On the Challenges of Identifying Benthic Dominance on Anthropocene Coral Reefs

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The concept of dominance is frequently used to describe changes in rapidly reconfiguring ecosystems, but the definition of dominance can vary widely among studies. Using coral reefs as a model, we use extensive benthic composition data to explore how variability in applying dominance concepts can shape perceptions. We reveal that coral dominance is sensitive to the exclusion of key algal groups and the categorization of other benthic groups, with ramifications for detecting an ecosystem phase shift. For example, ignoring algal turf inflates the dominance of hard and soft corals in the benthic habitats underpinning reef ecosystems. We need a consensus on how dominance concepts are applied so that we can build a more comprehensive understanding of ecosystem shifts across a broad range of aquatic and terrestrial settings. For reefs, we highlight the benefits of comprehensive and inclusive surveys for evaluating and managing the altered ecosystem states that are emerging in the Anthropocene.

Keywords: algal turf, benthic dominance, coral reef, macroalgae, phase shift

The concept of dominance has been discussed by ecologists for decades (McNaughton and Wolf 1970). In classical terms, *dominance* can refer to a relationship between individuals, where a subordinate defers to the dominant in situations such as contests (Kaufmann 1983). However, in ecological research, the term is also widely used when referring to the numerical prevalence of organisms in a community (Hart 1990, Hillebrand et al. 2008, Lohbeck et al. 2016), with numerous definitions and approaches for capturing this concept suggested over time (McNaughton and Wolf 1970, Ma and Ellison 2018). Increasingly, the notion of dominance has taken center stage in ecological circles as the world's ecosystems rapidly reconfigure in response to a growing range of anthropogenic stressors, with consequent changes in the relative abundance of different organisms (Klanderud and Totland 2005, Bruno et al. 2009, Vaughn 2010, Ling et al. 2015). This carries important implications for our understanding of ecosystems, because, if the dominant organisms in ecosystems alter, this could have substantial ramifications for how these ecosystems function, as well as their capacity to support the services on which people depend (Hillebrand et al. 2008, Lohbeck et al. 2016, Genung et al. 2020).

The application of dominance concepts has been particularly prevalent on the world's coral reefs. In these productive, shallow-water ecosystems a range of different organisms,

spanning a plethora of taxonomic groups, occupy the benthos, and contribute to the processes operating in these ecosystems (Brandl et al. 2019, Reverter et al. 2022). However, coral reefs are also among some of the most threatened ecosystems in the world, because a range of stressors from local to global scales act on them (Hughes et al. 2017, Andrello et al. 2022). In response to these stressors, coral reefs have experienced some of the most striking examples of ecosystem transformations (Gardner et al. 2003, Bellwood et al. 2004, Bruno and Selig 2007), with phase shifts between alternative configurations representing a severe form of change (Done 1992, Hughes 1994, Graham et al. 2015). Indeed, the collapse of coral reefs from coral-dominated to macroalgae-dominated configurations has become one of the archetypical examples of ecosystem decline within the broader ecological literature (e.g., Scheffer and Carpenter 2003, Folke et al. 2004, Conversi et al. 2015) and remains a prime example of change in coral reef research (e.g., Hughes et al. 2003, Bellwood et al. 2004, Mumby et al. 2007, Graham et al. 2015). However, at the heart of studies examining phase shifts and coral reef decline lays the concept of dominance, with this concept forming the foundations of phase shift definitions (for a review, see Crisp et al. 2022).

The literature concerning dominance on coral reefs, and our subsequent understanding of this concept, is far from

clear. For example, although the epitome of "healthy" or "pristine" coral reefs is still generally taken to be a coral-dominated state (Hughes et al. 2017), numerous studies have suggested it to be a "dangerous misnomer," with healthy seascapes composed of a range of benthic taxa (e.g., different types of algae and filter feeders; Vroom et al. 2006, Vroom 2011, Bruno et al. 2014, Smith et al. 2016). Moreover, a growing body of literature has suggested that, as coral cover declines, reefs may be increasingly dominated by the other benthic organisms, such as sessile invertebrates, including sponges and ascidians (Norström et al. 2009, Bell et al. 2021, Reverter et al. 2022). This variability in perspectives may, however, be heavily shaped by variation in how we approach the calculation of dominance, as well as how we classify abundant but often overlooked benthic components (e.g., grouping crustose coralline algae, algal turf, and bare space into a CTB category). Invariably, this draws into question the utility of dominance as a concept. Furthermore, if this concept is sensitive to variation in its application, one must ponder how applicable this concept is when trying to understand change on Anthropocene coral reefs. Unfortunately, what we mean by dominance on coral reefs, how we approach its quantification, and how this could subsequently shape our understanding of coral reefs, remains poorly resolved.

