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A Common Terminology to Unify Research and Conservation of Coralline Algae and the Habitats They Create

Victor L. Jardim[1] | Jacques Grall[1,2] | M. Beatriz Barros-Barreto[3] | Anaëlle Bizien[2] | Thomas Benoit[4] | Juan C. Braga[5] | Juliet Brodie[6] | Thomas Burel[1] | Andrea Cabrito[7] | Guillermo Diaz-Pulido[8] | Patrick Gagnon[9] | Jason M. Hall-Spencer[10,11] | Mathieu Helias[12,13] | Paulo Antunes Horta[14] | Siddhi Joshi[15] | Nick A. Kamenos[15,16] | Regina Kolzenburg[15] | Erik C. Krieger[17,18] | Erwann Legrand[19] | Tessa M. Page[20] | Viviana Peña[21] | Federica Ragazzola[22,23] | Lina M. Rasmusson[24] | Francesco Rendina[25] | Nadine Schubert[26] | João Silva[26] | Frederico T. S. Tâmega[27] | Adeline Tauran[28] | Heidi L. Burdett[15,16]

[1]Université de Brest, CNRS, IRD, Ifremer, LEMAR, IUEM, Plouzané, France | [2]UAR 3113, Observatoire Marin, Université de Brest, Plouzané, France | [3]Department of Botany, Federal University of Rio de Janeiro, Rio de Janeiro, Brazil | [4]Ifremer, Centre de Bretagne, DYNECO, Laboratory of Coastal Benthic Ecology, Plouzané, France | [5]Departamento de Estratigrafía y Paleontología, Universidad de Granada, Granada, Spain | [6]Natural History Museum, Research, London, UK | [7]Institut de Ciències del Mar (ICM), CSIC, Barcelona, Spain | [8]School of Environment and Science, Coastal & Marine Research Centre, Griffith University, Nathan, Queensland, Australia | [9]Department of Ocean Sciences, Ocean Sciences Centre, Memorial University of Newfoundland, St. John's, Newfoundland and Labrador, Canada | [10]School of Biological and Marine Sciences, University of Plymouth, Plymouth, UK | [11]Shimoda Marine Research Center, University of Tsukuba, Shimoda, Japan | [12]Conservatoire National des Arts et Métiers, INTECHMER, Cherbourg-en-Cotentin, France | [13]Normandie Université, UNICAEN, Laboratoire des Sciences Appliquées de Cherbourg, Cherbourg-en-Cotentin, France | [14]Departamento de Botânica, Universidade Federal de Santa Catarina, Florianópolis, Brazil | [15]Umeå Marine Sciences Centre, Umeå University, Umeå, Sweden | [16]Department of Ecology & Environmental Science, Umeå University, Umeå, Sweden | [17]Red Sea Research Center, King Abdullah University of Science and Technology, Thuwal, Saudi Arabia | [18]School of Biological Sciences, Victoria University of Wellington, Wellington, New Zealand | [19]Institute of Marine Research, Bergen, Norway | [20]School of Ocean and Earth Science, University of Southampton, National Oceanography Centre Southampton, Southampton, UK | [21]Facultad de Ciencias, BIOCOST Research Group, A Coruña, Spain | [22]Genoa Marine Center, Stazione Zoologica Anton Dohrn, Villa del Principe, Genoa, Italy | [23]National Biodiversity Future Center (NBFC), Palermo, Italy | [24]Department of Biological and Environmental Sciences, University of Gothenburg, Gothenburg, Sweden | [25]Department of Science and Technology, Laboratory of Marine Ecology, Centro Direzionale, University of Naples Parthenope, Naples, Italy | [26]Centre of Marine Sciences (CCMAR/CIMAR LA), Campus de Gambelas, Universidade do Algarve, Faro, Portugal | [27]Departamento de Biotecnologia Marinha, Instituto de Estudos do Mar Almirante Paulo Moreira (IEAPM), Arraial do Cabo, Brazil | [28]Université de Bordeaux, CNRS, Bordeaux INP, EPOC, UMR 5805, Station Marine d'Arcachon, Pessac, France

Correspondence: Victor L. Jardim (victor.leitejardim@univ-brest.fr)

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ABSTRACT

Linguistic uncertainty is a prime source of uncertainty pervading ecology and conservation. Coralline algae are a widespread and diverse group of calcifying red macroalgae that underpin coastal ecosystem function and service provision. Recent increasing interest in coralline algae in the scientific literature has revealed a diverse but confusing terminology at organism to habitat scales. Coralline algal research and conservation are international and multidisciplinary, so there are geographic and disciplinary imbalances in research and conservation efforts. To reach consensus and reduce uncertainty, we propose a unified terminology. We review trends in cultural and scientific use of coralline algal terms and propose a system based on six morphologies: (1) attached, (2) free-living geniculate, (3) encrusting and free-living nongeniculate coralline algae, the latter either being (4)

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nucleated or (5) non-nucleated thalli or (6) fragments. We take inspiration from other coastal systems that have achieved consensus through umbrella terms, such as 'coral' and 'kelp', to accelerate global progress in coralline algal research and conservation. We characterise 14 coralline algae–dominated habitat global types, falling within seven functional groups, four biomes and four realms: (1) freshwater coralline streams; (2) coralline tide pools; (3) intertidal coralline rims and (4) turf; (5) coralline sea caves; (6) coral–algal reefs; (7) algal ridges; (8) coralligenous reefs; subtidal (9) carbonate crusts, (10) coralline barrens and (11) turf; and (12) articulith, (13) maerl and (14) rhodolith beds, which fall into the coralline algal bed functional group. We hope this unified terminology promotes data comparison, enables cross-boundary and cross-sector sharing of best practices, develops capacity for meta-analyses and improves conservation strategies.

1 | Introduction

A subject with strong cultural, scientific and/or socio-economic connections is usually associated with a high diversity of terms to describe it, because language and human cognition and perception are deeply intertwined (Drew 2005; Klemfuss et al. 2012; Thierry 2016). Similarly, the stronger the connections of a people to a species or group of species, the higher the number of words to describe them (Drew 2005). This pattern can also be seen in scientific language. However, while a diverse terminology can enable specific descriptions, it can also hinder broader scientific understanding of the subject. This is due to increasing uncertainty (Kéfi et al. 2019; Kovalenko et al. 2012), where there is a lack of a unique and complete understanding of a subject. Uncertainty can arise from contrasting multiple knowledge—distinct but equally valid views (Brugnach et al. 2008). Linguistic uncertainty has been identified as one of the main classes of uncertainty that impairs ecological knowledge and effective conservation strategies (Regan et al. 2002; Kujala et al. 2013).

Coralline algae are a highly diversified, globally distributed group of red calcifying macroalgae (Corallinophycidae, Rhodophyta) that thrive in marine and locally in freshwater environments under a wide range of conditions (Johansen 1981; Žuljević et al. 2016). Following pioneering taxonomy-driven work at the end of the 19th century (Foslie 1894; Woelkerling et al. 2005; Woelkerling 2008), coralline algae have received increasing attention in the scientific literature (Figure 1). This interest came from the recognition of their global importance for coastal ecosystem function, service provision and biogeochemical cycling, their sensitivity to projected environmental change and their value in palaeoecological records (McCoy and Kamenos 2015). Similarly, given the biological resources provided by the habitats these coralline algae create, there is increasing concern related to their exploitation (Grall and Hall-Spencer 2003; Riosmena-Rodríguez 2017; Berchez 2022; Mógor et al. 2021; Ramos et al. 2023). Such recognition is driving conservation efforts, with coralline algae being increasingly included in marine management frameworks around the world (European Commission et al. 2016; Keith, Fragkopolou, et al. 2022; Brodie et al. 2023; Axelsson 2023).

