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Review

Photoautotrophic Euendoliths and Their Complex Ecological Effects in Marine Bioengineered Ecosystems

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Abstract: Photoautotrophic euendolithic microorganisms are ubiquitous where there are calcium carbonate substrates to bore into and sufficient light to sustain photosynthesis. The most diverse and abundant modern euendolithic communities can be found in the marine environment. Euendoliths, as microorganisms infesting inanimate substrates, were first thought to be ecologically irrelevant. Over the past three decades, numerous studies have subsequently shown that euendoliths can colonize living marine calcifying organisms, such as coral skeletons and bivalve shells, causing both sub-lethal and lethal damage. Moreover, under suitable environmental conditions, their presence can have surprising benefits for the host. Thus, infestation by photoautotrophic euendoliths has significant consequences for calcifying organisms that are of particular importance in the case of ecosystems underpinned by calcifying ecosystem engineers. In this review, we address the nature and diversity of marine euendoliths, as revealed recently through genetic techniques, their bioerosive mechanisms, how environmental conditions influence their incidence in marine ecosystems and their potential as bioindicators, how they affect live calcifiers, and the potential future of euendolithic infestation in the context of global climate change and ocean acidification.

Keywords: bioerosion; ecosystem engineers; parasitism; mutualism; boring microflora

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1. Introduction

Autotrophic (cyanobacteria, and red and green microalgae) and heterotrophic (fungi) euendolithic microorganisms, discovered in the 19th century [1], actively penetrate the hard substrates in which they live [2]. Euendolithic organisms have been present on Earth since the Proterozoic, 2500 to 541 million years ago [3], coinciding with the appearance of oxygen in Earth's atmosphere, and are thus thought to have played a major role in the development and evolution of life, as well as in the production and destruction of carbonates [4–6]. Euendoliths are ubiquitous, as they can be found in almost every environment, geographical location, or depth, where the appropriate substratum (e.g., relatively soluble carbonate and phosphate substrates) is available and their biological requirements are met [4,7–11]. For example, photoautotrophic euendoliths are restricted to the photic zone, where there is sufficient light to carry out photosynthesis, and are particularly diverse and ecologically significant in marine environments [7,8]. They colonize a wide variety of carbonate substrates, from inanimate and dead carbonates to the calcified structures of live animals, such as the skeletons of hard corals, bivalve shells, and the thalli of crustose coralline

algae [12–16]. Since their discovery, numerous studies have been conducted on the euendoliths colonizing inanimate and dead calcium carbonates [8,17–20]. Initially, researchers speculated that the bioerosive activities of euendoliths had little to no effect on infested live calcifying organisms [21]. However, an increasing number of more recent studies suggest that euendolithic infestation has both negative and, surprisingly, beneficial effects on live calcifying organisms [22–25]. Bivalves, corals, and coralline algae create persistent physical structures that provide habitats for a wide array of associated species [26,27]. Thus, they are referred to as 'ecosystem engineers' and can form the basis of entire ecosystems [28,29]. Such marine ecosystems are under multiple anthropogenic pressures, including overexploitation, chronic pollution, and population fragmentation, and their responses to ongoing global climate change and ocean acidification remain uncertain [30,31]. Under such circumstances, the negative and beneficial effects of euendolithic infestation on individual live calcifying organisms have the potential to reverberate at the population, community, or ecosystem level, with complex, and potentially unexpected, ecological outcomes [32,33]. Understanding how euendolithic infestation interacts with other environmental stressors, and how these interactions will change under future environmental conditions is critical to predicting the long-term fate of such ecosystems.

Here, we focus on photoautotrophic euendoliths in the marine environment and their complex ecological effects on live calcifying organisms and the bioengineered ecosystems they create. This review discusses: (1) the nature of marine euendoliths and the techniques used for their observation, (2) the mechanisms involved in their bioerosive activity, (3) their incidence and distribution in marine ecosystems, in relation to various environmental parameters, and their potential as ecological indicators (*sensu* [34]), (4) how they affect today's living calcifying organisms, with a focus on corals, coralline algae, and bivalves, and (5) how euendoliths are anticipated to respond to global climate change, and particularly to ocean acidification.

2. What Are Euendoliths and How Are They Observed?

Initially thought to be part of the substrate morphology [1], microborings observed in calcium carbonate substrates were later correctly attributed to the activities of microorganisms, such as algae and fungi [35–37], which became known as 'endoliths'. The term 'endolith' refers to a morphologically and physiologically heterogenous group of microorganisms living within a rock or other stony matter, such as coral skeletons or animal shells [38], and more specifically, to organisms that actively bore into relatively soluble substrates, such as phosphate and carbonate substrates [2,8,39] (Figure 1).

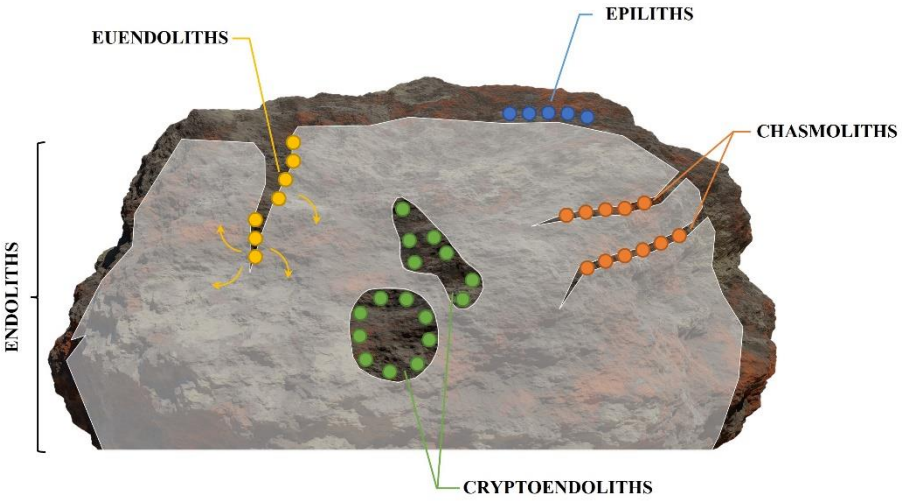

Figure 1. Types of endolithic organisms in relation to a hard rocky substrate (modified from [40]).

While more detailed classifications exist (e.g., [40]), a broad distinction is made among:

1. Epiliths that live on the surface of the substrate;
2. Chasmoliths that adhere to the surface of fissures and cracks in the substrate;
3. Cryptoendoliths that adhere to the surface of pre-existing cavities within porous rocks, including spaces produced and vacated by euendoliths, with no dissolution action;
4. Euendoliths that actively penetrate carbonate (and phosphate) substrates and reside partially or completely inside cavities of their own making.

These distinctions are not mutually exclusive as some organisms can display more than a single boring habit or may alter their habits during their life cycles. For example, several boring algae mature on the surface of shells and penetrate the substrate with endolithic filaments, while part of their thallus remains epilithic [41,42]. Endolithic green algae from the genus *Ostreobium* Bornet and Flahault (1889) switch to a chasmolithic lifestyle after reaching larger cavities within the substrate [43]. Some red algae from the genera *Porphyra* C. Agardh (1824) and *Bangia* Lyngbye (1819) can exhibit an endolithic lifestyle during the early stages of their life cycle, called the conchocelis phase, while occurring in a wide variety of habitats as adults [44,45].

The first descriptions of euendoliths were derived from dead mollusk shells gathered from the coast [35,46]. Euendolithic green algae were observed through a thin shell fragment, forming a horizontal layer parallel to the surface, with an underlying network of ramifications into the substrate. Relatively inaccessible (Figure 1), euendolithic microorganisms and their microborings require basic but specific techniques to be studied [8,42,47].

These include:

1. Isolation of endoliths. After fixing the sample (substrate and euendoliths of interest) in formaldehyde solution to prevent structural damage to enclosed euendolithic organisms, the surrounding carbonate substrate is usually dissolved using dilute acid. The released endolithic filaments can then be observed and identified under light microscopy or transmission electron microscopy (TEM) [8]. As the hard matrix supporting the euendolithic filaments is dissolved, the organic components of the boring collapse, making spatial relationships and growth arrangements difficult to reconstruct. This technique only allows a qualitative assessment of euendolithic communities but is still widely used to detect and identify euendoliths of interest [15,48,49].
2. In situ observations. Microborings can be studied in standard petrographic thin sections or sufficiently transparent fragments of shells using light microscopy [50] or scanning electron microscopy (SEM). The 2D visualization of microborings by petrographic thin sections is of limited use for the study of 3D objects, such as empty or filled euendolithic microborings, but allows their observation and the estimation of their true penetration depth in association with the surrounding matrix [42].
3. Cast-embedding of microboring networks [8,42,51]. Combined embedding and casting in polymerized resins preserves the spatial arrangements of boring tunnels (3D architecture) and the euendolithic organisms in situ [51], allowing proper examination after the dissolution of the surrounding substrate (routine protocol in [8], see Figure 2 in [42]). Such casts can then be observed using light microscopy or SEM. However, this technique is limited when microborings are filled by secondary carbonate precipitation following the death of the euendoliths [42].
4. Cultivation [48,52,53]. Natural samples (e.g., shell fragments, ooids) harboring euendoliths are used to inoculate agar plates containing a chemically defined culture medium. Once single colonies grow enough to be mechanically isolated, each colony is transferred into a liquid medium and stored under specific environmental conditions. While cultivation selects heavily for fast-growing microorganisms, it is a valuable tool to confirm taxonomic identification and to investigate the life history and physiology of euendoliths [44,45,54]. Cultivation also represents a necessary step to build the databases used for the identification of environmental DNA sequences [52].