What is dominance on coral reefs?

In coral reef research, we are far from a universally accepted definition of *dominance*. Indeed, the following thoughts of Vroom (2011) remain as true today as they did over a decade ago: "Is coral dominance: (1) a state where corals cover more than 50% of the substrate, (2) a state where, out of the numerous organisms that occur in reef settings, corals occupy a greater percent[age] of the substrate than any other type of organism (even though the actual percent[age] cover of coral may be low), or finally (3) a state where corals occupy a greater amount of substrate than only a select group of organisms (e.g., macroalgae)?"

Although we may not have a universally accepted definition of dominance, in the majority of recent literature (including in most studies on phase shifts on coral reefs; for a review, see Crisp et al. 2022), dominance aligns most closely with the second definition of Vroom (2011). That is, dominance is taken to be the most abundant benthic category (on the basis of percentage cover). This is the definition that we used in our assessments of dominance as a concept below. Importantly, because the measurement of percentage cover is ubiquitously used in coral reef monitoring globally (e.g., Aronson et al. 1994, Hill and Wilkinson 2004, Obura et al. 2019), our examination of dominance based on this definition may have far reaching implications for the understanding of coral reef change. However, this may be a problem for a high diversity ecosystem, where the most prominent benthic categories can occupy a small percentage of the space. Moreover, this definition of dominance will depend on what benthic groups we include or exclude

in the calculation and on how we classify benthic organisms and substrata on the reef.

To explore how sensitive our perceptions of dominance (based on the most abundant benthic category) might be to the inclusion or exclusion of different benthic categories, we used a global data set of 23,444 observations of complete benthic cover (i.e., 100% of reef cover) on coral reefs between 30 degrees north and 30 degrees south (figure 1a). This data set was compiled from six major publicly available databases, as well as a formal search of the literature (see supplemental text S1 and supplemental figures S5–S9 for full details). It should be noted that the sample sizes of data varied between sources and ocean realms (supplemental figures S6 and S9). Although this variability has the potential to shape results it is unlikely to have a major influence, especially given the large overall size of the data set and the fact that examination of subsets of the data (which were based on sample sizes approximately two to eight times smaller than the full data set) produced similar patterns as the full data set (see figures 1 and 2), suggesting our subsequent inferences are robust. The full benthic composition data set was composed of six benthic categories routinely included in surveys (hard corals, macroalgae, soft corals, other benthic organisms, sand, and a conglomeration of categories that represent surfaces generally covered by low-lying algae or cyanobacteria, such as turf and crustose coralline algae (i.e., crustose coralline algae, turf algae and bare space; see text S1 and supplemental figures S5–S9 for details). Where it was necessary, data were pooled into these benthic categories, and means were calculated for unique geographic coordinates within the same sampling year, depth, and habitat.

On the basis of these data, we could determine the most abundant benthic categories and recalculate this on the basis of the exclusion of certain groups (see supplemental text S2). For example, because sand is often considered an abiotic component of the benthos it may be excluded from calculations of all biotic categories (e.g., Alevizon and Porter 2015, Steneck et al. 2019, Reverter et al. 2022). After sand, the CTB category may be excluded (e.g., Reverter et al. 2022) because it is often poorly classified. Indeed, the CTB category is composed of components such as rock, dead coral, and rubble and is, therefore, frequently considered as an abiotic component of the reef (e.g., Leujak and Ormond 2007, Marcus et al. 2007, Sommer et al. 2011, Facon et al. 2016, Brown et al. 2017). However, it is critical to note that there is no such thing as bare space on a reef, and these "abiotic" categories are almost invariably covered by some form of biofilm or algae, particularly algal turfs (Smith et al. 2016, Wolfe et al. 2021).