As a consequence of increasing recognition and the unmatched morphological diversity of the group, the terminology used for coralline algae and the habitats they form has also become diverse, sometimes leading to linguistic uncertainty (McCoy and Kamenos 2015). The European Red List of Habitats (European Commission et al. 2016) exemplifies this linguistic uncertainty in coralline algal science and conservation. This document alone has 11 names for coralline algal habitats and includes numerous others in which coralline algae are notable components (Figure 2; Table S1). Among the terms used, some are polysemic (have multiple meanings) and context dependent, while some are synonymous. This linguistic uncertainty has the potential to lead to misunderstandings among researchers, decision-makers and other stakeholders, transcending into policy-making (Norton 1998; Milner-Gulland and Shea 2017) and public engagement (Vigliano Relva and Jung 2021).

Coralline algal research and conservation are inherently international and disciplinarily diverse due to the worldwide distribution and the diversity of the algal group. This leads to local and regional scale variations in priorities: Coralline algal research disciplines are not evenly developed worldwide (Rendina et al. 2022) and conservation efforts depend on local pressures and stakeholders (Keith, Ferrer-Paris, et al. 2022). Here, we highlight the importance of unification and community consensus as a tool for contextualisation, to ensure readers understand the meaning of a term (Crump et al. 1999). We review how coralline algal terminology has evolved since the 18th century at organism and habitat levels, identifying long-term trends in cultural and scientific usages of these terms and proposing a unified typology for coralline algal habitats, providing authors with terms that can make communication about these algae more efficient. We hope this will help advance coralline algal research and conservation by (1) facilitating observational and experimental data comparisons; (2) enabling cross-boundary and cross-sector sharing of technique developments, best practices and conservation strategies; and (3) improving meta-analyses, as synonyms can be missed in published literature leading to skewed results (Hodges 2008; Stroud et al. 2015; Cira et al. 2019).

2 | Facilitating Progress in Coralline Algal Research and Conservation Worldwide

A unified terminology for coralline algal habitats may foster better international research collaboration, accelerating the advancement of coralline algal research frontiers and base conservation strategies on a more coherent foundation. In other coastal systems, this has been achieved—'coral', 'kelp', 'seagrass' and 'mangrove' are umbrella terms for 10s–1000s of species with high intravariability, and all have similarly simple habitat terms. The cohesive terminology and grouping of such diverse habitats has facilitated their international recognition within research,

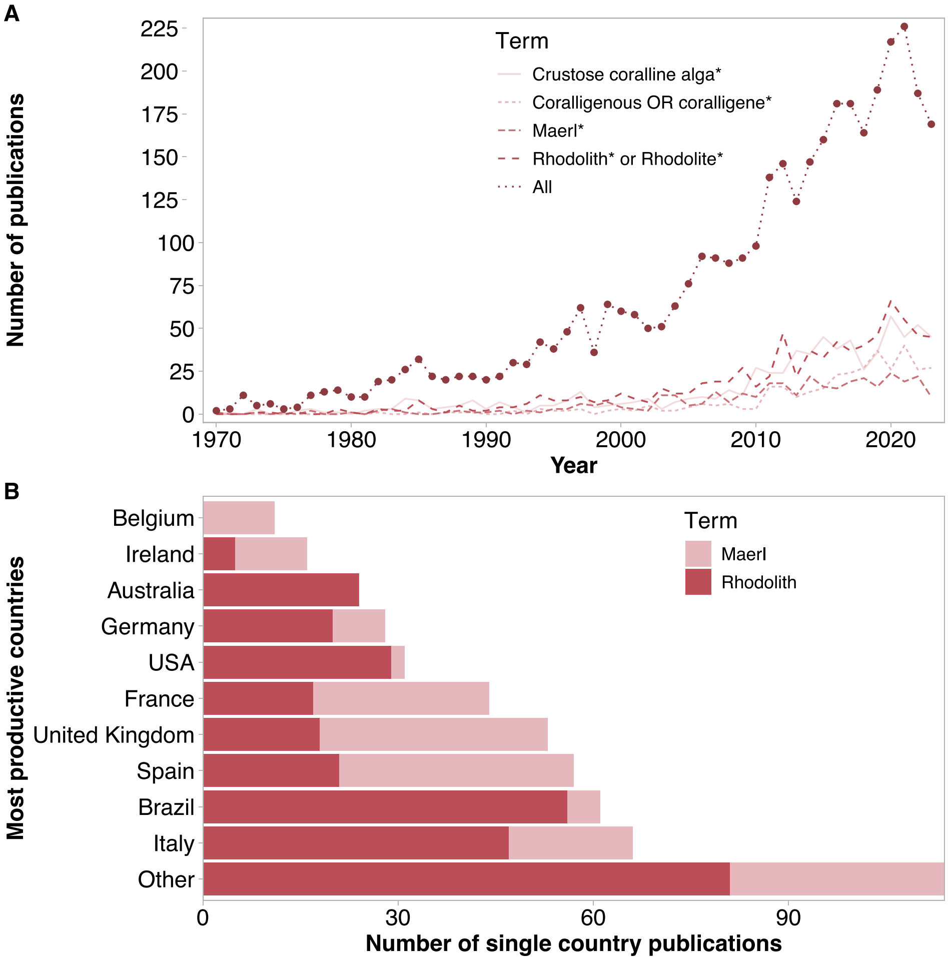


FIGURE 1 | Scopus search for publications containing coralline algal terms in the title, abstract or keywords from 1970 to 2023. (A) Search terms: 'coralline alga*' OR 'coralline red alga*' OR 'coralligene*' OR 'coralligenous' OR 'maerl*' OR 'rhodolite*' OR 'rhodolith*'. Total number of publications = 3713. Total and individual term trends are shown—note that one publication may contain more than one term. (B) Number of single-country publications containing the terms (maerl*) or rhodolith ('rhodolith*' OR 'rhodolite*'), showing the 10 most productive countries to illustrate regional and global trends, created with the 'bibliometrix' R package (Aria and Cuccurullo 2017; R Core Team 2024).

conservation and more widely, with numerous examples of global datasets and assessments (Hamilton and Casey 2016; Krumhansl et al. 2016; McKenzie et al. 2020; Sully et al. 2019; van Katwijk et al. 2016; van Woesik and Kratochwill 2022). Recognition for the importance of coralline algal research lags far behind—we believe due in part to the disparate terminology used at organism to habitat levels. Similarly, global datasets for coralline algae and the habitats they form are lacking, despite increasing academic attention (Figure 1).

Ecosystem conservation and management is typically implemented through local action, which may lead to both epistemic and linguistic uncertainty when aggregated at larger scales (Box 1; Keith, Ferrer-Paris, et al. 2022). However, international and interdisciplinary studies, which depend on a coordinated scientific community, enable cross-comparisons between baseline knowledge, ecological status and conservation efforts and help share successful policies and protect coralline algal habitats globally (Wilson et al. 2004; Brodie 2009; Tuya et al. 2023). Scaling-up local ecological data helps global conservation (Agardy 2005; Edgar et al. 2016, 2014; Rowland et al. 2020) and is needed for coralline algal conservation as at present, this is a data-deficient topic (Ferrigno et al. 2023; McCoy and Kamenos 2015; van der Heijden and Kamenos 2015; Rendina et al. 2022; Ferrigno et al. 2023). Addressing linguistic uncertainty will help resolve this and better set conservation objectives (Milner-Gulland and Shea 2017).

An increasing number of studies proposing unified terminologies to resolve language uncertainty in ecology often resort to trait-based and functional approaches (Bellwood et al. 2024; Ellison 2019; Keith, Ferrer-Paris, et al. 2022; Streit and Bellwood 2023). Here, we review the terms used for coralline algae and propose a unified typology at first the organism and then the habitat level. We then define coralline algae–dominated habitats based on the International Union for Conservation of Nature (IUCN) Global Ecosystem Typology (GET) (Keith, Ferrer-Paris, et al. 2022).