5. X-ray computed tomography (CT) and micro-computed tomography (micro-CT) (reviewed in [55]). These non-destructive 3D-visualization tools are firmly established for paleontological investigations, with their highest resolution encompassing the spatial magnitude of microborings [56–58]. They are, however, still relatively expensive and time-consuming, and require a high level of technical skill [55,58]. More affordable micro-CT and associated analyses can underestimate the extent of bioerosion by photoautotrophic euendoliths [57], as microborings range between 1 and 100 µm in diameter [32]. Micro-CT does, nonetheless, allow the investigation of microborings (empty or filled) within substrates that cannot be altered or dissolved (e.g., type material).

Most techniques used to observe euendoliths focus on the characteristic pattern of their microborings (i.e., form, diameter, direction, length, and pattern of the tunnel), which allows taxonomic identification even in the absence of the organism itself. Different euendolithic species boring into the same substrate and under uniform ecological conditions will produce distinctive boring patterns, in terms of size, shape, and mode of branching of tunnels [59]. Both biological and mineralogical factors should be considered in the characterization of microborings. While the size, frequency, and branching patterns of microborings are dictated by the size and properties of the euendolithic organism, the directions of growth and the fine sculpture of the inner surface of the microborings are influenced by the mineralogical properties of the substrate [8,59]. Critically, a single euendolithic species can display a large variety of morphologically different patterns when boring into different substrates or under different ecological conditions of light and water supply, amongst others [8]. For example, the microborings produced by intertidal euendolithic cyanobacteria are shallower and composed of straight tunnels where desiccation is high, in the supratidal or upper intertidal, while being deeper and tortuous in areas with stagnant water or lower on the shore [8]. These factors reduce the accuracy of taxonomic identification using microborings. Moreover, euendolithic organisms often exhibit few distinguishing morphological features, making taxonomic identification via direct observation equally unreliable [60]. While morphological features of the organism or its traces (i.e., microborings) are useful in the initial discovery of unknown entities, taxonomic identification is best achieved using genetic and molecular techniques [60] and/or cultivation [52].

Used as a complement to morphological descriptions, single- and multi-marker genetic approaches allow the identification of cryptic clades and/or species within euendolithic species complexes and provide tools to determine the composition of natural euendolithic communities. For example, two species within the green algal genus *Ostreobium* were described using morphological features [35,61], whereas up to 95 delimited cryptic species have been identified within this genus using genetic and molecular techniques [62–67]. Environmental DNA (eDNA) metabarcoding allows the automated identification of multiple euendolithic species from a single sample, either containing entire organisms or a piece of substrate containing degraded DNA/RNA (e.g., coral skeleton, bivalve shell), by targeting the amplification and sequencing of one or several specific DNA/RNA regions using universal primers [68]. The composition of euendolithic communities can be investigated using multiple markers, including 16S rRNA and 23S rDNA targeting bacteria and cyanobacteria [64,67,69,70], and 18S rRNA, rbc*L*, and *tuf* A targeting chlorophytes [54,63,65,67,71]. Moreover, the use of eDNA metabarcoding, in combination with other techniques, such as microscopy, spectrophotometry, and cultivation, has revealed previously undisclosed diversity of prokaryotic and eukaryotic endolithic organisms [52,64,67] and can help resolve their phylogenetic history [64]. For example, euendolithic green algae almost exclusively belong to the class Ulvophyceae, in which the ability to bore evolved independently over 20 times [64], while the cyanobacterium *Acaryochloris marina* Miyashita and Chihara (2003) has been recorded for the first time in the skeleton of live corals using eDNA [64] and produces chlorophyll-*d*, allowing it to use far-red light for photosynthesis and thus to occupy niches depleted of visible light [72]. Finally, the correct identification of the euendolithic species is fundamental in the study of euendolithic communities and

their impacts, as different strains within the same species complex (e.g., *Ostreobium quekettii* Bornet and Flahault, 1889) can differ in their physiology [73,74].

3. How Do Euendoliths Erode Calcium Carbonate?

To understand biologically mediated carbonate dissolution, the basis of biotic carbonate precipitation in its simplest form needs to be revisited. Through their metabolic activity, small cells or organisms indirectly create a microenvironment where the concentrations in the chemical species present increase the local precipitation of carbonate, such as calcification by photosynthetic cyanobacterial communities [75,76].

At slightly alkaline or neutral pH, oxygenic photosynthesis can be expressed as:

$$HCO_3^- + H^+ \rightarrow C(H_2O) + O_2 \quad (1)$$

Protons effectively consumed by oxygenic photosynthesis can then drive the thermodynamic equilibrium of carbonate dissolution–precipitation (with the equilibrium constant expressed as K_{s0}) toward the solid phase (indicated by (s); here, calcium carbonate):

$$CaCO_3\ (s) + H^+ \leftrightarrow Ca^{2+} + HCO_3^-\ ;\ K_{s0} \quad (2)$$

The free energy of dissolution ΔG is given by:

$$\Delta G = RTln(\frac{IAP}{K_{s0}}) \quad (3)$$

where R is the ideal gas constant (8.314 $J{\cdot}K^{-1}{\cdot}mol^{-1}$); T, the absolute temperature (in Kelvin); K_{s0}, the equilibrium constant of carbonate dissolution–precipitation; and IAP is the ion activity product [77]. If $IAP > K_{s0}$, carbonate precipitation will be thermodynamically favored whereas if $IAP < K_{s0}$, dissolution will be favored. Through their autotrophic metabolism, cyanobacteria and microalgae promote the alkalinization of the medium, increasing local carbonate precipitation. Furthermore, in the case of marine euendoliths, seawater is supersaturated with respect to calcite and aragonite, making carbonate dissolution thermodynamically unfavorable [78]. This leads to an apparent geomicrobial paradox in photoautotrophic euendolithic organisms [78]: how do they achieve local carbonate dissolution, essential for boring, although their autotrophic nature and their surrounding environment should enhance local carbonate precipitation?

The exact mechanisms by which euendolithic organisms bore into carbonate substrates have long remained elusive [4,46,78–81], with several possible mechanisms being suggested for euendolithic cyanobacteria and later discarded [78,82]. Indeed, suggested boring mechanisms in cyanobacteria need to be consistent with observations and physiological and geochemical principles [78]. Specifically, they need to fulfill three necessary conditions:

1. The dissolution process is thermodynamically unfavorable, as it mainly occurs in waters saturated with calcium carbonate (i.e., calcite and aragonite). Excavation then becomes an ATP-driven active process with an energetic cost;
2. The carbonate-dissolving mechanisms must be localized at the "head" of the microborer (i.e., apical cells) as dissolution produces true tunnels, with the typical "negative" shape of the borer [59];
3. The proposed mechanisms must allow for the conservation of mass and electrical charge as in chemical reactions, the mass and the electrical charge of the components before the reaction must be equal to the mass and the electrical charge of the components after the reaction.

Previously proposed mechanisms included the excretion of weak organic acids, the separation of antagonistic photosynthetic and boring activities, and enzymatic dissolution [79,80,83], but none fulfill all three conditions listed above [78,82].

Garcia-Pichel subsequently proposed an alternative boring mechanism, coined 'The Calcium Pump', which relies on the active transport of Ca^{2+} through the cyanobacterial trichome, leading to low concentrations of free Ca^{2+} at the end of the borehole, which in turn decreases ion activity product below levels that would make dissolution thermodynamically favorable (i.e., $IAP < K_{s0}$; Figure 2) [78]. The participation of P-type Ca^{2+} ATPases and evidence for transcellular Ca^{2+} transport have been demonstrated for strains of one of the most common cyanobacterial euendoliths, *Mastigocoleus testarum* Lagerheim ex Bornet and Flahault (1886) [82,84]. Long-range Ca^{2+} transport within the cyanobacterial filament is made possible through two unique cellular adaptations discovered in this cyanobacterium: active pumping of Ca^{2+} is orchestrated by the preferential localization of P-type Ca^{2+} ATPases at one pole of the cell, while specialized cells, called calcicytes, allow fast Ca^{2+} transport at low, nontoxic concentrations throughout undifferentiated cells (Figure 2). Calcicytes also act as a buffer against excessive, detrimental Ca^{2+} concentrations before final excretion from the borehole [84]. Furthermore, 'The Calcium Pump' model fulfills the three necessary conditions enumerated earlier: it is an active process, localized at the end of the borehole, which allows for the conservation of mass and electrical charge [78]. The model is also consistent with the observation of microetchings [79,85], which, in the absence of hard or moving parts in cyanobacteria, points towards carbonate dissolution by cation removal, and with the range of bored substrates, which share Ca^{2+} as a common denominator [78]. Finally, it alleviates reprecipitation of calcium carbonate within the borehole thanks to the intracellular transport of Ca^{2+} [78]. While these studies have shed light on the boring mechanism for euendolithic cyanobacteria [86], details regarding the boring mechanism carried out by other photoautotrophic euendoliths have still not been investigated in depth. However, Krause et al. have recently demonstrated the existence of active calcium uptake by the green alga *Ostreobium quekettii*, occurring at the apical tip of the siphonal thallus, in a process similar to that exhibited by cyanobacteria [87]. All microborers exclusively use chemical bioerosion [32,78] and with regards to these latest findings, further studies are required to reveal the exact boring mechanism of endolithic green and red algae.

