Structural Engineered Living Materials

Yang Geng, Zian Jia, and Ling Li*

Department of Mechanical Engineering, Virginia Polytechnic Institute and State University, 635 Prices Fork Road, Blacksburg, VA 24061, USA.

Abstract

Biological structural materials not only exhibit remarkable mechanical properties but also often embody dynamic characteristics such as environmental responsiveness, autonomy, and self-healing, which are difficult to achieve in conventional engineering materials. By merging materials science, synthetic biology, and other disciplines, Engineered Living Materials (ELMs) provide a promising solution to combine living organisms with abiotic components, thus facilitating the construction of functional "living" materials. Like natural materials, ELMs possess vitality and hold immense application potential in areas such as medicine, electronics, and construction, captivating increasing research attention recently. As an emerging branch of ELMs, structural ELMs aim to mimic living biological structural materials by achieving desired mechanical performance while maintaining important "living" characteristics. Here we summarize the recent progress and provide our perspectives for this emerging research area. We first elucidate the superiority of structural ELMs by reviewing biological structural materials and biomimetic material design strategies. Subsequently, we provide a systematic discussion on the definition and taxonomies of structural ELMs, their mechanical performance, and physiological behaviors. Finally, we summarize some critical challenges faced by structural ELMs and highlight directions of future development. We hope this review article can provide a timely summary of the state of the art and relevant perspectives for future development of structural ELMs.

Keywords

Structural materials, engineered living materials, structural ELMs, composites, mechanical properties.

1. Introduction

Within the broad spectrum of material science, the investigation of structural materials for load-bearing applications constitutes an important component. It primarily concerns the fundamental questions related to the mechanical properties of materials (such as stiffness, strength, fracture toughness, fatigue strength, and energy absorption), mechanical behavior and deformation mechanisms (such as dislocation motion, crack propagation, and phase transitions), which are also at the core of material science.[1] Because of the crucial role structural materials play in construction, transportation, energy, electronics, and aerospace, among others,[2]–[5] the progress of these materials is intrinsically tied to advancements in various modern industries and engineering fields. Therefore, one of the key objectives in materials science is the development of superior, environmentally-friendly structural materials to tackle increasingly complex application conditions and meet growing challenges.

Historically, structural materials, like other functional materials, are developed through experimental approaches by taking advantage of the processing-structure-property relationship, for example, testing alloy compositions or thermal treatment procedures for metallic structural materials. In the past several decades, material innovation enabled by computational modeling (e.g., finite element modeling and molecular dynamics modeling) and machine learning approaches has led to significant advancement in structural material development. More recently, drawing inspiration from nature has also proven to be an effective approach for material innovation.[6] In particular, nature is replete with ingeniously designed structural materials, which have evolved millions of years, facilitating organisms to cope with diverse environmental pressures and functional demands. It is widely acknowledged that the basic constituents of natural structural materials, including biopolymers (e.g., proteins and polysaccharides) and biominerals (e.g., calcite, aragonite, silica, and hydroxyapatite), exhibit inferior mechanical properties. Nevertheless, through hierarchically elegant structural "designs", from atomic to macroscopic scales, natural structural materials achieve exceptional mechanical properties, far beyond the rule of mixture from their constituent components. For instance, the nacreous layer of seashells, consisting of aragonite platelets and a protein matrix, forms a well-controlled "brick and mortar" structure, offering remarkable strength and fracture resistance.[7], [8] Bamboo, on the other hand, with its lightweight yet strong cellulose fibers, forms multiscale porous structures that support its towering stature.[9] Another fascinating feature of natural structural materials, in contrast to synthetic materials, is their balanced material properties to fulfill multiple functional requirements.[10] For example, mussel byssus achieves both toughness and wear resistance through a granular protein structure[11], and spider silk balances strength and flexibility for capturing prey efficently[12]. These natural structural materials provide a rich source of inspiration for us to design and develop novel bio-inspired analogs.[6] However, in addition to the challenge of replicating the multiscale structural complexity of natural materials, current bio-inspired structural materials often fail to respond "intelligently" to environmental stimuli, whereas natural structural materials are often able to sense, regulate, adapt, and even self-heal upon failure, thanks to the “living” components integrated within these materials. For example, vertebrate bones constantly remodel at multiple length scales due to a collection of specialized cells embedded in bone, such as osteoblasts, osteocytes, and osteoclasts.[13], [14]

