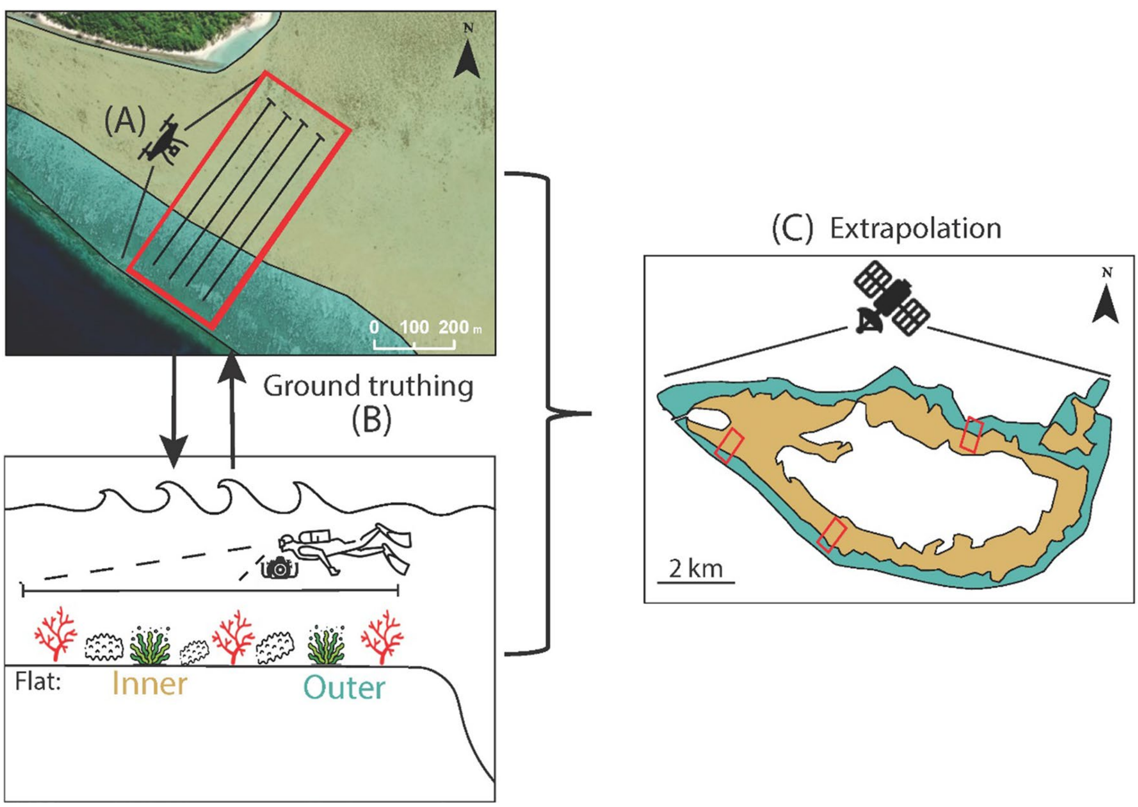

Fig. 6 Schematic summary outlining a potential approach using in-situ assessments, as well as multiple layers of sensors of varying resolution, to bridge scientific disciplines and upscale observations onto reef-scape scales. After multiple shallow reef areas are surveyed using a 'small-area-high resolution' sensor (**A**) and ground-truthed using in-situ assessments and sub-cm resolution in-water remote sensing technology (**B**), observations can be extrapolated and upscaled using a 'large-area-lower-resolution' sensor (**C**). Geomorphic map in (C) taken from (Phinn et al. 2012)