Our exploration of the relative dominance of benthic groups revealed that excluding abiotic or poorly defined benthic categories inflates the perception of dominance of corals on reefs (figure 1). When all groups were included, hard corals represented the dominant benthic category (i.e., most abundant) in 9% to 41% of observations from each realm, with CTB being the dominant category in most cases
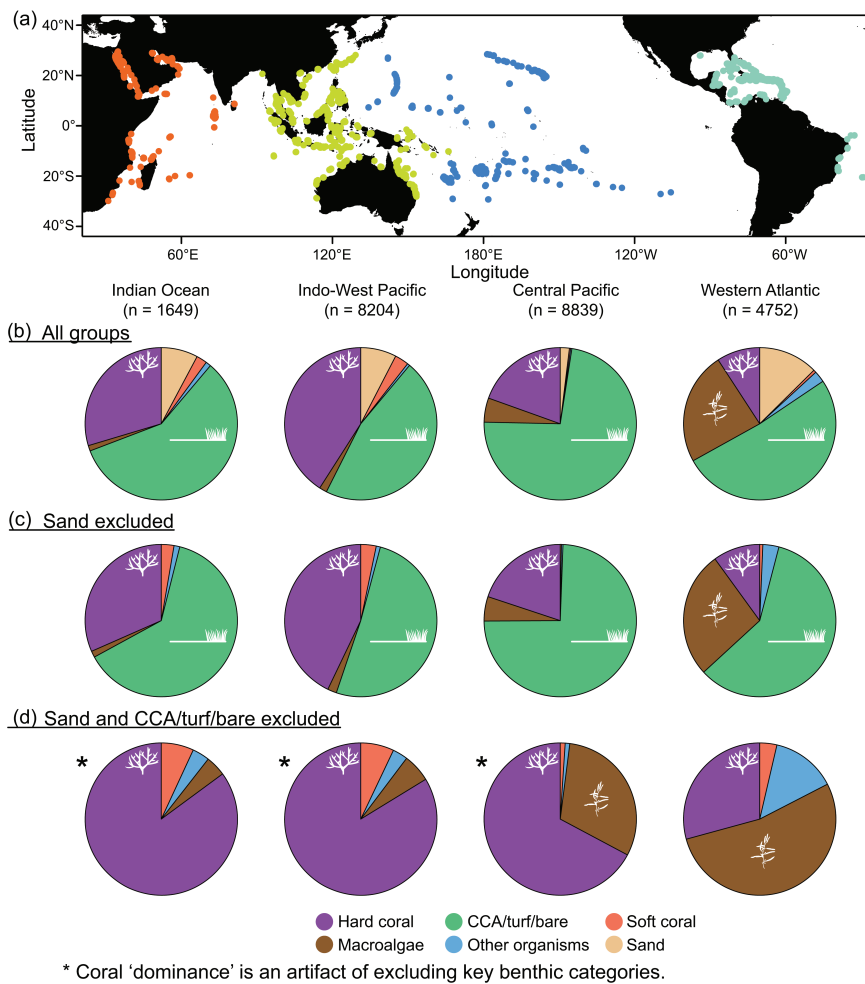
Figure 1. Variation in the relative dominance of different benthic components based on the inclusion or exclusion of categories. (a) The global distribution of the 23,444 coral reef benthic composition observations across four major coral reef realms, which are delineated by different colors. The relative dominance of benthic components when (b) all six categories were considered, (c) sand was excluded from calculations, and (d) when sand and the category composed of crustose coralline algae (CCA), algal turfs, rubble and "bare" substrata was also excluded. For the variation of dominance across habitats and through time, see supplemental figures S1 and S2.

of observations; figure 1). The exclusion of the CTB category also inflated the relative dominance of soft corals and other organisms (figure 1). Importantly, this inflation may lead to conclusions that organisms such as soft corals are relatively more abundant or dominant on reefs than is the case. Evidently, in this case, coral dominance was a product of removing a large proportion of the benthos from consideration.

Given the sensitivity of dominance calculations to the exclusion of benthic categories, this raises the question of whether such exclusion can be justified ecologically. In short, we posit that it cannot. The principal reason behind our conclusion is that the coral reef benthos is not composed of a subset of components. Instead, the coral reef benthos is composed of a range of interacting components all competing for limited space. Excluding components of the reef biases perceptions, enhancing subsets of the benthos that may not be that abundant in absolute terms (e.g., soft corals or other organisms) while overlooking benthic categories that may be very abundant and important in ecological processes. For example, removing the CTB category would exclude surfaces driving key functions such as productivity (Hatcher 1988, Klumpp and McKinnon 1992) and calcification (Adey 1998, Kench et al. 2022). Evidence of this oversight is seen in how poorly the CTB category has been quantified and categorized on coral reefs at a global scale (for a discussion, see Smith et al. 2016, Tebbett et al. 2023). However, given the sensitivity of dominance to the inclusion of the CTB benthic category it warrants further assessment of how the concept of dominance holds up to finer divisions of algae in this CTB category.