As to why euendoliths bore, Garcia-Pichel et al. suggested that they are metabolically dependent on the substrate for dissolved carbon dioxide CO_2 released during substrate excavation that can be used for photosynthesis [82]. Euendoliths preferentially fix carbon from the most readily available source, either from the atmospheric pool of dissolved CO_2 or the mineral substrate they bore into [88]. When dissolved CO_2 is limited, euendolithic microorganisms, such as *Mastigocoleus testarum*, grow preferentially as euendoliths and thus, derive most of their carbon from the mineral substrate they excavate [88]. By doing so, euendoliths can complete their geomicrobial action on the substrate and potentially gain a competitive advantage over photosynthetic epiliths, which may suffer from limited dissolved CO_2 access as the epilithic biofilm thickens [88]. Considering a variety of possible selection pressures (e.g., nutrient acquisition, protection from UV and/or predators), Cockell and Herrera suggested that the boring behaviors of euendoliths could also have originated as mechanisms against entombment by mineralization, especially in substrates with high mineralization rates [81].

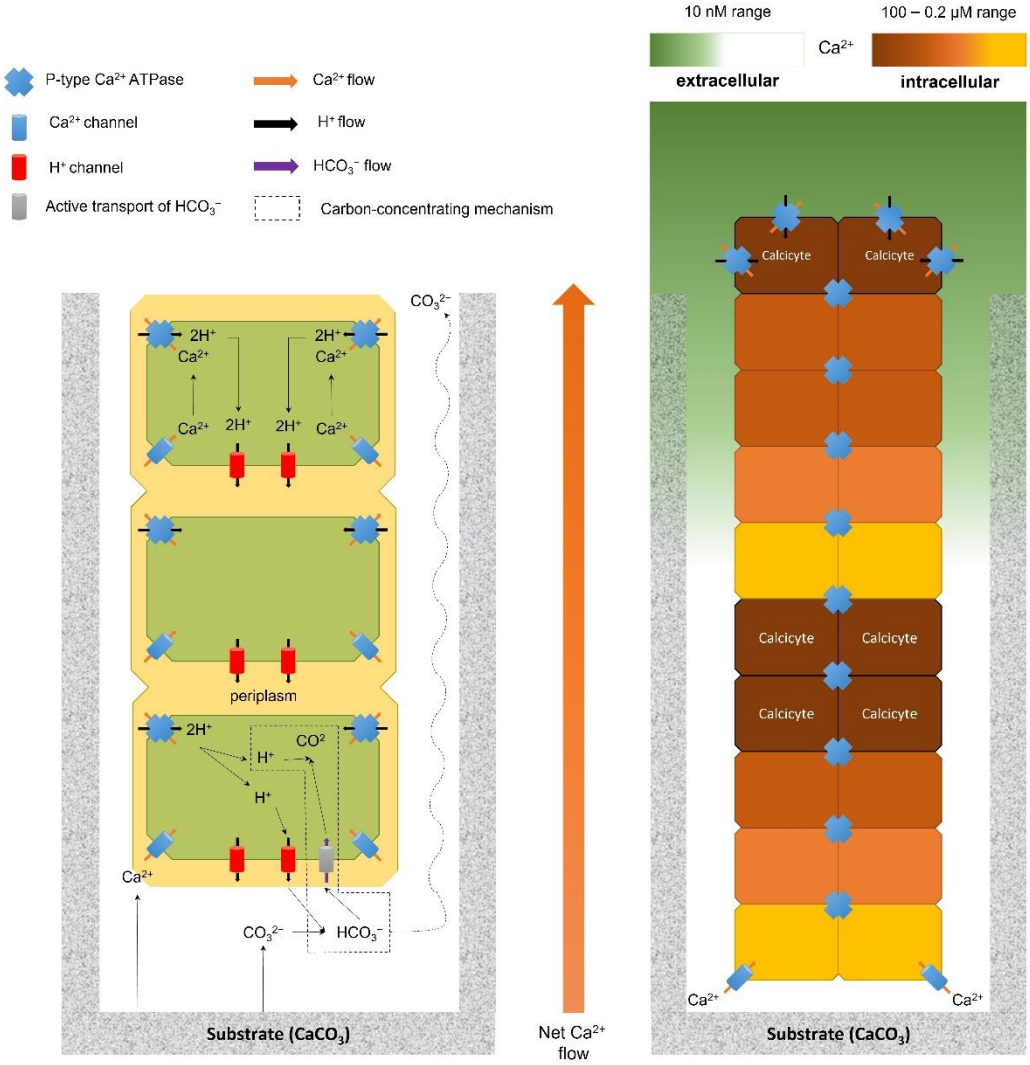

Figure 2. (Right panel). Proposed 'Calcium Pump' transport mechanism within the trichome of euendolithic cyanobacteria (both filamentous and pseudofilamentous), with the inferred distributions of transporter components (legend in the upper left corner) and the potential fates of the calcite dissolution products (Ca^{2+} and CO_3^{2-}). The calcium transport unit consists of repeating individual bipolar cells, where one pole is specialized for calcium uptake and the opposite for calcium extrusion. Conversion of carbonate ions CO_3^{2-} released from calcite into HCO_3^- is promoted by the counter-transported protons. This HCO_3^- is then actively transported within the cell, where it is converted into CO_2 through the carbon-concentrating mechanisms and can then be used in photosynthesis [89]. (Left panel) Holistic calcium ion localization during boring, with relative calcium concentrations within each compartment indicated. Calcicytes allow a higher proportion of cells within the trichome to remain photosynthetically active by controlling intrafilamentous calcium flow (modified from [90]).

4. Incidence of Photoautotrophic Euendoliths in Marine Ecosystems

Photoautotrophic euendoliths have a cosmopolitan geographical distribution and have been recorded in a variety of habitats, including terrestrial [9,91], freshwater and volcanic lakes [11,92], brackish [93], and marine environments [4,94]. Euendoliths are ubiquitous in the marine environment, occurring in enclosed seas, such as the Adriatic Sea [16] and the Mediterranean Sea [95,96], in cold-temperate [97–99], tropical waters [13,100–102], as well as in the Arctic and Antarctic [94,103]. Present essentially anywhere, there is sufficient light to allow for photosynthesis and a carbonate substrate to bore into; euendolithic communities play an important role in ecological processes in the marine environment [4,104]. Although they appear to erode virtually all suitable substrates, the distribution of eu-

endoliths and the composition of euendolithic communities are extremely variable and depend on light availability, the nature of the substrate, and a variety of abiotic and biotic environmental factors acting in synergy [19,52,105].

4.1. Light Availability

As photosynthetic organisms, light availability is the major determinant of euendolithic activity and distribution and has a strong influence on the composition of euendolithic communities [105], reflecting the specific light requirements of different species [106]. In most marine habitats, light availability is highly variable and is influenced by the topography of the area, the presence of 3D structures, the nature of the substrate, and water depth.

Euendoliths are more abundant, and erosion more severe, in microhabitats with high light availability, such as sun-exposed surfaces in the intertidal, mostly horizontal, and moderately inclined surfaces high on the shore [14,107–109], or in shallow waters [105], compared to microhabitats with low light availability, such as down-facing and shaded substrates [107,110,111]. Reduction of light availability at polluted sites [112,113] or in habitats at greater depths [101,105] similarly reduces euendolith abundance. Geographically, photoautotrophic euendoliths are more abundant, and erosion more severe, at lower latitudes than higher latitudes, in both the intertidal and underwater [33,111,114,115]. As boring by euendoliths is an active mechanism, it is often restricted to environmental conditions optimal for growth [116]. As solar irradiance increases and cloud cover decreases, the depth of the photic zone increases towards lower latitudes [114]. At higher latitudes, temperatures and light availability are generally low and highly seasonal [115], with a prolonged night and ice cover towards the poles [94,103,117] and a condensed photic zone [111,114]. Combined, these unfavorable environmental conditions slow down euendolithic infestation and limit photoautotrophic euendolithic communities to a few specialist species capable of coping with such adverse conditions.

While the composition of euendolithic communities shifts as light availability decreases with increasing depth, their bathymetric distribution is consistent around the world (see Tables 1 and 2 in [42]) [8,19,105,110,111,114,118–123]. Euendoliths are ubiquitous in the supratidal, intertidal, and wave spray zones [124], where assemblages are dominated by cyanobacteria and chlorophytes, referred to as the CyChlo-association [105], in sediments [101] as well as mollusk shells and coral skeletons [14,97,105]. In the shallow photic zones, the additional conchocelis stages of rhodophytes can be observed (CyChloRho-association) in the early stages of colonization [105]. In the disphotic zone or in shaded microhabitats, where light availability is dramatically reduced, only heterotrophs and low-light specialists amongst the photoautotrophs occur, forming the so-called OstPleHet-association [10,97,105]. These include the cyanobacterium *Plectonema terebans* Bornet and Flahault ex Gomont (1892) and the chlorophyte *Ostreobium quekettii* that have been recorded down to about 300 m [125–127]. Finally, heterotrophic organisms (i.e., fungi and bacteria) dominate the benthic assemblages of the deep, aphotic zone. At a finer scale, different clades within the same euendolithic species can be distributed along a depth gradient, suggesting different physiological traits [63]. Not only does the composition of euendolithic communities change with depth, but also with time, as mature euendolithic communities, even in shallow, clear waters, are dominated by the OstPleHet-association [105].