3 | The Emergence of a Diverse Terminology

All orders within the Corallinophycidae (Phylum: Rhodophyta), except the Rhodogorgonales, fall under the umbrella term 'coralline algae'—almost all of which have- extensive calcification in the cell walls (Jeong et al. 2021). The Rhodogorgonales have a very different calcification process and a gorgonian-like filamentous morphology (Fredericq and Norris 1995). The

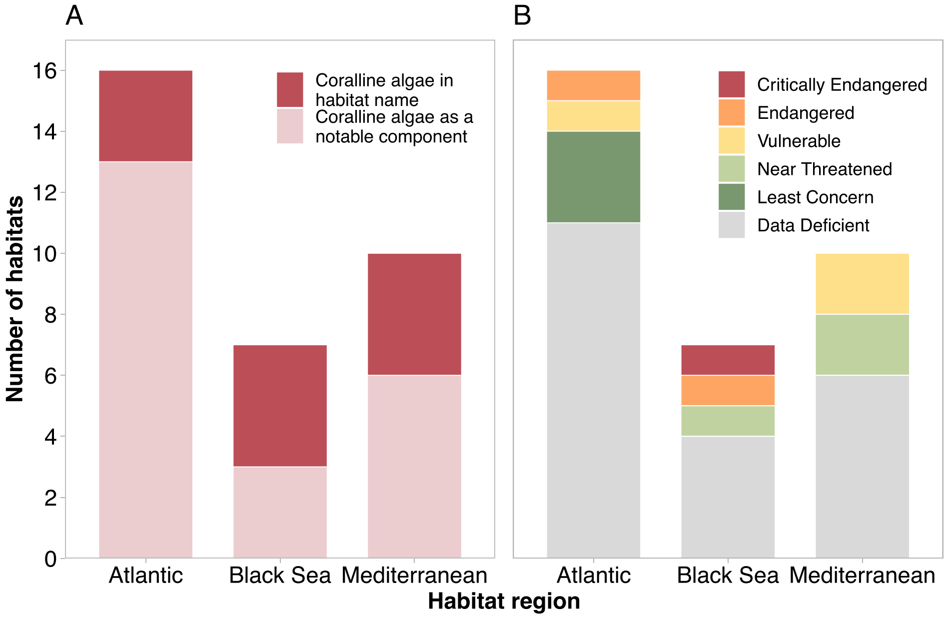


FIGURE 2 | Coralline algae in the European Red List of Habitats (European Commission et al. 2016). (A) The number of habitats where coralline algae are in the habitat name ($n = 11$) or are listed as a notable component in the habitat description ($n = 22$) and (B) the current conservation status of coralline algal-associated habitats across the Mediterranean, Black Sea and Atlantic regions. Further information on each habitat is provided in Table S1.

coralline algae are divided into two groups based on morphology (Figure 3): geniculate (erect fronds with uncalcified segments known as genicula) and nongeniculate (thalli lacking uncalcified segments). However, this morphological division is not reflected in their phylogeny. The order Corallinales has both geniculate and nongeniculate taxa, sometimes in a single genus, assuming evolutionary reversals of some taxa to the ancestral, nongeniculate state (Hind et al. 2018). Nongeniculate coralline algae can have a free-living or encrusting morphology, the latter being flat or with branch-like protuberances (Irvine and Chamberlain 1994). Some species are exclusively encrusting, while others can be found both free-living or encrusting (Hernandez-Kantun et al. 2016).

Besides the presence of genicula, coralline algae present great morphological and functional diversity. They greatly vary in size, thickness and shape, varying from (small) to (large). The group also presents several life strategies: parasitic, semiendophytic, epilithic, epiphytic, epizoic or live as epibionts on man-made surfaces such as glass, plastic and metal (Adey and Sperapani 1971; Adey and Macintyre 1973; Harvey et al. 2005; Dean et al. 2015; McCoy and Kamenos 2015). This diversity is thought to be at least partially due to the presence of secondary pits and vegetative cell fusions that allow the translocation of photosynthates to living cells beneath photosynthetic tissues, allowing lateral growth (Steneck 1983, 1986). The morphological and functional diversity of the group has contributed to the proliferation of terms used to describe coralline algae.

3.1 | Free-Living Nongeniculate Coralline Algae

Free-living, nodule forming, nongeniculate coralline algae have been documented since the mid-18th century (e.g., Linnaeus 1758; Ellis and Solander 1786), although they were thought to be animals that looked like plants (zoophytes) until Philippi (1837) identified them as photosynthetic organisms. Initially classified as *Millepora* hydrocorals (Ellis and Solander 1786; Pallas 1766) and later as *Nullipora* zoophytes (Lamarck 1801), they were then identified as coralline algae of the genera *Lithothamnion* Heydrich and *Lithophyllum* Philippi, in the mid-late 1800s (Wiegmann 1837; Chauvin 1842; Foslie 1894). Since then, multiple terms have arisen from both traditional and scientific ecological knowledge, with varying consensus over their interchangeability such as coatings, nodules, maerl, rhodoliths, rhodolites or rhodoids; there are at least 12 terms used in the academic literature for free-living coralline algae (Riosmena-Rodríguez 2017).

For example, in the early 20th century the Breton word maerl (*maërl*, in French) started gaining popularity in the scientific community (Lemoine 1910), although it had been used for centuries by Celtic and French people in reference to the coralline algae exploited for soil treatment—as a variant of 'marne' the word for calcareous rocks (Augris and Berthou 1990). The terms 'maerl' and 'maerl beds' have been historically used for unattached coralline algal habitats created by *L. corallioides* (P.Crouan & H.Crouan) P. Crouan & H. Crouan, *Boreolithothamnion glaciale* (Kjellman) P.W.Gabrielson, Maneveldt, Hughey & V. Peña (previously *Lithothamnion glaciale*) and *P. calcareum* (Pallas) W.H.Adey & D.L.McKibbin ex Woelkering & L.M.Irvine in the Northeast (NE) Atlantic and subarctic seas (Cabioch 1969; Adey and Macintyre 1973; Barbera et al. 2003; Wilson et al. 2004; Hinojosa-Arango et al. 2009; Peña et al. 2014; Jenkins et al. 2021). These species often lack a nucleus, the main reason why many now consider only such forms as maerl (sensu stricto). At least 13 different maerl-forming species have been identified in the NE Atlantic with many different growth forms (Peña et al. 2013, 2021; Pardo et al. 2014; Qui-Minet et al. 2021; Helias and Burel 2023). The term maerl sensu lato has sometimes been

Box 1. Rhodolith/maerl beds: a tale of detrimental linguistic uncertainty in conservation efforts and how human connection may improve it

An example of linguistic uncertainty affecting conservation is a lack of cohesion on free-living non-geniculate coralline algae terminology. The European Red List of Habitats (Table S1) uses the term 'maerl beds' for the Atlantic but "rhodolith beds" for the Mediterranean, although both are defined as "*sedimentary bottoms characterised by any morphology and species of unattached non-geniculate calcareous red algae*" (European Commission et al., 2016). Curiously, *Lithothamnion corallioides* and *Phymatolithon calcareum*, typically associated with the term 'maerl' in the Atlantic, are explicitly listed in the European Red List as the main species found in "Mediterranean rhodolith beds". The latest OSPAR commission Benthic Habitats report recognises maerl beds as threatened and/or in decline, but does not consider rhodolith beds (OSPAR, 2023).

While maerl beds in the Atlantic are recognised as Endangered or Vulnerable, Mediterranean rhodolith beds are considered 'data deficient' on the European Red List of Habitats (European Commission et al., 2016), despite extensive research conducted on Mediterranean coralline algal beds (Jacquotte, 1962; Pérès and Picard, 1964; Basso, 1998; Barbera et al., 2003; Bordehore et al., 2003; Ordines and Massutí, 2009; Sciberras et al., 2009; Sanz-Lázaro et al., 2011; Barberá et al., 2012; Micallef et al., 2012; Savini et al., 2012; Martin et al., 2014). Therefore, linguistic uncertainty is probably partly responsible for the 'data deficient' status. Indeed, Mediterranean coralline algal beds may be facing even more extreme conditions than those in the Atlantic zone and may deserve a higher conservative status (Rindi et al., 2019).