(figure 1b). This suggests that large areas of "coral" reefs are occupied by inconspicuous and poorly identified groups of algae that are often combined. Excluding sand from the analyses resulted in negligible changes to the relative dominance of benthic categories across most ocean realms. Although, an exception was the Western Atlantic, where excluding sand resulted in an increase in dominance from 51% to 59% of observations for the CTB category (figure 1c). By far the largest effect on how we perceive dominance on coral reefs resulted from the exclusion of the CTB category (figure 1d). This inflated the relative dominance of hard corals that now appeared to dominate across all Indo-Pacific Realms (67%–85% of observations), with macroalgae apparently dominating the benthos in the Western Atlantic (53%

The role of algae classification in dominance

Despite different types of algae (a term inclusive of cyanobacteria, which are not true algae) having been recognized as pivotal components of reef ecosystems for decades (Odum and Odum 1955, Adey 1998), they have typically received less research attention than hard corals. This longstanding neglect has resulted in algae often being lumped into an all-encompassing algae category (e.g., *Status of Coral Reefs of the World* report; Souter et al. 2021). However, the wide diversity of algal forms interact with corals and other organisms differently (McCook et al. 2001, Birrell et al. 2008) and have
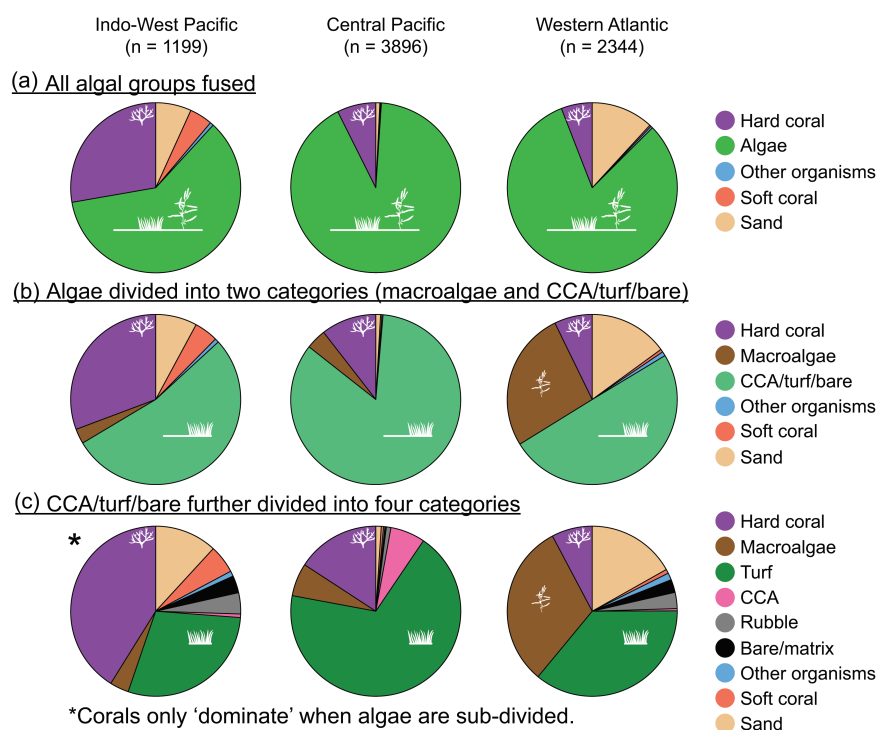
Figure 2. Variation in the relative dominance of different benthic components based on differences in algal classification across 7439 observations of benthic composition across three major coral reef realms. The relative dominance of benthic components when (a) algae was grouped in a single all-encompassing category, (b) algae was divided into macroalgae and a category composed of crustose coralline algae (CCA), algal turf, rubble and "bare" space (CCA/Turf/Bare), and (c) when the components of the CCA/Turf/Bare category were divided into four individual categories. Note the increase in coral dominance as algae are subdivided occurs because dominance is based on the most abundant category so the finer division of algae waters down the chance of any one algal category being considered dominant. Also note the Indian Ocean realm was not included because of a paucity of data. For the variation of dominance across habitats and through time, see supplemental figures S3 and S4.