4.2. Nature of the Substrate

Photoautotrophic euendoliths colonize a wide range of carbonate substrates, from compact limestone and loose sediments to living calcifying organisms or their fragmented remains [8]. Euendoliths have been recorded in the skeletons of corals [13,32,128] and coralline algae [15,16,129], in the shells of mollusks [14,100,130] and brachiopods [131], in the tests of foraminifera [124], in the calcareous tubes of annelids [99] and the plates of barnacles [103], and in sclerosponges [132].

Colonization by and distribution of euendoliths is intrinsically influenced by the nature and physical properties of the substrate, such as its mineralogy, porosity, translucency, density, or architecture [39,52,101]. While most euendoliths appear to be generalists, substrate preferences are found in some, such as the cyanobacterium *Mastigocoleus testarum* that bores into calcium carbonate substrates but not into other carbonates [39,116]. Skeletal remains of calcifying organisms are more susceptible to euendolithic infestation than other carbonate substrates [43,50,101,133], with the highest levels of an infestation occurring in the densest and least porous substrates. Within skeletal remains, the high-Mg calcite skeleton of crustose coralline algae is more susceptible to dissolution than the skeletons of massive or branching corals or bivalve shells, which are mostly composed of aragonite [134,135]. In shallow waters, the depth of penetration of euendoliths in dead coral skeletons nearly approximates that in live bivalve shells [19,100–102]. This is a result of the higher porosity and translucency of the coral skeleton [32], and the presence of organic lamellae (i.e., conchiolin) within bivalve shells that slow down excavation by photoautotrophic euendoliths [50]. Only heterotrophic euendoliths, such as fungi, can penetrate and proliferate into organic lamellae, as they feed on the organic matter [50,100,136].

In live calcifying hosts (e.g., corals, coralline algae, bivalves), a wide range of defenses prevents the colonization of the calcified parts by euendoliths. Coral skeletons are protected by the polyp tissue [13,121,137], while coralline algae have the capacity of sloughing their protective epithelial cells to prevent biofouling [138]. Bivalve, brachiopod, and other mollusk shells have a protective layer, the periostracum, which deters fouling organisms [139–143]. Nonetheless, the incidence of euendolithic infestation in live calcifying organisms is high around the world, independent of the location or the substrate. Nearly all corals around the world have been recorded as infested by euendoliths [13,128,132], while up to 90% of bivalves shells are infested on rocky shores worldwide [14,96,107,108]. After the death of the calcifying organisms, colonization becomes more intense, as euendoliths do not have to overcome the active or passive defense mechanisms of the host or adjust their boring performances to carbonate accretion rates of living organisms [13,15,101,137]. In newly available dead carbonate substrates, a succession of microborer communities can be observed, boring from the surface down into the substrate [13,144–146]: (i) pioneer species, such as the large chlorophyte *Phaeophila* sp. Hauck (1876) and the cyanobacterium *Mastigocoleus testarum*, settle within the first three months, (ii) these are followed by an intermediate stage, between 3 and 6 months, where the chlorophyte *Ostreobium* sp. starts to dominate euendolithic communities, and (iii) the final stage, largely dominated by *Ostreobium*, after more than 6 months of exposure.

4.3. Biotic and Abiotic Environmental Factors

In addition to light, biotic, and abiotic environmental factors can act in synergy to influence the composition and density of euendolithic communities, as well as their rates of microbioerosion. In the intertidal, the abrasive effects of sand and other sediments carried by the winds or the waves favor the initial colonization of the substrate by euendoliths, and ultimately increase the severity of infestation in mussels [14]. Meanwhile, in shallow waters, nutrient concentration, epilithic cover, and the presence of macroborers and macrograzers interact to shape euendolithic communities [19,147–149]. This interaction operates through several mechanisms:

1. Photoautotrophic euendoliths penetrate the substrate until they reach their compensation depth, where photosynthesis balances respiration, after which boring either stops or proceeds parallel to the surface [19,122,150];
2. Grazers are attracted to the substrate by the presence of photoautotrophic euendoliths, as these represent a renewable source of food [15,19,151]. The boring activity of euendoliths weakens the superficial layers of the substrate, which can facilitate the settlement of macroborers with their own bioerosive activity, as well as grazing;
3. On the one hand, macrograzers constantly remove the superficial layers of the substrate, thus extending the depth to which the light can penetrate and, therefore,

the depth to which the endoliths can bore, increasing microboring rates [150,152]. Grazing also reduces the settlement and growth of epilithic organisms that compete with euendoliths for space and diminish light availability [17]. On the other hand, macroborers excrete different waste products within the infested substrate, such as ammonium, phosphates, or CO_2. Such waste products act as fertilizer for euendolithic communities, which increase in abundance, biomass, and productivity in the vicinity of macroborers [149,152,153].

Under intense grazing pressure, euendolithic growth and boring rates cannot keep pace with the rapid removal of the substratum by grazers, resulting in lower microboring rates [119]. If grazing exceeds euendolithic boring rates, the food resource is eventually exhausted, and the denuded surface must be recolonized: intense grazing impedes the development of euendolithic communities so that they rarely reach maturity [18,119]. Different groups of organisms are more or less efficient at grazing [113]. Sea urchins are efficient grazers compared to fish, and remove a larger portion of the carbonate substrate, resulting in a lower measurable boring activity of euendoliths in sites with higher densities of sea urchins than of fish [113,119,154,155].

Depending on its nature, the epilithic communities covering the bored substrate can also influence the abundance and composition of euendolithic communities, by diminishing light availability and attracting/deterring macrograzers [105,113,119,122,156]. With time, epiliths start to colonize the surface of the bored substrate and become denser, filtering out light for the underlying euendolithic communities. Interactions between epilithic cover and euendolithic communities are generally reported for substrates exposed for long periods of time, usually >6 months [105,122,157,158]. Under low grazing pressure, the pioneer species *Mastigocoleus testarum* dominates euendolithic communities on experimental substrates covered with algal turfs, joined by the low-light specialists *Plectonema terebrans* and *Ostreobium quekettii* on shaded substrates covered with crustose coralline algae or macroalgae [113,119]. Depending on its nature, the epilithic cover can influence the intensity of macrograzing on the bored substrate: algal turfs attract macrograzers while crustose coralline algae and macroalgae, which are unpalatable or inedible for most grazers, act as a deterrent [119,151,154].

Nutrient concentrations in the surrounding environment influence the abundance, species composition, and microbioerosion rates of euendolithic communities, as well as the density and species composition of the epilithic communities [112,119]. At sites subjected to eutrophication, microbioerosion rates by euendoliths are higher than in more oligotrophic waters, in association with either low [119] or high grazing pressure [152]. Conversely, nutrient-enriched turbid inshore waters are characterized by lower microbioerosion rates compared to clear oligotrophic offshore waters at the Great Barrier Reef, suggesting that increased turbidity resulting from the entrapment of sediments in the epilithic cover at inshore sites diminishes light availability and, thus, restricts euendolithic colonization, even at high nutrient concentrations [113]. Elevated concentrations of inorganic nutrients (e.g., nitrogen, phosphorus) drastically increase the severity of colonization, the depth of penetration, and ultimately the microbioerosion rates of euendolithic communities, especially in the absence of macrograzing [156–158]. Different euendolithic taxa display variable responses to the addition of nutrients, depending on the nature of the nutrient and the specific limitations of the euendoliths; while heterotrophic euendoliths increase in abundance when exposed to increased levels of organic matter, euendolithic green algae and cyanobacteria react to higher levels of nitrogen and phosphate, respectively [156–158]. In live calcifying substrates, the effects of nutrient addition on euendolithic communities can be mitigated by the host response to the same nutrients. For example, when phosphorus is added, the skeletal growth rates of hard corals increase and "dilute" euendolithic communities, as they are unable to keep up with increased coral growth [159]. Additionally, nutrient concentrations can influence the species composition and density of epilithic communities [112], with an indirect impact on the underlying euendolithic communities [105,119,122]. In coral reefs with low nutrient loads, the epilithic cover is dominated by algal turfs associated with

pioneer euendolithic species that require high light intensities, while in reefs subjected to eutrophication, the dominance shifts to macroalgae and crustose coralline algae, diminishing light availability for an underlying euendolithic community abundant in low-light specialists [119].

4.4. Photoautotrophic Euendoliths as Bioindicators

With their specific niche specializations, in terms of nutrition, light, temperature, nutrient concentrations, and other physical parameters, and the characteristic microborings they produce, photoautotrophic and heterotrophic euendoliths can be used as present geographical, water quality, and paleobathymetric bioindicators at the species or community level [8,124]. Similarly, fossil euendoliths could potentially be used as indicators of past temperatures, salinity levels, or trophic dynamics, but more research is still needed [42]. Some euendoliths, such as members of the genus *Ostreobium*, display a complex biogeographical distribution. *Ostreobium* has been found in abundance on temperate coasts but becomes rare in tropical waters [50,133], showing a clear latitudinal pattern. Within the genus, *Ostreobium quekettii* dominates endolithic assemblages in nearly all corals, while *O. constrictum* K.J. Lukas (1974) and *O. brabantium* Weber Bosse (1932) have only been found in the Atlantic and Pacific Oceans, respectively [61]. More recently, del Campo et al. revealed a complex biogeographical distribution of three identified clades within the genus *Ostreobium* across coral reefs [160]. However, there is a need for more recent and detailed regional comparisons of the incidence of individual euendolithic species and the composition of euendolithic assemblages, as advances in molecular genetic techniques and the use of polyphasic approaches allow better detection and taxonomic identification of euendolithic specimens [52,64,67].