Besides baseline scientific knowledge, the deep historical roots and cultural connections humans have with the ocean cannot be overstated and might be reflected on the different levels of protection given to coralline algal beds worldwide (Poe et al., 2013; Bennett, 2019). For instance, the term 'maerl' has an important historical and cultural heritage value in many places in the North Atlantic, especially in Brittany, France. A local festival called '*La fête du maërl*' takes place every four years in Plougastel-Daoulas in the Bay of Brest, attracting more than 5000 people with art exhibits, traditional dancing and historical re-enactments to remember those who extracted coralline algae for a living, and to raise awareness of the ecological and socioeconomic importance of these habitats (Friant and Marie, 2010; Péron and Marie, 2010; Noisette, 2013).

used to include nucleated growth forms of unattached coralline algae and the habitats they form in the Mediterranean (Barberá et al. 2017) and NE Atlantic (Axelsson 2023).

In the second half of the 20th century, the terms rhodolith and rhodolith beds were first introduced to describe 'unattached aggregations of calcareous red algae' (Barnes et al. 1970, 1971). This broad definition could, therefore, include free-living thalli of noncoralline calcifying red algae such as Peyssonneliaceae (subcl. Rhodymeniophycidae) species (Buchbinder and Halley 1985). However, these other calcifying red algae are usually associated with corallines and are seldom the dominant nodule-forming component, with exceptions in transition zones (Ballesteros 1994; Basso 2012; Bianchi and Morri 2025; V. A. Bracchi, Bazziacalupo, et al. 2022; Deinhart et al. 2022). The terms rhodolite and rhodoid were also proposed at the time (Bosellini and Ginsburg 1971; Peryt 1983), but because these had previously been used to describe a variety of red garnets and other coated grains, they were discarded for coralline algal nodules (Adey and Macintyre 1973; Ginsburg and Bosellini 1973). Since then, rhodolith has become the most widely used term for free-living nongeniculate coralline algae (Rendina et al. 2022) except in Europe, where maerl is more commonly used (Figure 1B). Although the first definitions of rhodolith sensu lato did not distinguish among nucleated and non-nucleated nodular calcifying red algal growths, Steneck (1986) only consider those that grow around a nucleus as rhodoliths sensu stricto. Nucleated nodules can also be further classified based on the relative contribution of the coralline algal component to the whole nodule structure into coatings (< 50%) or rhodoliths

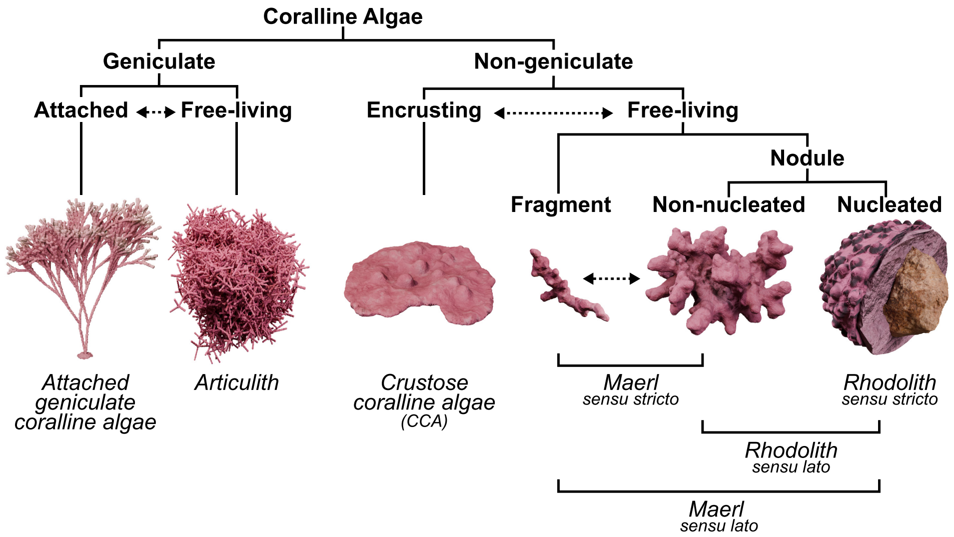


FIGURE 3 | Proposed morphological organismal typology for coralline algae. Note that rhodolith and maerl both have historically been given both strict and broad definitions. Rhodolith sensu stricto only includes nucleated nodules, while maerl sensu stricto includes only non-nucleated forms. While rhodolith sensu lato includes only nodular forms, maerl sensu lato also includes nonnodular fragments. Here, we present historical uses so that authors can be specific about which morphotypes are referred to when using any of the terms. The represented morphologies are examples of the variety in growth forms. Arrows represent reproductive strategies that enable shifts between different types: Attached algae can grow into free-living forms, while free-living reproductive forms can produce spores that will grow into attached forms.

(> 50%) (Steneck 1983; Basso 1998). The nucleus can be of biotic or abiotic origin, and nucleated rhodoliths can be composed of one or several thalli, often with multiple species on individual nodules (Riosmena-Rodríguez 2017). There is growing use of rhodoliths sensu lato as a general term for coralline algal nodules, particularly those with nuclei, while maerl sensu stricto remains the term commonly used for non-nucleated free-living nongeniculate coralline algae (Foster 2001; Arnold et al. 2021; Bélanger and Gagnon 2023).

Subclassifications have been created to reflect the morphological diversity of free-living nongeniculate coralline algae and introduce a rich terminology that can be source of linguistic uncertainty. For instance, both Bosence (1983) and Basso (1998) proposed the term 'boxwork' for different types of nodules. Bosence (1983) distinguished them in three classes: branching, columnar and laminar, with the latter being divided into concentric and nonconcentric nodules (boxwork). Basso (1998) proposed three classes: boxwork rhodoliths (large, multispecific, laminar to columnar nucleated nodules with multiple voids), *prâlines* (small, monospecific, laminar, branching or columnar nucleated nodules) and unattached branches (small, monospecific, unattached non-nucleated branches). Although useful to describe specific morphologies, when using subclassifications, authors should be explicit about their meanings to avoid confusion.

3.2 | Encrusting Nongeniculate Coralline Algae

Much like free-living forms of nongeniculate coralline algae, descriptions of encrusting forms date back to the 1700s. Pérès and Picard (1964) provide a wealth of information on the variety of habitats these algae can form and an evocative variety of French terms used to describe these habitats. The term crustose coralline algae became popular at the end of the 20th century, when it was initially used as a synonym for nongeniculate coralline algae (Adey and Macintyre 1973; Bosence 1983; Steneck 1986). Nowadays, crustose coralline algae usually refers to encrusting (sessile) nongeniculate corallines only (McCoy and Kamenos 2015), although free-living forms are sometimes also referred to as crustose coralline algae (Amado-Filho et al. 2012; Pereira-Filho et al. 2012; V. Bracchi, Caronni, et al. 2022; Rebelo et al. 2022). This ambiguity is understandable since many encrusting species may grow on mobile substrata (biogenic, lithic or man-made) to create nucleated free-living specimens (Foster 2001). The term 'crustose' can also be misleading as many nongeniculate species have calcified upright branches (Woelkerling et al. 2005). Additionally, many geniculate species can be confused with encrusting nongeniculate species in early development stages, as they present a nongeniculate basal crust preceding the formation of upright geniculate fronds (Irvine and Chamberlain 1994).