Indo-West Pacific, Central Pacific and Western Atlantic, respectively) that had separate categories for algal turf, CCA, rubble and a bare space or recently dead coral or matrix category (see supplemental text S3 and figure S9 for details). This represents approximately a third of the available data, emphasizing the large number of surveys that pool these categories (note the data set would have been even smaller—$n = 737$ observations—if we only included data from monitoring schemes with no spurious categories, such as dead coral, that are also likely to be covered in these algae; see text S3 for details). By relying on this subset of data we explored how our perceptions of dominance would be changed by different schemes for the classification of CTB algae. This exploration included a single all-encompassing algae category, two algal categories (macroalgae and CTB), and then a five-category scheme (macroalgae, algal turf, CCA, rubble, bare or matrix; see supplemental text S4 for details). Importantly, we did not change the categorization of other benthic groups, even though the finer division of algae would be equivalent to also separating hard corals into separate groups on the basis of their morphology and thereby decreasing the likelihood of corals being detected as dominant. Once again, dominance was taken to be the most abundant benthic category, as it was above.

By treating algae as a single group, between 60% and 92% of all observations made on reefs would consider them to be algae-dominated systems (figure 2a). In contrast, coral-dominated reefs ranged from just 6% to 28% of observations in each realm. The division of algae into two groups (macroalgae and CTB) resulted in minor changes in dominance, with these two groups together accounting for 56% to 88% of observations across realms, although the CTB category alone was overwhelmingly dominate in all realms (figure 2b). The maximum increase in coral dominance was just 3% of observations on Central Pacific Reefs. Importantly, our five-category scheme for algal groups again suggested that one of the algal groups was dominant on reefs in 41% to 82% of observations in each realm (figure 2c). Because dominance was based on the most abundant category, these finer divisions of algae led to an increase in coral dominance (figure 2c). The maximum increase in coral dominance occurred in the Indo-West Pacific from 31% to 41% of observations. This is interesting because in this scheme of

varied functional roles (Steneck and Dethier 1994, Fulton et al. 2019). From the different algal functional forms, however, fleshy erect macroalgae (e.g., Sargassaceae, Dictyotales) has received growing attention in the literature because of its association with phase shifts (Hughes 1994, Bellwood et al. 2004) but also as an important habitat in tropical ecosystems (Fulton et al. 2019, 2020). However, other functional groups such as algal turfs and CCA are still often overlooked in benthic monitoring schemes with their classification remaining highly variable or with precedent often being given to the substrata they cover (e.g., rock, dead coral, rubble; for a discussion, see Smith et al. 2016).

Because of the poor resolution of algal categorization in the literature, it was necessary to use a single category (CTB) for the full global-scale comparison. However, to assess how sensitive dominance could be to more nuanced classification of these algae, we used a subset of the data ($n = 7439$ observations; $n = 1199$, 3896, and 2344 in the

five algal categories the chance of any algae being dominant had been watered down substantially, but a group of algae (or a substratum likely to be covered by algae or a biofilm or cyanobacteria) was still dominant in most cases (figure 2c). Furthermore, it is particularly interesting to note the overall prevalence of algal turfs on reefs, especially in the Central Pacific (figure 2c). Clearly, this benthic group of algae (algal turfs) disproportionally covers a substantial area of benthic space in coral reef ecosystems.

Our examination of the sensitivity of dominance calculations to algal categorization supports earlier research that suggested algal groups are often the most abundant component of coral reefs (Vroom et al. 2006, Vroom 2011, Bruno et al. 2014, Smith et al. 2016). Furthermore, despite treating other organisms as a single group in our examination (which maximized the chance of this group being considered dominant), the data suggests that, when the reef benthos is viewed in its entirety, these organisms are generally only a minor component compared with algae (figures 1 and 2). It is only when the benthos likely to be covered in algal turfs and crustose coralline algae is excluded entirely from dominance calculations that these other organisms emerge as more prominent components of reef dynamics (figure 1). Indeed, studies that have documented increases in these other organisms often still find that they only cover relatively small areas, with absolute benthic cover being low compared with groups such as algal turfs (Norström et al. 2009, Tebbett et al. 2019, Bell et al. 2021). Clearly, our perceptions of the benthic components that dominate reefs has the potential to be heavily skewed by how we categorize the benthos and, particularly, how different algal groups are treated in terms of their inclusion in calculations.

What do changes in dominance mean?