Photoautotrophic euendoliths have the potential to be employed as indicators of water quality and/or pollution [156–158,161,162]. The composition of euendolithic communities shifts depending on the concentrations of inorganic nutrients and organic matter in the surrounding environment [156–158]. In the Arabian Gulf, oil pollution is responsible for a dramatic decrease in the abundance of live euendoliths and microbioerosion rates on foraminifera [161], while in Italy, benthic foraminifera demonstrate increased levels of euendolithic infestation by photoautotrophic euendoliths in sites with heavy metal pollution [162,163].

Modern euendolithic bathymetric distribution can be reliably used as an indicator of the current depth, as it can be cross-checked by direct measurements of the physical parameters. Through their boring activity, microbial euendoliths leave traces, as an "instant fossil" in the sedimentary record, each with its own bathymetric range [124] and remarkable constancy through time. While single fossil traces can be used for the identification of individual ichnotaxa, the study of euendolithic trace communities (or ichnocoenoses) within the substrate allows for paleobathymetric and paleoecological reconstructions over geological time scales [8,20]. The light-dependence of photoautotrophic euendoliths thus reveals itself as a useful tool to determine the limit between past photic and aphotic zones [20]. The study of fossil trace assemblages in paleodepth reconstruction allows for a finer detection of past sea level variations than other commonly used methods [120], such as the analyses of the successive coralgal communities [164]. However, fossil microborings should be compared with modern microborings from similar substrate types [120,122] and the ichnocoenoses described must be directly compared with modern assemblages for interpretation [8]. Indeed, a bathymetric ichnocoenoses index could provide misleading paleobathymetric conclusions in shallow waters when 3D-underwater structures (e.g., reefs) create heterogeneous light conditions on the infested substrate (i.e., illuminated, shaded, and cryptic habitats) at the same depth [98,110,165]. Similarly, the investigated substrate could have been translocated from shallow depths to its deposition site [42]. Thus, fossil microborings should be viewed as semiquantitative rather than absolute indicators of paleophotic zones [165,166].

5. Photoautotrophic Euendoliths in Marine Bioengineered Ecosystems

While numerous studies have assessed euendolith-induced biodegradation of carbonate skeletal materials, until recently, severe harm to living host organisms was understood to be limited to the erosive activity of invertebrates or fungal borers [21]. Due to low light penetration within the substratum, photoautotrophic euendoliths were generally thought to be unable to inflict significant structural damage on live organisms, as they eroded only the uppermost layers of the carbonate substrate [21]. Over the last three decades, mounting evidence has shown that the eroding activity of photoautotrophic euendoliths can be the source of severe, often lethal, damage to living calcifying organisms [22,24,107]. However, the presence of euendoliths has also been observed to have beneficial effects [23,25,108].

Here, we focus on three groups of calcifying organisms, i.e., corals, crustose coralline algae, and bivalves, and describe the process of colonization by euendoliths in live hosts, their incidence, and their detrimental and beneficial effects on the individual host, as well as on the bioengineered ecosystem (summarized in Table 1), i.e., coral reefs, coralline algal mats, and bivalve beds.

Table 1. Summary of the negative and positive effects observed and suspected (underlined) of euendolithic infestation on the physiological parameters, calcified structures, biological interactions, and bioengineering qualities of main live calcifying hosts.

Responses to Endolithic Infestation	Live Calcifying Hosts				References
	Corals	Coralline Algae	Bivalves	Others	
Physiological Parameters					
Growth	↓ =		↓	↓	[22,24,143,167–169]
General condition	=		↓		[22,96,107,167,170–172]
Reproduction			↓	=	[22,168,173,174]
Attachment strength			↓		[107,172,173]
General survival	↑ =		↓ †	↓	[14,22,73,143,144,170,171,173,175,176]
Individual survival to heat stress	↑ (lim)		↑ (lim)		[23,25,33,108,109,115,177,178]
Calcified structures					
Microbioerosion	↑	↑↓	↑	↑	[13,15,22,108,129,143,169,179]
Thickness	↑		↓ †	↓	[22,24,98,143]
Strength	↓		↓ †	↓	[22,107,143,169,172,174–176,180]
Porosity	↑	↑	↑		[13,15,24,108]
Deformations	↑		↑ †	↑	[14,24,96,174,181–183]
Maintenance costs	↑		↑	↑	[22,24,96,98,143,168,181]
Mineralogy		~	~		[96,135]
Biological interactions					
Epibionts			↑		[172]
Predators	↑		↑		[107]
Grazers	↑		↑	↑	[151,176]
Photoautotrophic euendoliths	↔	↔	↔		[15,24,108,144,170,171]
Bioengineered ecosystems					
Architectural complexity		↑↓	↓		[129,135]
Coastal protection from waves and other stressors	↓	↑↓	↓	↓	[107,129,135,174,175,179]
Mitigation of environmental stressors for associated species			↑		[33,109,115]
Resistance to anthropogenic stressors			↓		[175,184]

Symbols for effects: (=)—no effect; (↑)—positive effect, reinforcement; (↓)—negative effect, reduction; (↓↑)—variable responses depending on the host species and/or environmental conditions; (~)—alteration in the composition of the parameter; (†)—mortality observed in the host species; (↔)—mutualistic relationship; (lim)—effect observed during unusual harsh environmental conditions (i.e., heatwaves). Please note that some effects presented in this table are based on observations of a single species or different life cycle stages of the host species.

5.1. Corals and Crustose Coralline Algae

In live corals, the colonization of the skeleton by euendoliths from the water column is prevented by the polyp tissue [121,137,181]. In young coral recruits, the entire corallite (i.e., part of the skeleton elaborated by a single polyp) is tightly covered with polyp tissue [128,167,185], which efficiently protects the underlying calcareous skeleton from infestation by other life stages of endolithic organisms (e.g., propagules, epilithic biofilms), thanks to its superficial mucus and cnidocysts. In some instances, the polyp tissue retracts towards the proximal portions of the coral colony, either temporarily when corals are under major thermal stress [186] or permanently in the case of solitary corals [187], leaving the skeleton unprotected. Therefore, photoautotrophic euendoliths have the ability to colonize the coral skeleton from its base, as soon as the larvae settle on an already-infested substrate [167], or to enter through the exposed skeleton through lateral fissures or when the polyp tissue retracts [186,187]. In live crustose coralline algae (Corallinophycidae), colonization by photoautotrophic euendoliths from the surface is prevented by the presence of live cells (as for corals), capable of 'sloughing' as a defense against biofouling [138,188]. With crustose coralline algae (CCA) growing apically, the live tissue remains in the upper part of the thallus, giving it a red color, leaving empty calcified cell walls at the basal layer of the thallus, which turns whitish-gray [15,16]. Without the protective live tissue, euendoliths colonize CCA from its basal layer, which can be in direct contact with an already-infested substrate [15,16]. Thereafter, photoautotrophic euendoliths have to match or exceed skeletal calcification rates, by positive phototrophic growth orientation (i.e., growing from the inside of the skeleton towards the surface) and high rates of growth and carbonate penetration [13,15]. Only a few euendolithic organisms have adapted to low-light conditions, such as the cyanobacterium *Plectonema terebrans*, the chlorophyte *Ostreobium quekettii*, and less frequently some conchocelis stages of Bangial rhodophytes, are known to keep pace with coral growth [13,61,63,137,181,189,190]. In addition, the cyanobacterium *Mastigocoleus testarum* can be found in live CCA crusts [15,16,128], and *P. terebrans* has been observed boring directly into CCA calcified cell walls [191]. Areas of dense euendolithic growth are often correlated with areas of slower growth in corals, as shown by the patterns of colored bands in massive, slow-growing corals [13,192–194]. In fast-growing corals, such patterns are less clear [195], with euendoliths being more abundant in the middle part of the skeleton [159]. The distribution of euendolithic organisms is, however, not limited to the colored bands as they can be present in most regions of the skeleton although in insufficient densities to be visible [13]. In the same fashion, euendolithic infestation in live CCA crusts forms a green band underneath the live tissue [15]. Photoautotrophic euendoliths are ubiquitous in live zooxanthellate corals (Symbiodiniaceae [196]), with 100% of Atlantic, Indian, and Pacific corals being infested [13,132,144,192,193]. In the southern Chilean fjords, 83% of the colonies of the azooxanthellate *Desmophyllum dianthus* Esper (1974) were infested in the euphotic zone [128]. Photoautotrophic euendoliths have been recorded from live crustose coralline algae in the Mediterranean Sea and the Pacific Ocean [15,16].