Recently, Engineered Living Materials (ELMs) become an emerging class of novel materials that are developed through an interdisciplinary effort, combining materials science and engineering, synthetic biology, and other disciplines.[15] Unlike traditional artificial materials, ELMs possess a unique nature, namely “living”, since they not only mimic the static structural features of organisms but also harness their biochemical and physiological characteristics. By integrating living cells, tissues, or even organisms with abiotic components, these living materials are able to grow, adapt to environmental changes, and self-repair when damaged. With the vitality, they can be produced under environmentally-friendly conditions, even utilizing certain waste materials as raw resources. What’s more, the genetic tractability of the living cells endows the ELMs with tailorable functionalities. In the past decade, ELMs have been increasingly applied in therapeutics, electronics, construction, etc.[16] However, while providing opportunities for the design and development of new materials, ELMs also face challenges, such as controlling and optimizing the growth and behavior of living components and ensuring their stability and safety under various environmental conditions.

In the family of ELMs, Structural Engineered Living Materials (Structural ELMs) constitute a more recent yet important category, focusing specifically on the multiscale structures and mechanical properties of ELMs. Similar to other ELMs, structural ELMs possess the characteristic of being "living". This attribute precisely addresses the issues, as previously mentioned, faced by traditional structural materials, such as the inability to react to environmental changes and challenges in sustainable manufacturing. Hence, Structural ELMs may possess a substantial potential for applications in future construction, infrastructure, and other domains and may profoundly impact our vision and utilization of structural materials.

While many excellent reviews are available on ELMs[16]–[18], comprehensive reviews on structural ELMs are limited. This is primarily because the initial interest in ELMs predominantly emerged within the field of synthetic biology, with a vast application potential in therapeutics, leaving the attention and detailed investigation of the mechanical properties of ELMs lacking. Given the potential and advantages of ELMs as compared to traditional structural materials research, it is essential to thoroughly review the past development of structural ELMs, summarize key challenges, and provide perspectives for future development. Therefore, in this review, we will first provide an overview of natural structural materials and the problems posed by conventional bio-inspired structural materials. We will then introduce the latest research progress in structural ELMs based on different living components (including bacteria, fungi, plants, mammalian cells, and consortia), and discuss their mechanical properties and physiological behaviors. Finally, potential applications will be summarized and potential future research focus will be discussed.

2. Structural materials in nature and bio-inspired material design

2.1 Structural materials in nature

Biological materials are perfect examples of living structural materials. Two features distinguish them from conventional engineered materials, i.e., their complex hierarchical microstructures and the inherent interaction between their living and structural components (**Fig. 1a, b**). A complete biological materials system can be divided into the living component comprising cells, bacteria, algae, fungi, etc., and the structural component, encompassing specific microstructures (**Fig. 1b**). Biological materials are "structural" — they have developed complex microstructures at multiple length scales, such hierarchical structures serve as the foundation for their impressive mechanical and functional properties, accommodating and safeguarding the living components. Biological materials are "living" — they are produced by living organisms, regulated by living components, and can dynamically send signals, respond, change, and adapt.