Invariably, the sensitivity of dominance to calculation approaches raises questions about the use of this concept in understanding reefs and associated change in the Anthropocene. In this respect, the notion of dominance lies at the heart of phase shift concepts, with the occurrence of these shifts requiring a change in the dominant benthic category on a reef (for a review, see Crisp et al. 2022). To explore this type of change in more detail, we interrogated the high-resolution algal data, as we did above, to explore the relative frequency of shifts in dominance between hard corals and two key groups of algae (macroalgae and algal turf) at the same locations (see supplemental text S5 and supplemental figure S10 for details). We also set different thresholds to explore the magnitude of this change in dominance. Specifically, we set thresholds that meant the difference in cover between the groups had to be at least 10% or 25% of the benthos before and after the change in dominance occurred (as above, dominance reflected the most abundant category). This was to ensure the change in dominance was associated with a substantial change in benthic cover rather than just minor fluctuations (e.g., a decrease in hard coral

cover from 40% to 39% and an increase in algal turfs from 39% to 40%).

By considering changes in dominance at the same location through time, the data suggested that changes from hard corals to algal turfs occurred relatively frequently (19% of sites; figure 3a). In contrast, changes in dominance from hard corals to macroalgae were relatively rare (just 2% of sites; figure 3a). However, these conclusions were found to be sensitive to the two different thresholds (figure 3b, 3c). Indeed, it appeared most changes in dominance represented minor changes in benthic cover, rather than reflecting substantial change (figure 3). This is particularly interesting given that there is currently no agreed threshold in the phase shift literature that defines when a change in dominance should be considered substantial (for a review, see Crisp et al. 2022). In reef research, we frequently perceive a change in dominance to represent a substantial change in benthic composition. However, without an agreed threshold for a major change in benthic dominance, the data suggest that changes in dominance alone are not particularly meaningful (figure 3). Considering persistence and trends through time (e.g., Graham et al. 2015), as well as direct consideration of potential drivers (e.g., Arif et al. 2022), may account for some of these issues.

The other interesting point that emerged from this examination of changes in benthic dominance was the fact that shifts from algal groups to hard corals were not as rare as one might expect. Importantly, although this does not necessarily contrast previous literature on coral cover decline (e.g., Hughes 1994, Bellwood et al. 2004, Jackson et al. 2014, Tebbett et al. 2023), because shifts from coral to algal turf dominance were still more common (figure 3), it does suggest that shifts to coral dominance can still occur. Interestingly, this also aligns with results from a recent assessment of potential phase shifts using independent long-term monitoring data from Australia's Great Barrier Reef (Crisp et al. 2022). The expectation that shifts from algae to coral dominance are exceedingly rare could be due to the fact that virtually all past studies of phase shifts on coral reefs focused on a reef location that was initially dominated by corals (for a review, see Crisp et al. 2022). Therefore, in most cases, change in this past research could only take one direction (i.e., a decline in coral dominance). This raises an interesting point about our approach to monitoring coral reef change. Rarely are studies focused on habitats initially dominated by algae, where there is a larger chance of documenting a phase shift to corals (but for examples of topicalization on temperate reef from algae to corals, see Vergés et al. 2014). Moreover, it is important to note that seasonal variability may also shape how we perceive dominance as a given location could appear coral-dominated in winter or algal-dominated in summer, if seasonal canopy forming macroalgae are present in that location (Schaffelke and Klumpp 1997, Fulton et al. 2014). Therefore, it could be that changes from algae to hard coral dominance can occur relatively frequently and that our focus on declines in coral
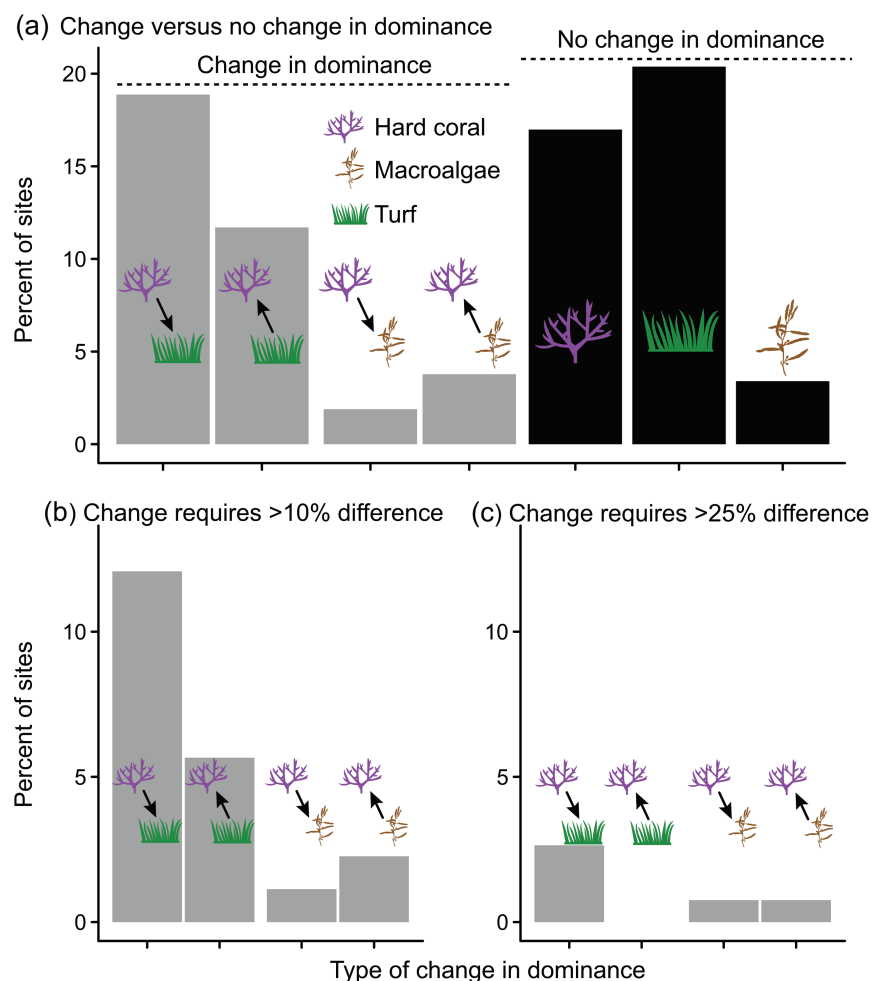
Figure 3. The frequency of changes in benthic composition on coral reefs. (a) The relative frequency by which 265 reef sites shifted between dominance by hard corals versus either macroalgae or algal turfs, as well as the relative number of sites that were consistently dominated (i.e., no change detected) by specific benthic components. The relative number of sites where a change in dominance occurred and the difference between the benthic groups was at least (b) 10% and (c) 25% of benthic cover both before and after the shift in dominance occurred.