The negative effects of endolithic infestation on live corals have largely been demonstrated in azooxanthellate corals, which do not benefit from a symbiosis with zooxanthellae. However, given their similar calcification rates [197], it is reasonable to expect that azooxanthellate and zooxanthellate corals will display similar negative effects to infestation by photoautotrophic euendoliths. Euendolithic infestation affects apical growth and skeletal structure of adult coral colonies [24]; however, it does not slow the extension rates and fitness of coral recruits [167]. Heavily infested areas of the coral *Desmophyllum dianthus* display a thicker but more porous skeletal structure, reduced apical extension, and enhanced skeletal deformations [24]. Thus, euendolithic infestation alters the calcification pattern of the coral and unbalances the energetic budget towards the maintenance of skeletal integrity, at the expense of the vertical growth of the polyp and other essential biological processes, such as reproduction. Skeletal deformations, resulting from the secondary deposition of aragonite on the coral skeleton, can act as a mechanical barrier to endolithic infestation [24,181], but are linked to increased coral mortality and reduced coral growth and

reproduction, thus reducing the overall fitness of the coral [198,199]. As a source of food for grazing organisms [124], euendoliths attract excavating invertebrates and vertebrates, enhancing overall bioerosion activity in coral reefs and leading to deeper damage to the substrate [19,113]. Finally, filamentous cyanobacteria associated with the Black Band Disease have been observed actively boring through both coral skeleton and tissue, indicating a potential relationship between endolithic organisms within the coral skeleton and coral diseases [200]. As euendoliths accelerate internal bioerosion rates in CCA, their infestation is likely to increase CCA porosity [15], with consequences similar to those in corals. As microbioerosion is lower in CCA than in corals (7.9% vs. 25% of the bored substrate) [13,15], its negative effects on CCA might also not be detectable or significant.

As early as the 1950s, Odum and Odum suspected another kind of relationship between photoautotrophic euendoliths and their live coral hosts, one that is positive and mutualistic rather than negative, which they termed 'ectosymbiosis' [144]. Forty years later, Schlichter et al. first demonstrated the translocation of photoassimilates from the euendolithic algae living in the coral skeleton to the coral tissue via the uptake mechanisms for dissolved organic substances of cnidarians in the azooxanthellate coral *Tubastraea micranthus* Ehrenberg (1834) [170]. This interaction increases the polyp's fitness by increasing productivity and biomass, while in return, the metabolic end products of the coral can be used by the endolithic algae. Subsequently, Schlichter et al. highlighted the role of the green euendolithic alga *Ostreobium quekettii* in intra-colonial nutrient recycling in two zooxanthellate coral species, though this was considered to be minor compared to the contribution made by zooxanthellae [171].

In live coral skeletons, three main factors influence the availability of light to euendolithic organisms [193,201]:

1. Between 0.1 and 10% of the photosynthetically active radiation (PAR) penetrates and reaches the zone of the endolithic algae, the main part of PAR being absorbed by the zooxanthellae in the coral tissue [171,202–204];
2. Light transmission is affected by the architecture of the coral's skeleton. Corallites on the top of coral colonies guide light deeper into the coral skeleton, while for corallites on the side of the colony, light enters at an angle, reducing its penetration into the skeleton [193];
3. Water depth.

Low light intensities within the coral skeleton suggest an adaptation to shaded environments for euendoliths and, thus, low euendolithic photosynthetic production and a low contribution to the metabolism of healthy zooxanthellate corals [171,190,201,205]. For example, respiration and photosynthetic rates of endolithic algae in the zooxanthellate coral *Porites compressa* Dana (1846) represent, respectively, only 1.4% and 6% of those of the zooxanthellae, corresponding to the amount of PAR effectively reaching the endoliths [171,205]. During bleaching events, however, corals lose their symbiotic zooxanthellae and their shading effect to the endolithic layer (Figure 3c,d). Photoautotrophic euendoliths then acclimate to the increased solar irradiance penetrating the skeleton [177] and start blooming [206]. Two to three weeks after the onset of bleaching, characteristic greenish (*Ostreobium quekettii*) and reddish (*Plectonema terebrans*) pigments of photoautotrophic euendoliths become visible through the now transparent coral tissue (Figure 3d) [23,98,128]. Following this increase in photosynthetic activity, increased quantities of photoassimilates are continuously translocated between the euendoliths and the coral tissue, thanks to the close contact between euendolithic filaments and coral tissue; the cytoplasmic compartments of corals and euendolithic algae are only separated by a cell membrane and by a cell wall and membrane, respectively [170]. On the one hand, due to the capacity of coral cells to absorb dissolved organic substances, such as sugars and amino-acids [207], these photosynthetic products can be readily used by the coral tissue when released by euendoliths, and contribute to the metabolic demands of the coral, especially during bleaching events [23,170,208]. On the other hand, euendoliths may benefit from the internal CO_2 pool and nitrogen-containing metabolites of the coral, using these as a source of inorganic carbon for photosynthesis

and nitrogen, respectively [209]. Although euendolithic sources of energy are nutritionally less important than those of zooxanthellae [171,208] and insufficient to support sexual reproduction by the coral [210], the bloom of euendolithic organisms in the coral skeleton can promote the survival of zooxanthellate corals during bleaching events until new zooxanthellae are recruited [206]. In the event of a rapid bleaching event, however, high light intensities coupled with high temperatures cause the photoinhibition of euendolithic activity [178]. Moreover, the increased abundance of euendoliths in the coral skeleton during bleaching events can result in a corresponding increase in bioerosion rates, further increasing the porosity of the coral skeleton [148]. Thus, photoautotrophic euendolithic communities can sustain coral survival through a critical supply of organic carbon and nutrients during periods of environmental change but slowly weaken the structural integrity of the coral skeleton, increasing its vulnerability to mechanical damage. Conversely, in live CCA crusts, euendolithic infestation can reduce the susceptibility of CCA skeletons to dissolution, especially under ocean acidification and global climate change [129,135]. Through their boring activity, photoautotrophic euendoliths remove highly soluble magnesium calcite from the skeleton, indirectly increasing internal interstitial pH [179], thereby promoting internal secondary precipitation of minerals [211] and increasing the relative abundance of dolomite in the skeleton [135]. CCA skeletons rich in dolomite are less susceptible to dissolution and skeletal disruption [134,135], as dolomite is a more stable form of carbonate and some euendoliths (such as *Mastigocoleus testarum*) are unable to bore through it [116]. Because live CCA crusts are only moderately bored compared to corals, it appears that the beneficial effects of euendolithic infestation could largely outweigh their negative effects, even under heat and acidification stress.

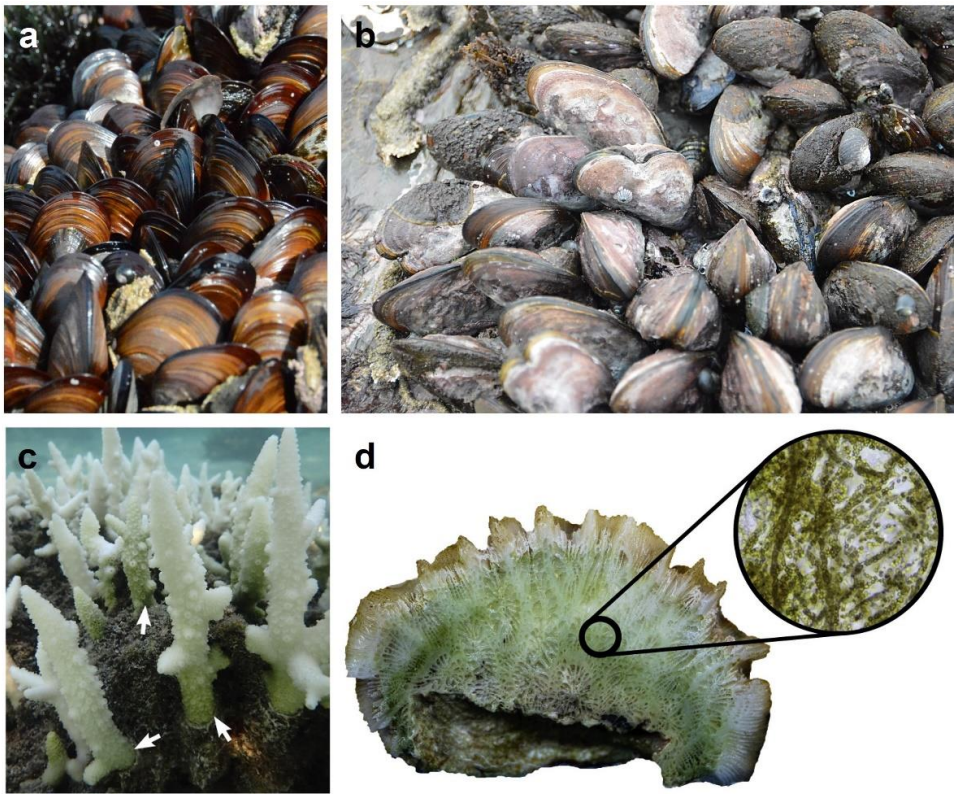

Figure 3. Signs of infestation by euendolithic microborers in live marine calcifiers. (**a**) Non-infested *Perna perna* bed. (**b**) *Perna perna* mussels showing extremely eroded shells due to the action of euendolithic cyanobacteria. (**c**) Bleached coral with evident *Ostreobium* bloom (indicated by white arrows). (**d**) Cross-section of *Paragoniastrea australensis* coral showing *Ostreobium* that inhabits the skeleton. The inset shows Ostreobium filaments after skeletal decalcification. Copyright: © Alexia DIEVART (**a**,**b**), © Alexander Fordyce (**c**). Images (**c**,**d**) from [74].