Much of the diversity of terms regarding encrusting nongeniculate coralline algae stems from the wide variety of habitats that they form. These include coralline algal rims, buttresses, platforms, cornices and *trottoirs*, coralline algal-dominated tide pools and sea caves, coral–algal reefs, coralline algal carbonate crusts (or cor-stromes) and coralligenous reefs, the latter also being known as coralligenous assemblages, formations, concretions, coralligène or simply coralligenous (Marion 1883). The similarities and differences among these habitats are discussed below, in the habitat typology section.

3.3 | Geniculate Coralline Algae

Geniculate coralline algae were first described as zoophytes in the 18th century (Linnaeus 1758). The name comes from their genicula, an uncalcified, joint-like cell structure, separating two intergenicula, the calcified segments of the upright fronds usually developed from a nongeniculate basal disc. The term genicula was initially employed for *Equisetum* plants (Blackstone 1746), then for Cnidarians by Linnaeus (1758) and Ellis and Solander (1786), and was subsequently applied to corallines (Harvey 1847).

The Corallinales is the only order of coralline algae with geniculate species (Walker et al. 2009). The presence of genicula was long considered the most important character for taxonomic distinction (Johansen 1981). However, the presence of genicula is a derived character that has arisen in the descendants of nongeniculate coralline algae multiple times (Aguirre et al. 2010; Peña et al. 2020). Hind et al. (2018) also suggest that evolutionary reversals have occurred within the subfamily Corallinoideae, twice within the geniculate genus *Bossiella* P.C. Silva.

The genicula development pattern differs from one genus to another, either through the development of uncalcified cells (apical growth for the Metagoniolithoideae or subapical growth for the genus *Lithothrix* Gray) and/or by decalcification (important in Lithophylloideae) (McCoy et al. 2023). The genicula grant these algae some degree of physical flexibility and were initially called *articulis* by Linnaeus—hence the popularity of the alternative term 'articulated coralline algae' (Johansen 1981).

Geniculate taxa are usually epilithic and typically occur in the intertidal and subtidal zones from polar to tropical environments (Stewart 1982; Kelaher et al. 2001), although species can also be epiphytic or epizoic. They are often strongly attached by crustose or stoloniferous holdfasts, which can be extensive and sometimes confused for an encrusting nongeniculate coralline algae base (Brodie et al. 2013). Some geniculate corallines can be free-living and create extensive habitats similar to free-living nongeniculate coralline algae beds—these understudied growth forms have been recently named 'articuliths' (Tâmega et al. 2017, 2021).

3.4 | Creating International Cohesion Through a Unified Typology

As coralline algal science and interest from conservation and policy sectors have grown, the diversity of terms used to describe these algae and their associated habitats has also increased. Although a diversity of terms enables specificity in organismal/habitat descriptions, the definition of terms and the extent of 'interchangeability' between terms is not internationally consistent, creating uncertainty. Adoption of specific terms (and rejection or delineation of others), namely, in policy documents, creates uncertainty and places coralline algal habitats at greater risk of inadequate protection measures.

4 | Proposed Organismal Typology

Some terms, such as crustose coralline algae and nongeniculate coralline algae, have been used interchangeably when they designate organisms with different life histories and ecological functions. On the other hand, organisms with similar traits and functions have been named differently on cultural and morphological bases, as in the case of the free-living nongeniculate coralline algae. Informed by both terminology history and morphological differentiation (discussed above), we propose a unified organismal typology (Box 2 and Figure 3).

In this typology, coralline algae are initially distinguished by their structural morphology, leading to the categorisation of geniculate and nongeniculate forms. The mode of attachment is then used to further differentiate these forms. This includes attached and free-living geniculate forms, as well as encrusting (sessile) and free-living nongeniculate forms. Free-living nongeniculate types can be nodules or fragments—the latter having only one long axis (Figure 3). Encrusting nongeniculate forms may have branches which, when detached, can become free-living fragments or non-nucleated nodules—referred to as 'maerl' in the strictest sense. The broader term 'maerl' can encompass all free-living forms, including nucleated and non-nucleated nodules and fragments. Conversely, the term 'rhodolith' in its broadest sense and following the original definition by Barnes et al. (1971) may include noncoralline calcifying red algae and encompasses all free-living nodules, while in its strictest sense, it specifically refers only to nucleated nodules of free-living nongeniculate coralline algae. Importantly, we do not prescribe authors necessarily use the terms sensu lato and sensu stricto when referring to maerl or rhodoliths, but instead, advocate authors are explicit about which type of coralline algae is being referred to (nucleated nodules, non-nucleated nodules or fragments) whenever they use one term or the other—as many definitions exist.

5 | Proposed Habitat Typology

International cohesion among coralline terminology might be even more important at the habitat level for conservation and management. When different terms are employed to habitats with similar ecological traits and functions, dissimilar protection levels might be applied (Kujala et al. 2013). In this sense, a functional approach could be an effective alternative basis for a unified terminology (Hattam et al. 2021; Streit and Bellwood 2023). Many coralline algal species can be considered multi-influence engineers, as they can affect several biotic and abiotic processes and resultant ecosystem functions (Byers 2022). Therefore, we propose a unified morphofunctional habitat typology in which we describe and group coralline algae–dominated habitats following the IUCN's GET (global-ecosystems.org). The GET units are based on (1) ecosystem functions and ecological processes, (2) their characteristic biota, (3) conceptual consistency throughout the whole biosphere, (4) a scalable structure, (5) spatially explicit units and (6) descriptive parsimony (Keith, Ferrer-Paris, et al. 2022).

5.1 | IUCN's Global Typology

The GET has three upper hierarchical levels (Figure 4): 11 realms (Level 1), including atmospheric (which is taken into account but has no lower hierarchical units), freshwater, marine, terrestrial, subterranean and six transitional realms not relevant here; 25 functional biomes (Level 2); and 110 functional groups (Level 3). Biomes are components of a realm with similar ecosystem structure and one or a few common major ecological drivers

Box 2. Coralline algae organismal typology and definition key

- Coralline algae 1
  - Geniculate 2
    - Attached 3
    - Free-living 4
  - Non-geniculate 5
    - Encrusting 6
    - Free-living 7
      - Fragment[a,b] 8
      - Nodule 9
        - Nucleated[c,d] 10
        - Non-nucleated[a,b,d] 11

1. Calcifying benthic red algae within the Corallinophycidae (exc. Rhodogorgonales, Rhodophyta)
2. Corallinales species with calcified frond segments separated by genicula (uncalcified cells)
3. Geniculate coralline algae attached to substrata by crustose or stoloniferous holdfasts
4. Geniculate coralline algae living unattached in nodular forms known as articuliths
5. Fully calcified coralline algae lacking genicula
6. Non-geniculate coralline algae attached to substrata, also known as Crustose Coralline Algae
7. Non-geniculate coralline algae living unattached as fragments or nodules
8. Fragments of branching encrusting and free-living non-geniculate coralline algae
9. Nodular growths of free-living non-geniculate coralline algae
10. Free-living non-geniculate coralline algae growing as nodules over a biogenic or abiotic nucleus.
11. Free-living non-geniculate coralline algae growing in nodular forms from unattached fragments

a. Maerl *sensu stricto*. Includes non-nucleated nodules of free-living non-geniculate coralline algae and fragments of branching non-geniculate coralline algae
b. Maerl *sensu lato*. Includes all free-living non-geniculate coralline algae.
c. Rhodolith *sensu stricto*. Includes nucleated nodules of free-living non-geniculate coralline algae.
d. Rhodolith *sensu lato*. Includes all nodules of non-geniculate coralline algae and other non-coralline calcareous red algae of the presence of nuclei.

and functions. Functional groups are similar systems within a biome that share common ecological drivers and present similar biotic traits. Functional groups can be further divided into three bottom hierarchical levels: regional subgroups (Level 4), global types (Level 5) and subglobal types (Level 6). Level 4 units are based on ecoregions and are not applied here because many regions are data deficient for coralline algae (European Commission et al. 2016; Rendina et al. 2022; Brodie et al. 2023). Lower Levels 5 and 6 are independent of Level 4 and have a bottom-up hierarchy. Global types (Level 5) are defined by the aggregation of subglobal types (Level 6, regional expressions of functional groups) based on compositional resemblance. Global types grouped into the same functional group share similar ecological processes, drivers and services but present different biotic composition.