dominance may have resulted in a partial understanding of reef dynamics and reef change in the Anthropocene.

Looking forward and conclusions

By exploring the concept of dominance, the data suggests that there are several conceptual pitfalls that could lead to substantial variability in how we perceive change on coral reefs. Given the sensitivity of conclusions to how dominance concepts are implemented, and the current lack of any consensus about how to approach dominance calculations for the coral reef benthos, the future of dominance-based assessments needs to be evaluated. At the very least, our evaluation suggests applying the concept of dominance to coral reef benthic data should be performed with caution. Careful consideration needs to be given to which benthic groups

are included and at what level benthic categories are categorized or pooled to ensure they are comparable across broad taxonomic groups such as corals and algae. In this respect, it appears prudent to consider the coral reef benthos in its entirety because coral reef functioning is not based on a subset of benthic components but is instead based on the entire ecosystem. Indeed, an appreciation that coral reefs are just one component of the broader tropical seascape, requires that all ecosystem components are considered (Fulton et al. 2020). Essentially, we may be at a point in coral reef studies where we need to reassess the application of the term *dominance*, and view change in these dynamic systems from a more comprehensive, continuous, perspective.

In the future, it is likely to be increasingly important to understand what levels of relative benthic cover underpin the functioning of reef ecosystems, which, in turn, support the types of goods and services we expect from tropical reefs (Darling et al. 2019). Could it be that 10% coral cover is sufficient to underpin the functioning of the reef? The answer will likely depend on the ecosystem service or services of interest (e.g., biodiversity, net productivity, fishery yields). In this respect, viewing the nature of the coral reef benthos as a dynamic continuum, and examining how the relative amounts of different benthic components relate to key ecosystem processes and services may hold the key to effective management actions (cf. Hemingson et al. 2022).

As opposed to the current research paradigm, the data shows that most of the world's reefs are dominated by algal groups (figures 1–3). Given the central role different groups of algae play in the functioning of coral reefs and other tropical ecosystems (Klumpp and McKinnon 1992, Adey 1998, Fulton et al. 2019, Kench et al. 2022, Wilson et al. 2022), an understanding of these organisms is likely to be key to understanding future coral reefs. Indeed, in the Anthropocene, reefs in decline do not necessarily shift to algal dominance as algae are often already present and dominant on reefs (see supplemental figures S2 and S4 for temporal trends in dominance). In this respect, algal turfs clearly represent one of the most abundant groups of benthic space holders on coral reefs, but our understanding of this group is still in its infancy compared with hard corals. Because the abundance of these algae means they play large and potentially critical roles in

reef ecosystems, a better understanding of these algae in monitoring and management appears prudent.