Coral reefs are amongst the most diverse and complex marine ecosystems in the world, providing a habitat for countless associated species [27], as well as providing many services to mankind, such as commercial fishing, tourism, and coastal protection against storms and cyclones [27,212]. In tropical reefs, CCA are critical biological and geological components [188], cementing together sand, dead corals, and debris to create a stable substratum [213]. This substratum facilitates the settlement of coral larvae and other invertebrates of commercial value, such as abalone and sea urchins [135,214,215]. Overall, the maintenance of healthy coral reef ecosystems is critically dependent on the balance between constructive forces, such as calcification by corals and encrusting coralline algae, and destructive forces, including bioerosion [216]. Severe euendolithic infestation of individual coral skeletons can fragilize whole coral reefs, increasing their susceptibility to damage by cyclones and storms [212], El Niño events [217,218], and predators, such as the crown-of-thorns starfish [12], and diminishing the coastal protection they offer to other ecosystems and mankind. However, during extreme heat waves, euendolithic infestation of corals can mitigate the effects of bleaching and promote coral survival [23,170,171,178]. In live CCA crusts, euendolithic infestation promotes long-term survival by altering the mineralogical composition of the skeleton [134,135]. Finally, by affecting the inanimate substrates composing the ecosystem as well, endolithic infestation plays a role in shore bioerosion in interaction with grazers [113]. For more detail about the role of boring microflora in modern coral reef ecosystems, see [32].

5.2. Bivalves

In live bivalves, the colonization of the shell by photoautotrophic euendoliths is prevented by the periostracum, a well-defined external proteinaceous coating of variable thickness that constitutes the outermost layer of the shell (Figure 3a) [14,22,93,219]. The early developmental stages of bivalves are largely free of endoliths [94,107], as their protective periostracum is still intact. Over time, the periostracum can be abraded, by contact with neighboring mussels within a bed and/or by sediment particles carried by waves [14,107] or by the activity of macrograzers [94]. Once the periostracum is removed, photoautotrophic euendoliths colonize the bivalve shell from the outside in, in a similar fashion to dead substrates. This involves a succession of microboring species through time [14,49,100]: (i) pioneer species within the first months, such as the cyanobacteria *Mastigocoleus testarum* and *Plectonema terebrans*, and the chlorophyte *Phaeophila* sp., (ii) an intermediate stage after the pioneer species are established, with the addition of the cyanobacterium *Solentia stratosa* Ercegovic (1927), and (iii) a late successional stage, after more than 6 months of exposure, with the addition of the cyanobacteria *Hyella* sp. Bornet and Flahault (1888) and/or *Pleurocapsa* sp. Thuret (1885), and the chlorophyte *Ostreobium quekettii*, which replaces *Phaeophila*. In some instances, infested bivalve shells take a greenish color when euendolithic infestation is dense [93,94]. The spatial distribution of cyanobacterial euendoliths in bivalve shells reflects this succession in time, as the last colonizers are only found towards the older parts of the shell, where they co-occur with pioneer species [49]. The succession of microborer communities does not necessarily involve the replacement of euendolithic species by others [100], but rather their addition [14,49]. Consequently, euendolithic infestation is stronger on the oldest parts of the shell (i.e., umbo and central shell), and with increasing shell length, as a proxy of age [22,33,94,96,100,172]. Most studies have focused on the succession of cyanobacterial euendolithic communities on bivalve shells [14,49], so less detail is available for chlorophytes and other photoautotrophic euendoliths [96,100,220]. Photoautotrophic euendoliths colonize intertidal bivalve shells around the world, independent of their location or the nature of the shore [14,94,221]. On South African rocky shores, the incidence of endolith-infested shells in the brown mussel *Perna perna* Linnaeus (1758) and the blue mussel *Mytilus galloprovincialis* Lamarck (1819) varied between 23% and 95% on sheltered shores within bays and on shores exposed to the open ocean, respectively [14,107,221]. In California, between 60% and 90% of the shells of the Californian mussels, *Mytilus californianus* Conrad (1837), were infested by euendoliths,

depending on their position with respect to height on the shore [108], while 93% of the shells of the bearded horse mussel, *Modiolus barbatus* Linnaeus (1758), were infested in the Adriatic Sea [96].

As euendoliths bore into the shell, bivalves need to repair the shell and maintain carbonate structures through secondary carbonate deposition [22], an energetically demanding process requiring 25–50% of their energy budget [222,223]. The bivalve's energetic budgeting then shifts towards self-repair with time, at the expense of growth, reproduction, attachment strength, and overall condition [22,107,168,173,220]. The severity of euendolithic infestation and its negative effects on bivalves is, however, species-specific. In South Africa, the invasive blue mussel, *Mytilus galloprovincialis*, exhibits greater infestation levels and negative effects than the native brown mussel, *Perna perna* [107,221]. Regardless of the rate of shell deposition in infested bivalves (up to two times that of non-infested bivalves), it is never enough to compensate for the degradation caused by euendoliths [22]. Ultimately, infestation becomes so severe that bivalves fracture their own shells with the force applied by their adductor muscles [14]. Thus, endolithic infestation can at times account for more than 50% of total mortality in highly infested populations [22].

Moreover, damage to the individual bivalve exceeds simple structural damage and has critical consequences at the population and community levels. Through their boring activity, euendoliths reduce shell strength and thickness, increasing vulnerability to predation, wave action [22], or trampling [175]. Similarly, shell microtopography and its antifouling characteristics [142] can be altered by euendoliths, which could lead to higher settlement of epibionts such as barnacles (as hypothesized in [172]). Infestations by larger epibionts increase a bivalve's vulnerability to drag forces and predators [224], while these epibionts' boring actions could further enhance euendolithic infestation [172,225]. In addition, by creating a more complex, rougher shell surface, euendolithic infestation influences the hydrodynamic properties of mussel beds, leading to greater ingestion rates of microplastics by mussels within infested mussel beds, and greater retention of microplastic on infested mussel shells and within infested mussel beds [184]. Moreover, infested mussels produce fewer byssal threads for attachment to the substratum, making them more vulnerable to drag forces [107,173] and creating an architecturally less complex mussel bed for the associated infauna. Gonad mass, and thus reproductive capacity, are also negatively affected by euendolithic infestation [22,107,173,220]. Larger mussels, responsible for the bulk of gamete output from the population, are the most susceptible to mortality through shell collapse and suffer the greatest decrease of gonad tissue due to endolithic infestation [22], thus reducing population reproductive output.

Shell-boring photoautotrophic euendoliths have, however, also been shown to have beneficial effects on the bivalve host under certain environmental conditions [25,33,108]. Infested mussels lose their dark color through the loss of the periostracum, which exposes the pale nacreous layer underneath and the deposition of excess calcium on the outside of the shell by euendoliths (Figure 3b) [14,25,49,108]. Infested mussel shells, being paler, absorb around 10% less sunlight energy than non-infested shells, resulting in lower body temperatures (up to 5 °C lower) and greater water retention [25,108]. During heat waves, infested mussels can experience lower short-term mortality rates [25,108], as they warm up slower and reach lower body temperatures than non-infested mussels during aerial exposure [115]. The beneficial effects of endolithic infestation can extend to neighboring mussels within a bed: mussel beds mostly composed of infested mussels exhibit lower temperatures and higher humidity in the interstitial space [33,115]. The beneficial effects of euendoliths are regulated by particular topographic and meteorological conditions [33,109,115]. Thermal buffering by euendoliths is greatest when bivalves occur on horizontal or moderately inclined, mostly sun-exposed, surfaces, and under conditions of high solar irradiance and air temperature, low wind speed, and moderate humidity [109,115]. Thus, thermal buffering by euendoliths is the strongest and most ecologically significant when (and where) bivalves suffer from stressful environmental conditions, particularly in the summer and at lower latitudes [33,109,115]. The protection offered to associated species by the bioengineering

effects of mussel beds is thus likely to be enhanced by endolith-induced improvements in within-bed humidity and temperature, especially in the upper intertidal zone where mussel beds are typically mono-layered and thermal refuges are scarce [108].

Worldwide, bivalves are the most prominent ecosystem engineers on intertidal rocky shores [226], providing a functional habitat and refuge to a wide array of associated species in a physiologically stressful environment characterized by high temperature and low humidity during emersion [226–229]. Bivalve beds offer a refuge from thermal and desiccation stresses [229,230], and predators [227,231], a habitat for epibionts [226], and participate in the transport of solutes and organic particles in the near-shore environment [26,232]. Bivalve beds provide many ecosystem services, such as fishing, other resources, protection against the waves, and stabilization of the coastline [233,234]. Euendolithic infestation of bivalve beds increases the susceptibility of these ecosystems to damage by waves and anthropogenic stressors, such as trampling and plastic pollution [175,184], while reducing their vulnerability to heat waves [25,115].

5.3. Other Groups

While limited information is available on the incidence and distribution of photoautotrophic euendoliths in calcifying organisms, the physiological, biological, and ecological impacts of endolithic infestation have not been documented outside of commercially or structurally important calcifiers, such as corals, CCA, and bivalves (see [32]).