Based on how the structural part interacts with the living part, biological living materials can be divided into three categories shown schematically in **Fig. 1a**. The first type is represented by materials like seashells, hairs, and teeth, where living components only exist at the growing front, and the grown structural components operate on themselves with little or no interaction with the living cells (**Fig. 1a1**). Such biological materials are typically dense composites and function akin to conventional "inert" engineering materials. The second type, illustrated in **Fig. 1a2,** represents the most common relationship between the living and structural components in biological materials, where living components are accommodated within structural components as seen in bones, leaves, skin, and many soft tissues. The structural component is typically porous, which could be hard like cancellous bone and echinoderm skeletons, soft like the extracellular matrix of soft tissues, or a combination of hard skeletons and soft membranes like the chicken eggshells. In these materials, the living cells are attached to structural scaffolds, enabling vibrant proliferation, migration, and differentiation. Finally, some biological materials lack clear structural elements, and the living components themselves serve the structural function (**Fig. 1a3**). For example, the living mechanical tissue of plants, collenchyma, contains cellulose, hemicellulose, and pectin in its cell walls, providing mechanical support to the growing parts of plants. Among the above three categories, the second type, with manifest structural and living parts and massive structure-living cell interfaces, represent the most sophisticated biological materials. Its advantages include robust mechanical properties, large design space, and efficient bioactive functions, making it the most suitable motif for engineering bio-inspired living materials. Hence, our focus in this paper will primarily be on the second type.

The structural component of biological materials is hierarchical, nature's primary solution to achieve diverse functions using only limited resources of materials.[19]–[21] By controlling the material distribution at different length scales, microstructured materials can achieve superior mechanical properties including high specific stiffness, strength, toughness, and special mechanical functions.[21], [22] For example, human bones possess an extremely complex microstructure with at least 12 levels of hierarchy, enabling high strength and toughness.[23] The skeletons of echinoderms like starfish use much simpler microstructures (three levels of hierarchy) but possess a porous, dual-scale crystalline structure for high strength and damage tolerance[24]. Animal skins are soft living composites stratified in layers, where curved collagen, elastin, and reticulum fiber networks within the dermis provide high tear resistance[23–25]. Beyond mechanical functions (**Fig. 2a, b**), material microstructures also enable optical, microfluidic, water-collection, and active functions (**Fig. 2c-i**), as seen in examples like butterfly wings[25], starfish ossicles [24], insect exoskeleton[26], [27], plant leaves, seeds and stems[28]–[31].

Building upon the functions enabled by the structures of biological materials, the living part further enables biological materials to sense and respond, self-renew and adapt, self-replicate and evolve. The dynamic nature of living cells imbues materials with a wide spectrum of temporal events, ranging from milliseconds to millions of years (MYS), as depicted in **Fig. 1c**. Fast dynamic processes, such as signal transmission, muscle fibers contraction, and chemical release, occur within a second. For instance, the stomatopods deliver lightning-fast attacks with their dactyl clubs in milliseconds, fast-twitch muscle fibers can contract in 0.1 seconds (twitching 30-70 times per second), and the remarkable color-changing abilities of chameleons and cuttlefish manifest within seconds. On an intermediate time scale, spanning from minutes to months, living materials exhibit the capability to transform, self-heal, and adapt. Examples include the healing of skins in days, the service life of eggshells lasting weeks, spores capable of remaining dormant for weeks to months, and the regeneration of broken bones and sea urchin spines occurring over months. Moreover, in the long-time scale, living materials undergo adaption to environmental changes and evolve over generations. Fossil records have unveiled the evolution of hard-shell eggs from soft ones, with progressive developments of microstructures[32]. In fact, over the course of millions of years, all biological materials perpetually evolve, driven by selection pressures like improved functionality and reduced energy expenditure. Thus, biological materials epitomize dynamic systems that operate across multiple time scales, seamlessly incorporating rapid responses, long-term development, and evolutionary adaptations.