The monitoring and management of coral reefs would be facilitated substantially by a unified framework for quantifying benthic cover, globally. A rational starting point for this endeavor would be to identify which of the higher-order (i.e., finer-scale) categories we should universally prioritize in benthic surveys that align with the categorization scheme developed under the CATAMI classification scheme (for *collaborative and automated tools for analysis of marine imagery*; see Althaus et al. 2015). This would need to be balanced against ease of application to ensure consistency of classification by field observers. We suggest particular attention should be given to key groups of algae, such as turfs. This is because, despite algal turfs being the most abundant benthic cover on most coral reefs (figure 2c), current definitions are often unclear, potentially exacerbating inconsistent monitoring (see Connell et al. 2014). Addressing such inconsistencies would be assisted by input from a working group with members that had expertise in different coral reef fauna and flora, as well as different backgrounds (i.e., specialized coral reef ecologists through to coordinators of citizen science monitoring programs). Indeed, such a collaborative approach could be critical as current inconsistencies in benthic categorization may stem from the fact that most research teams on coral reefs have specific expertise about a subset of benthic organisms (often corals) rather than broad expertise. A more general coral reef ecology perspective may, therefore, be key for transitioning from a coral-focused view of coral reefs to a broader appreciation of the entire benthic community (cf. Vroom 2011).

In respect to quantifying the coral reef benthos, it is also important to note that current approaches to the quantification of corals versus groups such as algal turfs and CCA are biased. This is because the most common methods for quantifying the reef benthos involve planform (i.e., looking from above) approaches (e.g., point–intercept–transects; supplemental figure S7). However, such approaches to quantifying benthic cover on reefs result in strong canopy effects, whereby the benthic cover directly on the substratum (e.g., algal turfs) is overlooked and unquantified as it is hidden underneath the canopy of corals (especially plate corals) or macroalgae (Goatley and Bellwood 2011, Bruno et al. 2014, Smith et al. 2022). Canopy-forming coral and macroalgae cover, therefore, is highly likely to have been historically overestimated on reefs relative to the cover of lower-lying algal groups such as turfs and invertebrates (including encrusting corals). Furthermore, surveys conducted on coral reefs typically center around the slope and crest habitats (see supplemental figure S8 and Bellwood et al. 2020), potentially biasing our perception of ecological patterns. Indeed, coral dominance is often higher on these slope and crest habitats compared with habitats such as the reef flat where algae and sand often dominate (supplemental figures S1 and S3). This means that the overall dominance of corals may be overrepresented in the actual spatial composition of reefs. Moreover, if one considers a broader seascape view of tropical reef systems the area covered by coral may be dwarfed by that covered by other groups such as macroalgae. For example, in New Caledonia and Ningaloo (Western Australia) the hectare cover of coral-dominated shallow reef area (at 6%–8%) can be overshadowed by macroalgal coverage (23%–46%; Garrigue 1995, Kobryn et al. 2013). Therefore, although tropical marine studies are often focused on reefs that predominantly support living corals, this habitat can be spatially limited when one considers shallow tropical seascapes in their entirety.

Overall, the data suggests that we may need to carefully consider how the concept of dominance applies to coral reefs going forward. It appears that our understanding will benefit from the consideration of a broader spectrum of benthic categories, especially algae. A better consideration of different algae will enable us to understand and manage the risks and benefits of altered reef communities that are emerging in the Anthropocene (Hughes et al. 2017, Bellwood et al. 2019, Williams et al. 2019). At a global scale, we may need to reconsider the types of benthic categories that are being identified, recorded, and prioritized as ecosystem indicators, with a broader push to understand coral reef systems in their entirety rather than being focused on subsets of benthic components such as hard corals. In doing so, this will help address apparent variability in the conclusions of studies as well as mismatches between what is focused on in the literature and what changes are most common (for a discussion, see Bell et al. 2021, Reverter et al. 2022). Aligning our efforts and unifying how concepts are applied will represent an important step toward a more comprehensive understanding of the drivers underpinning change in reef ecosystems and the consequences for the functions and services that tropical reefs support.

Supplemental Material
Supplemental data are available at *BIOSCI* online.

Disclosure statement

The authors have no competing interests to declare.

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