Level 6 units are regional expressions of functional groups that are explicitly linked to local knowledge and are aggregated based on subglobal classifications. Aggregation of subglobal units to broader global units (Level 5) is based on compositional

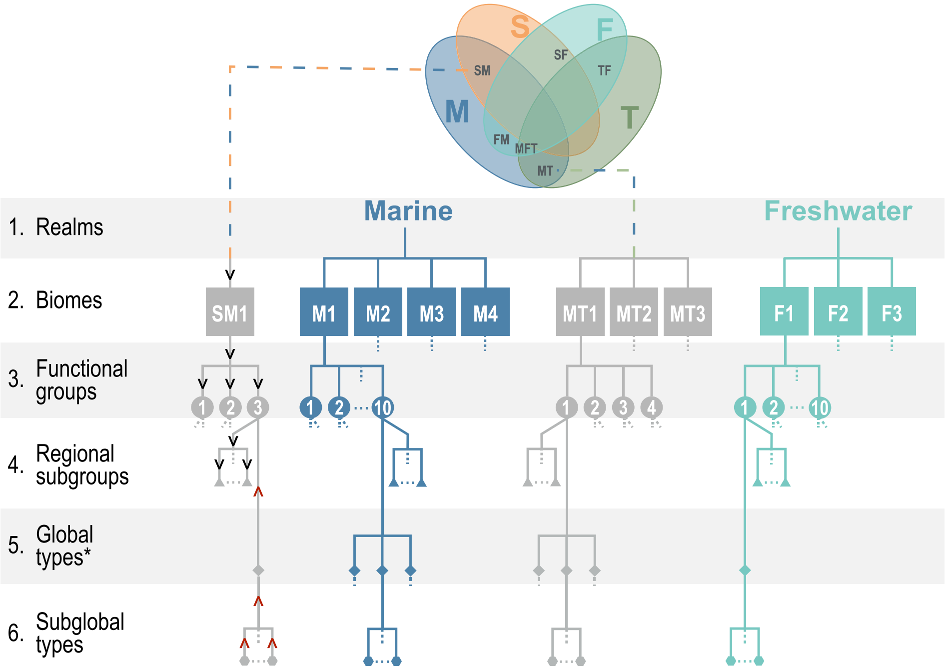


FIGURE 4 | Simplified IUCN's Global Ecosystem Typology (GET) showing only the realms containing coralline algal habitats. There are three upper hierarchical levels: 1—realms, 2—biomes and 3—functional groups. Level 3 levels can be further divided into 4—regional subgroups, 5—global types and 6—subglobal types. Four core realms represent major components of the biosphere: terrestrial, freshwater, marine and subterranean (the atmospheric realm is also taken into account but has no lower level units). Six additional transitional realms are defined as combinations of the four core realms. Core realms are coloured, while transitional realms are grey. Whenever a unit presents more than four lower levels, dashed lines are used to represent them. Lower levels of a single unit at each upper level are shown to simplify the diagram. Arrows indicate top-down (black) and bottom-up (red) structures. F = freshwater; M = marine; S = subterranean; T = terrestrial. Adapted from Keith, Ferrer-Paris, et al. (2022). Unit names are shown in Figure 5.

resemblance and is necessary to address uncertainty from contrasting multiple knowledge (Brugnach et al. 2008; Keith, Ferrer-Paris, et al. 2022). Therefore, under the post-2020 Global Biodiversity Framework, the IUCN's Red List Index of Ecosystems (RLIE) is used to inform the IUCN's Red List of Ecosystems and takes GET into account (Bland et al. 2019; Nicholson et al. 2021). The RLIE summarises the risk status and trends of ecosystems and can be reported at national or global levels and disaggregated by ecosystem type, using the GET (Rowland et al. 2020).

We characterise a nonexhaustive list of 10 coralline algae–dominated global types, falling within seven IUCN functional groups, four biomes and four realms (Figure 5). The global types we propose are based on subglobal habitats (GET Level 6) and grouped based on the main coralline algae morphologies (cf. Box 2 and Figure 3) and their compositional and functional resemblances.

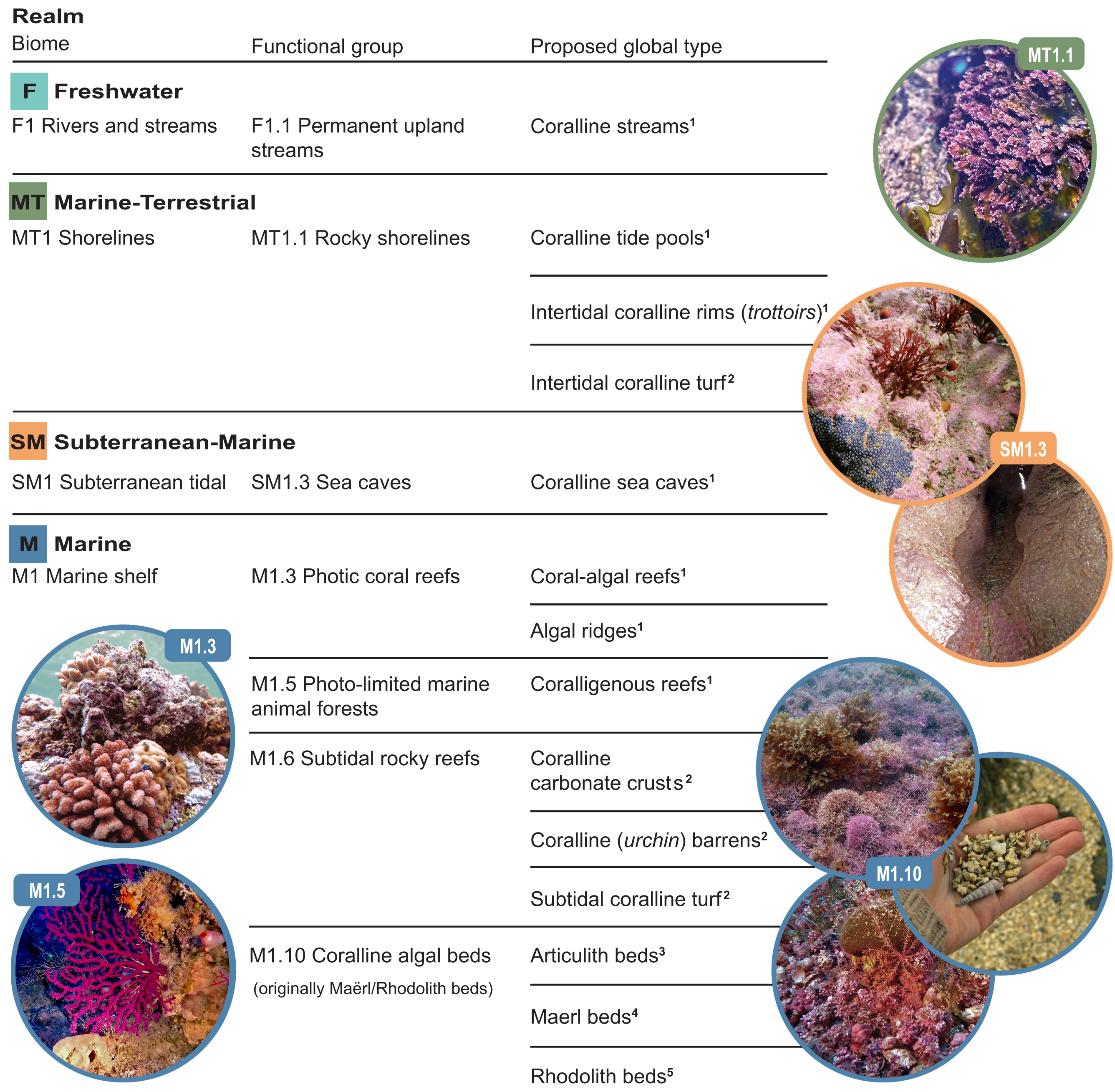
5.2 | The Freshwater Realm (F)