In soft corals, the chlorophytes *Ostreobium quekettii* and *Ulvella endozoica* (Goldberg, Makemson, and Colley) R. Nielsen, C.J. O'Kelly, and B. Wysor (2013) are associated with lower tensile strength and elasticity of the endoskeleton [174], and necrosis of the surrounding live tissue in two species of gorgonian corals [182,183]. In brachiopods, the presence of conchocelis stages of the red algae *Porphyra* or *Bangia* recorded in the outer layer of the shell [131,169,235] was linked to the potential disruption of growth and shell weakening, as biomineralization processes are disturbed and 'blisters' appeared at the areas of shell repair, as in bivalves [169]. Limpet and snail shells are infested by euendolithic cyanobacteria, such as *Mastigocoleus testarum* or *Hyella caespitosa* Bornet and Flahault (1888) [143], and green and red algae, such as *Phaeophila* or *Porphyra* [94,176,236], and become thinner and more fragile due to bioerosion (similar to bivalves). Infested limpets and snails suffer higher mortality rates, especially in adverse environments (i.e., open coast) [176,237]. In barnacles, the chlorophyte *O. quekettii*, the cyanobacterium *M. testarum*, *Hyella* sp. and *Plectonema terebrans*, and conchocelis stages of *Bangia* red algae were found in the plates [44,103,117,238]. Euendolithic infestation starts from the apex of the shell down to the base, weakening the barnacle shell and channeling its energy towards self-repair [238]. In foraminifera, the shell is infested by the same euendolithic species as barnacles, which increases their susceptibility to mechanical breakage and fragmentation and can potentially attract grazers [239]. By contrast, euendoliths at the test surface can promote the formation of a micritic crust around infested tests through secondary carbonate deposition [240], potentially increasing the potential of the test for preservation [241].

While the effects of euendolithic infestation on live calcifying organisms, such as foraminifera, limpets, brachiopods, or barnacles, could be simply underexplored, the sparsity of studies could also be an artifact of lower levels of euendolithic infestation in these organisms, which could translate in less detectable negative effects on the host.

6. Photoautotrophic Euendoliths in the Anthropocene

Marine calcifiers and their future relationship with photoautotrophic euendoliths will be influenced by global climate change (GCC) [32,242–244]. GCC is caused by the increase in the emission of anthropogenic greenhouse gases, such as CO_2, and manifests as an increase in air and sea surface temperatures (SST), and changes in rainfall regimes [245]. As air temperatures rise, cloud cover is predicted to decrease at the planetary scale, which increases the amount of solar radiation reaching the surface, increasing temperatures even more [245]. For the past 200 years, the world's oceans have absorbed about one-third of

the CO_2 released into the atmosphere, which has led to ocean acidification (OA), with a reduction of the pH of surface seawater of 0.1 units [246–248]. If global anthropogenic CO_2 emissions continue to rise in line with current trends, the average pH of the ocean's surface could further decrease by 0.7 units in the next millennium, with a rate of change one hundred times greater than in the past 300 M years [247,249]. For marine calcifiers, rising SST, ocean acidification, and the increase in solar radiation will negatively impact calcification, survival, growth, and reproduction, and diminish their resistance to other environmental stressors, such as pollution [30,250–253]. With decreasing calcification and a weakening of existing calcified structures due to passive dissolution in a more acidic ocean, marine calcifying organisms will become more susceptible to bioerosion [244]. Understanding how photoautotrophic euendoliths will behave in our changing world thus becomes important for understanding the fate of many bioengineered marine ecosystems [32,244].

Euendolithic infestation by photoautotrophs of carbonate substrates, especially those of live calcifying organisms, is expected to increase in prevalence with increased SST, solar radiation, and OA [109,115,129,179,254,255]. Surveys at sites with natural pH gradients, such as volcanic vents [162,254,255], and a series of mesocosm experiments controlling SST and pH [135,179,256–260] confirm this trend in experimental and dead substrates. Photoautotrophic euendoliths are expected to increase in biomass and cover, and to penetrate deeper and faster into the substrate, thus promoting microbioerosion, with a shift in communities under predicted future oceanic conditions of increased SST and reduced pH. The increase in frequency and intensity of marine heat waves in response to GCC will likely be associated with mass mortality events in bivalves [107,252], and coral and CCA reefs [135]. Such mortality events ultimately increase the availability of dead carbonate substrates for photoautotrophic euendoliths. Although manipulative experiments are scarce [259], hypotheses can be formulated on the future of photoautotrophic euendoliths that colonize live marine calcifiers by capitalizing on the knowledge compiled in this review. In a similar fashion to dead substrates, photoautotrophic euendoliths are expected to increase in abundance and biomass in live calcifying organisms with increasing SST and solar radiation. Under OA and GCC, marine calcifiers are more vulnerable to microbioerosion [242] and heat waves [135,252]. With favorable environmental change and the weakening of calcifying organisms, the negative effects of euendolithic infestation [22,24,107,167] are expected to be magnified in the future. In the worst-case scenario, the combined influence of GCC and euendolithic infestation is expected to increase microbioerosion rates by up to 150% in reefs by 2100 [129,156–158,179]. This equates to about two-thirds of reef carbonate deposited per year being dissolved by the action of microborers by 2100 [258].

As the negative effects of euendolithic infestation on live calcifying organisms are expected to increase in intensity under future oceanic conditions, so might the beneficial effects. Photoautotrophic euendoliths can contribute to host survival under OA and heat waves. In corals, photoassimilates are translocated directly from the euendoliths to the host until symbiotic zooxanthellae recolonize the coral tissue [23,170,171,210]. However, this mutualistic relationship is limited in the case of rapid heat wave-induced bleaching events, as high light intensities coupled with high temperatures inhibit euendolithic photosynthetic activity [178]. In bivalves, photoautotrophic euendoliths indirectly enhance the albedo of the shell, thus reducing the overall body temperature and the mortality rates experienced by infested bivalves [25,108,115]. The beneficial effects of euendoliths can extend to neighboring mussels, further increasing the thermal buffering provided by mussel beds to associated species on rocky shores [33,115]. In CCA crusts, photoautotrophic euendoliths preferentially remove the highly dissoluble fraction of the carbonate skeleton, thus increasing its resistance to bioerosion, either due to OA or photoautotrophic euendoliths themselves [116,129,134,135]. Both detrimental and beneficial effects of euendolithic infestation in live calcifying organisms are expected to increase in intensity with the ongoing GCC and OA. Nevertheless, in the long term, euendolithic infestation is detrimental to its calcifying hosts, ultimately leading to their death.

7. Conclusions

As discussed, photoautotrophic euendoliths are significant biological components of marine ecosystems. Photoautotrophic euendoliths, which are relatively inaccessible without specific observational techniques, are ubiquitous, found wherever there is a calcium carbonate substrate and suitable environmental conditions for survival. Through their boring activity, they leave long-lasting traces in the substrate that allow their identification. As each species has its own ecological requirements, the presence and abundance of euendolithic species and the composition of euendolithic communities are influenced by abiotic (e.g., light availability, nature of the substrate, water quality) and biotic parameters (e.g., grazers, epibiotic communities). Therefore, euendolithic species or entire communities can be employed as geographical, water quality, or paleobathymetric indicators. Photoautotrophic euendoliths colonize both inanimate calcium carbonate substrates and the calcified structures of live organisms. In live calcifying organisms, endolithic infestation has both detrimental and beneficial effects: while euendoliths bore into the calcified structure, the host's energy is allocated to secondary structural repair at the expenses of growth, survival, and reproduction; but endolithic infestation can mitigate temperature stress of the host or provide an alternative source of nutrition in the case of corals. However, in the long term, endolithic infestation ultimately leads to the host's death. In the future, the prevalence and severity of endolithic infestation are predicted to increase, which could lead to higher levels of microbioerosion in marine carbonate substrates, either inanimate or alive, and thus profoundly modify the dynamics of ecosystems founded on marine calcifiers.

Infestation by photoautotrophic euendoliths in live calcifying ecosystem engineers can significantly influence the phenotype, physiology, and biology of individual host specimens, and thus the quality of the habitat they collectively provide (e.g., mussel beds, coral reefs). Research on photoautotrophic euendoliths, especially in live substrates, could beneficiate from the following directions in the future:

1. Update and standardize the taxonomy of known photoautotrophic euendolithic species, including morphological descriptions, ecological requirements, and molecular-based approaches to taxonomy;
2. Determine the boring mechanisms for euendolithic species, such as red and green algae, and how these processes may be affected by environmental change, including OA and GCC;
3. Investigate euendolithic communities (e.g., species composition, abundance, biomass), and the prevalence and severity of euendolithic infestation in less-investigated marine calcifiers (e.g., brachiopods, barnacles, limpets, snails), under different environmental conditions and timescales, and using a combination of approaches;
4. Develop a standardized experimental framework, including ex situ and in situ experiments, to evaluate and compare the modalities of euendolithic infestation and how infestation may be influenced by various abiotic and biotic parameters (e.g., nutrient concentrations, light availability, presence of grazers and predators);
5. Determine the detrimental and beneficial effects of euendolithic infestation on live marine calcifiers, using manipulative experiments when possible;
6. Centralize available information on euendoliths (including heterotrophs) in a publicly accessible database (e.g., Ocean Acidification International Coordination Centre).

When researching marine calcifiers, the presence of euendolithic communities and their effects on host species and ecosystems should be acknowledged and, if possible, quantified. As euendolithic infestation has significant effects on marine calcifiers, failing to consider photoautotrophic euendoliths could lead to biases in the results or their interpretation, even when they are not the main research focus.

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