1. Standardizing procedures in coral reef ecology to enhance data reproducibility, facilitating robust comparisons across scales and disciplines. While local and regional ecological monitoring protocols may be standardized, global standardization will improve comparability. The MERMAID project (https://datamermaid.org/), an open-source application that gathers and manages real-time coral reef health data, provides an example of this approach. However, existing long-term benthic databases such as Caribbean Coastal Marine Productivity or National Oceanic and Atmospheric Administration lack uniformity, hindering cross-validation, particularly for finer-resolution benthos categorization (Tebbett et al. 2023a, 2023b). Consolidating these datasets under a common protocol would increase the value of data for training and validation of remote sensing mapping algorithms (Lyons et al. 2020).
2. The reliable recording and reporting of survey sites is crucial to data sharing and study replication. Therefore, including the survey start location using global positioning system (GPS) and indicating the direction of the surveys would significantly improve the spatial accuracy and reproducibility of ecological studies.
3. Technological advances, especially in the field of remote sensing, have opened numerous new frontiers in the marine realm. However, moving forwards, we need to ensure that new techniques are responding to critical questions. Despite increasing spatial resolution, current methodological advances are largely used for the same applications. To fully harness the capacity of recent technological innovations and advance our understanding of coral reef functioning in the Anthropocene, we must ensure that critical questions are being addressed and that technology is being developed to address these key questions, rather than retrofitting questions to new tools. We need to move beyond traditional studies that describe patterns to a deeper understanding of the functional and mechanistic basis of change. Integrating remote sensing and coral ecology studies may not directly yield causal insights. However, it has the potential to enhance our comprehension of complex relationships (Wedding et al. 2019). This integration, particularly when spatially explicit, can offer insights into seascape dynamics.
4. Just as certain parameters of coral biology, such as coral respiration, can only be accurately measured in controlled laboratory experiments, with specialized equipment, there are certain parameters of coral reef processes that cannot be reliably measured using broadscale remote sensing methods, no matter how advanced the technology becomes. For instance, discerning fine-scale rugosity (< 1 m) of coral colonies or distinguishing between live corals and dead corals coated in filamentous algae can be challenging using aerial and satellite remote sensing data, often necessitating optimal conditions. Therefore, it is crucial for coral reef ecologists, biologists, and remote sensing scientists to collaborate and develop new and meaningful indicators or proxies for coral reef processes that are applicable to both remote sensing and ecological methods and that operate at shared scales. Recent success has been shown in employing high-resolution (< 1 m) airborne sensors such as LiDAR to accurately describe broadscale coral habitat complexity (Asner et al. 2020; Harris et al. 2023). Furthermore, the utilization of automated image annotation for coral reef monitoring, which demonstrates accurate estimations of benthic abundance with a high agreement of 97%, significantly expedites data analysis by over 200 times and reduces costs by 99% (González-Rivero et al. 2020). Approaches like these enable the translation of detailed in-water measurements to broadscale remotely sensed methods with increased accuracy and relevance.
5. To advance our understanding of ecosystems and their vulnerability in the Anthropocene, increased public availability of datasets is crucial (Calders et al. 2020). However, despite the benefits of open science, data sharing lacks incentivisation and it is often perceived to have potential negative ramifications (Perrier et al. 2020; Gomes et al. 2022). To promote public availability of datasets, data source citations in perpetuity, a growing component in the field of remote sensing, as well as open-source databases such as MERMAID, could provide incentives that would ensure collaboration, promotion, recognition, and reward. Without these incentives, the collection of new data is likely to be impeded.

Overall, our review of studies investigating the benthic habitat of shallow water tropical reefs suggests that a gap exists between traditional coral reef ecology and remote sensing studies. Although advances have been made, especially through in-water photogrammetry, drones, and high-resolution satellite mapping, a more concentrated approach is recommended to effectively bridge this gap, especially at large scales. Coral reef ecologists rely on detailed observations that may not match the spatial scale needed for robust, broadly applicable inferences about complex and dynamic relationships within seascapes. Bound by logistical challenges and resource-intensive high-detail data, they often focus on a subset of habitats, inevitably creating scale artifacts. Remote sensing studies can supply continuous datasets across a range of scales and broader extents, offering a potential way to assess and study the scale of changes in the Anthropocene. However, they need ongoing spatially and temporally matched ecological data to ground-truth observations, ensure accuracy, and start the process of exploring mechanistic explanations for change. As anthropogenically caused stressors continue to escalate in scale, our study suggests that bridging these two scientific disciplines will be challenging but offers promising ways to upscale observations to entire reef-scape scales. We identify potential avenues for increasing the utility of each field, recognizing limitations and emphasizing collaborative approaches. In a world characterized by intensifying global change, such bridged approaches, integrating multiple tools at varying levels of resolution and scale, will be crucial to advance our understanding and management of coral reef functioning in the Anthropocene.

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Declarations

Competing interests The authors have no competing interests to declare.

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