In the freshwater realm (F), classified under the rivers and streams biome (F1) and the permanent upland streams functional group (F1.1), a unique encrusting nongeniculate coralline algae habitat has been documented in the Cetina river karst watershed in Croatia (Žuljević et al. 2016; Koletić et al. 2020). It is formed by *Pneophyllum cetinaensis*, the only known freshwater member of the Corallinales, colonising every hard substratum available as well as roots and mollusc shells (Žuljević et al. 2016; Necchi and Vis 2021). No studies have yet investigated the role of this coralline algae freshwater habitat on shaping associated assemblages. Unfortunately, this habitat is under strong human pressures, as the river crosses two cities and has several hydroelectric power plants, dams and artificial lakes along its course (Žuljević et al. 2016).

5.3 | The Marine–Terrestrial Transitional Realm (MT)

In the marine–terrestrial transitional realm (MT), three coralline global types are identified, all included in the shorelines biome and rocky shorelines functional group (MT1.1). Geniculate coralline algae can be a dominant part of rocky shoreline habitats. They are autogenic ecosystem engineers, forming turf that provides shelter to well-developed macrofaunal and macroalgal communities (Stewart 1982; Grahame and Hanna 1989; Kelaher et al. 2001; Nelson 2009). However, they are increasingly at threat from rising seawater water temperature, marine heatwaves and ocean acidification (Brodie et al. 2014; Williamson et al. 2014; Rendina et al. 2019; Kolzenburg et al. 2021).

Encrusting nongeniculate coralline algae may also be the main habitat-forming species in rocky shorelines, forming coralline algae–coated tide pools or intertidal encrusting coralline algae rims depending on their position in the shoreline and spatial organisation. Tide pools dominated by encrusting nongeniculate coralline algae can be found up to the upper intertidal zone,



Realm Biome	Functional group	Proposed global type
F Freshwater		
F1 Rivers and streams	F1.1 Permanent upland streams	Coralline streams[1]
MT Marine-Terrestrial		
MT1 Shorelines	MT1.1 Rocky shorelines	Coralline tide pools[1]
		Intertidal coralline rims (*trottoirs*)[1]
		Intertidal coralline turf[2]
SM Subterranean-Marine		
SM1 Subterranean tidal	SM1.3 Sea caves	Coralline sea caves[1]
M Marine		
M1 Marine shelf	M1.3 Photic coral reefs	Coral-algal reefs[1]
		Algal ridges[1]
	M1.5 Photo-limited marine animal forests	Coralligenous reefs[1]
	M1.6 Subtidal rocky reefs	Coralline carbonate crusts[2]
		Coralline (*urchin*) barrens[2]
		Subtidal coralline turf[2]
	M1.10 Coralline algal beds (originally Maërl/Rhodolith beds)	Articulith beds[3]
		Maerl beds[4]
		Rhodolith beds[5]

FIGURE 5 | Coralline algae–associated habitat nomenclature and typology, following the IUCN's Global Ecosystem Typology. New global types are proposed here, based on functional and compositional resemblances among subglobal types. Recommended habitat names are proposed as global types for consistency within the coralline algae community. Superscript numbers represent the dominant morphotypes of habitat-forming coralline algae, as described in Figure 3: 1 = encrusting nongeniculate coralline algae; 2 = attached geniculate coralline algae; 3 = free-living geniculate coralline algae nodules; 4 = free-living nongeniculate coralline algae nodules and fragments; 5 = free-living calcifying coralline algae nodules (including noncoralline species). Exemplary habitat photographs: MT1.1 = intertidal coralline turf, Brittany, France (credit: Victor L. Jardim); SM1.3 = coralline algae sea cave, Brittany France (credit: Jacques Grall); M1.3 = coral–algal reef, Great Barrier Reef, Australia (credit: Tessa Page); M1.5 = coralligenous reef, Sorrento, Italy (credit: Francesco Rendina); M1.10 (from top to bottom) = articulith bed, Rio de Janeiro, Brazil (credit: Frederico Tamega), Carraroe maerl beach composed mostly of nongeniculate coralline algae fragments, County Galway, Ireland (credit: Siddhi Joshi) and rhodolith bed Capri, Italy (credit: Francesco Rendina).

making them environmentally variable habitats characterised by distinct seasonal and diurnal cycles (Legrand et al. 2018) and intense biotic pressures, such as grazing (Steneck et al. 1991; Wai and Williams 2006). Coralline algae–dominated tide pools are usually dominated by a few species of encrusting nongeniculate coralline species (Wai and Williams 2006; Dorey et al. 2023). Although tide pools usually present low diversity of associated organisms when compared to subtidal communities, they are more diverse than the surrounding emergent rock habitats (Firth et al. 2014).

Intertidal encrusting nongeniculate coralline algae rims are formed through the coalescence of numerous coralline algae thalli on vertical or subvertical rocky surfaces (Verlaque 2010).

Coralline algae rims usually present a porous upper layer of living coralline algae over dead algae, an intermediate hardened multilayered sedimentary matrix with filled-up interstices and a highly colonised lower eroded matrix of dead crustose coralline algae (Pezzolesi et al. 2017). These habitats, also known as *trottoirs* in the Mediterranean, are understudied and face numerous threats, namely, sea-level rise, human mechanical impact and pollution, which grants them Vulnerable status on the European Red List of Habitats (European Commission et al. 2016; Blanfuné et al. 2023).

5.4 | The Subterranean-Marine Transitional Real (SM)

In the subterranean-marine transitional real (SM), sea caves (SM1.3) are special refuge habitats acting as biodiversity reservoirs (Bussotti et al. 2006; Gerovasileiou and Bianchi 2021). They are formed in a variety of rock types and can include biogenic habitats dominated by encrusting nongeniculate coralline algae (Adey and Vassar 1975; Gerovasileiou and Bianchi 2021). Sea caves have strong biotic zonation due to gradients in light and hydrography, with low-light communities dominated by coralline algae in cave entrances (Guido et al. 2019; Gerovasileiou and Bianchi 2021). Although highly diverse, sea caves are considered low resilient habitats and face many threats, including invasive species, global change and local human impacts (Tillin 2015; Gerovasileiou and Bianchi 2021).

5.5 | The Marine Realm (M)

In the marine realm (M), we identify six global habitat types in which coralline algae are the main biogenic component, all of them in the marine shelf (M1) biome. In photic coral reefs (M1.3), encrusting nongeniculate coralline algae dominate forming coral–algal reefs. Tropical coral–algal reefs (also known as algal reefs) form thick, mostly calcified frameworks of coralline algal crusts, corals, foraminifera, vermetids, serpulids and boring organisms (Littler 1973; Adey 1978, 1998). Encrusting nongeniculate coralline algae can characterise both inshore and fringing reefs, as well as mid and outer-shelf reefs, and thick coralline algal crusts are often more abundant in outer-shelf reefs (Dean et al. 2015). In the tropics, encrusting nongeniculate coralline algae often dominate the windward most exposed crests of reefs, sometimes accounting for up to 90% of the composition of reef crests, creating algal ridges (Adey and McKibbin 1970; Adey 1998). Coralline algae can contribute more than corals to coral reef carbonate production in some reefs (Cornwall et al. 2023). The Taoyuan Algal Reef (Taiwan) is the largest known subtropical intertidal algal reef; it spans over 27 km on a tidal flat and is approximately 4 m thick (Liou et al. 2017; Zhan et al. 2022). It is thought to harbour high coralline algal endemism and overall diversity but is threatened by coastal development and industrial waste run-off (Kuo et al. 2020; Heard et al. 2021; Chen et al. 2022; Zhan et al. 2022). All tropical coral reefs assessed on the IUCN's Red List of Habitats are either endangered or critically endangered (Bland et al. 2019, 2017). Their conservation status is primarily based on increased frequency and severity of warming-induced coral bleaching events (Hughes et al. 2017; Sully et al. 2019; Andrello et al. 2022). The impacts of warming on tropical coralline algae per se are varied, but overall, encrusting nongeniculate coralline algae seem less sensitive to warming stress than scleractinian corals (Cornwall et al. 2022). However, the impacts of global change and human activities on coralline algae need to be better understood and integrated when discussing the vulnerability of coralline algal habitats (Kuffner et al. 2008; Diaz-Pulido et al. 2012; Webster et al. 2013; Cornwall et al. 2017; Heard et al. 2021; Kluibenschedl et al. 2023).

Coralline algae are the deepest known macroalgae and have been found at 268-m depth (Littler et al. 1985), with encrusting nongeniculate coralline algae often being the dominant component of photo-limited marine animal forests (M1.5), forming coralligenous reefs. Coralligenous reefs (also known as coralligenous assemblages, formations, concretions or simply coralligenous) are typical mesophotic habitats of the Mediterranean Sea (Ballesteros 2006). They are among some of the best studied coralline algal habitats (Ferrigno et al. 2023) and were first described by Marion (1883). The term comes from the French word *coralligène*, which means 'coral maker', and is used to describe coralline algae dominated hard bottom communities (Basso et al. 2022). Coralligenous reefs are usually characterised by several layers of encrusting nongeniculate coralline algae (from a few centimetres to several metres thickness) over several kilometres on either rocky walls in the intertidal or subhorizontal sedimentary or rocky substrata in the subtidal, occurring at depths of over 150 m (Bosence 1983; Basso et al. 2022).

Subtidal rocky reefs (M1.6) are often dominated by coralline algae in the photic zone. In Subarctic and Arctic regions, encrusting nongeniculate coralline algae coat most subtidal rocky surfaces and can form thick carbonate crusts (or cor-stromes) that can be as thick as 0.5 m. Coralline algal carbonate crusts occur both in the Atlantic and Pacific ocean basins and may be composed of different taxa, although *Clathromorphum* Foslie and *Boreolithothamnion* species are the most abundant (Adey et al. 2013). In the Arctic, these carbonate crusts may be extremely long-lived, with *Clathromorphum* specimens aged up to 1200 years BP (Adey et al. 2015). This, in combination with their capacity to incorporate certain elements and isotopes in their band-like growth structures, can be useful for biogeochemical analyses and paleoclimate reconstructions (Adey et al. 2013; Halfar et al. 2013; Gould et al. 2022). Carbonate crusts are highly diverse habitats, harbouring macrobenthic communities as diverse as those found in surrounding habitats dominated by canopy macroalgae (Chenelot et al. 2011).

Similarly, encrusting nongeniculate coralline algae are the main biogenic components of subtidal rocky reef habitats usually known as 'urchin barrens'. These often-extensive habitats are distributed worldwide and emerge from a stable-state shift from structurally complex, macroalgae-dominated seascapes (such as kelp forests) to expanses of coralline-encrusted rock due to intense sea urchin grazing (Filbee-Dexter and Scheibling 2014). Even after the drivers of sea urchin outbreaks subside, these barrens often persist, sometimes maintained by other grazers such as limpets (Melis et al. 2019; Piazzi et al. 2016). While often associated with a loss of key ecosystem functions (Eger et al. 2024), coralline barrens are not devoid of life. They support diverse assemblages of benthic mega-invertebrates and can present structurally complex nongeniculate coralline species that provide habitat for a variety of organisms (Agnetta et al. 2024; Ramos et al. 2025).

Geniculate coralline algae are also major colonisers of rocky shores, forming coralline turfs. This habitat can be found worldwide across diverse environments, ranging from polar to tropical regions (Nelson 2009). Geniculate coralline algal turf habitats are characterised by the dense aggregation of geniculate fronds, forming cohesive mats that can reach heights of up to 15 cm (Connell et al. 2014). Their thalli, composed of stiff branches, provide a substratum for the attachment of numerous epiphytes (Soltan et al. 2001) while their three-dimensional structure fosters a high diversity of organisms, particularly small invertebrates (Kelaher and Castilla 2005; Berthelsen et al. 2014; Marchini et al. 2019; Ragazzola et al. 2021).

Finally, the IUCN GET recognises 'Rhodolith/Maerl beds' (M1.10) (Keith, Fragkopolou, et al. 2022). These coralline algal beds are aggregations of alive and dead free-living nongeniculate coralline algae that cover extensive benthic areas (Riosmena-Rodríguez 2017) and are common in fossil deposits (Aguirre et al. 2017). They are distributed worldwide and have a wide-depth range from intertidal to mesophotic zones (Davies et al. 2004; Wilson and Blake 2011; Pereira-Filho et al. 2012; Basso et al. 2016; Veras et al. 2020; Pierri et al. 2024). Here, we propose that FEG M1.10 is renamed as coralline algal beds—also including articulith beds (formed by geniculate coralline algal nodules) and removing linguistic uncertainty related to different morphotypes and locations. In the global typology, GET M1.10 is defined as benthic carbonate systems dominated by free-living, slow-growing, long-lived coralline algae covering 30%–100% of the seafloor within the beds, providing autochthonous energy to the system. In the GET definition, only nongeniculate coralline algae are included; however, the ecosystem properties, resources, ambient environmental conditions, disturbance regimes and biotic interactions used to define them could also be applied to free-living geniculate coralline algae (Keith, Fragkopolou, et al. 2022). For instance, rhodolith and maerl beds are grouped on the basis of moderate productivity (Martin et al. 2005; Riosmena-Rodríguez 2017; Qui-Minet et al. 2022), high associated biodiversity (Peña et al. 2014; Boyé et al. 2019; Helias and Burel 2023) and high structural complexity (Jardim et al. 2022; Bélanger and Gagnon 2023; Cabrito et al. 2024). Although understudied and possibly rare, articulith beds probably share most of these characteristics, are formed through similar processes and face similar pressures (Tâmega et al. 2017, 2021). Little is known, however, about the durability of the structure of articuliths, which may not be as long-lasting as the thalli formed by nongeniculate corallines—although closely packed thalli can protect geniculate corallines from breakage, a feature that may be enhanced in articuliths (Martone and Denny 2008a, 2008b).

6 | Conclusion

Inconsistent definitions can lead to ecological uncertainty and variable conservation policies for habitats with similar traits, functions and services and facing similar anthropic pressures. We have suggested a consistent set of terms to describe coralline algae and coralline algal habitats to help put them into a global context to support local actions and decision-making (Keith, Ferrer-Paris, et al. 2022). We highlight the importance of clarifying uncertain terms and simplifying dichotomies through contextualisation when using polysemic or synonymous terms. We resolve, in an integrative and adaptive way, a long-lasting debate on the use of the terms 'maerl' and 'rhodolith' through the umbrella term 'coralline algal beds' and explicit definitions that allow established terms in local and global scientific and management frameworks to coexist without creating uncertainty. Language is adaptative and ever-changing, and while a diverse coralline algal terminology reflects the widespread distribution and growing scientific and conservation relevance of the group, authors must have a contextualisation tool to simplify and clarify the terms they use. In this context, we urge the scientific community to adopt a more cohesive terminology for coralline algae, to improve scientific progression and international collaborations and to facilitate conservation, public understanding and stakeholder engagement.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

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

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.