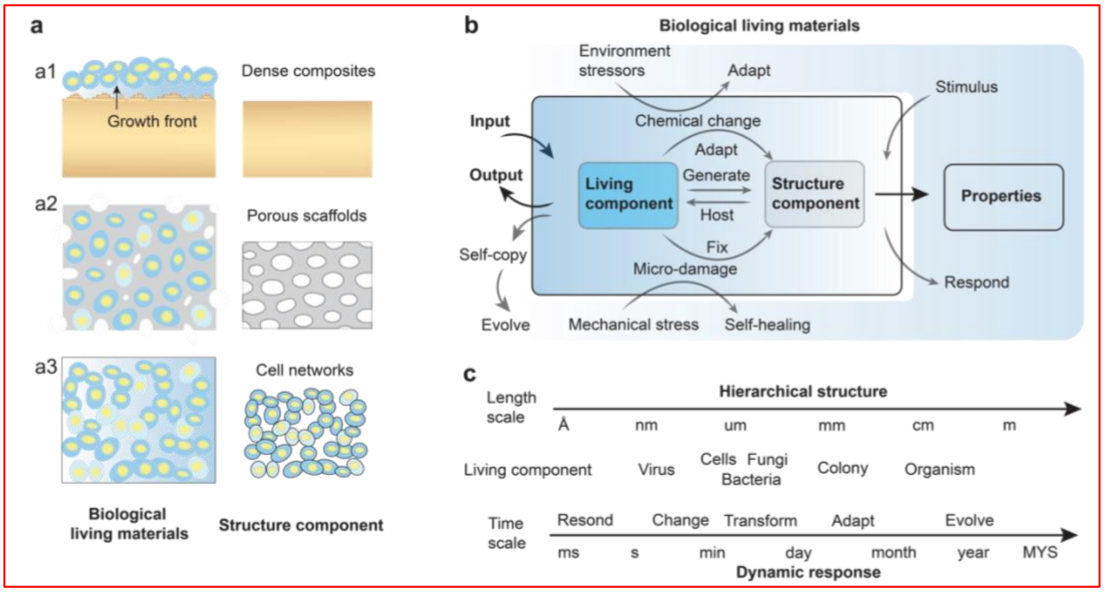

Fig. 1 Biological structural materials as living structural materials: (a) Three types of biological structural materials based on how the structural part interacts with the living part. (b) The “living component-structure component-property” relationship of biological materials. (c) The integration of living components and structural elements endows biological materials with mastery over space and time.

The integration of living components and structural elements endows biological materials with mastery over both space and time: the structural parts control materials distribution in space down to the atomic scale while the living parts govern the dynamic response across multiple time scales. Although designing microorganism–structural interactions is highly challenging in engineering living materials, it is a natural outcome in biological materials. The structural components of biological materials are customized based on the hosting living cells, ensuring biocompatibility, nutrition supply, and functionality. Factors including structural porosity, elastic and viscoelastic properties, permeability, and feature sizes are important traits of the cellular structure, which in turn regulates the distribution, connection, and grouping of cells in space, facilitating signaling and synergism among cells[33]. For example, the porous skeleton of sea sponge *Aphrocallistes vastus* possesses a hierarchical porosity with pore sizes of both 1 mm and 100 μm, simultaneously optimizing cell accommodation and fluid transport.[34] Similar hierarchical porosities are ubiquitously found in bamboo and other plant stems.[31]

Moreover, the living cells generate and regulate the substrate structure while the substrate properties affect cell performance. For instance, neurons extend much better on soft matrices like the brain, which is different from most tissue cells that spread better on harder substrates[35]. Neurons are also constrained to tubular spaces, presumably aiding signal transmission. In living biological materials, cells can actively adjust and fix the damaged structural component. For example, in damaged bones, cells like chondroblasts and osteoblasts resorb calcified cartilage, fill cavities with the Haversian system, and developed into fracture callus. This is followed by a remodeling process where osteoclasts further resorb bone, refining the bone microstructure, and restoring the bone's original shape and performance.[36]

The interaction between living and structural components enables complex functions in biological materials. One example is the physiological force sensor in the ear, where the hair structure amplifies the sound-induced vibration, which is further detected by the hair cell as neural impulses. This synergy between structure and cells enables high sensing capabilities of the ear. Another example of complex programmed function is observed in the Venus flytrap, where the cells can sense prey contact and trigger the saddle-shaped shellular structure to close rapidly within 0.1 seconds.[29] The fence-like structure of Venus flytrap then seals the chamber and prevents the prey from escaping, allowing the cells to secrete venom and digest the prey. [29]

2.2 Bio-inspired structural material

The delicate microstructures and outstanding properties of biological materials have inspired scientists and engineers to make biomimetic microstructured engineering materials for decades[6], [37]–[40]. However, bio-inspired materials engineering mostly focused on replicating the "inert" structural parts of biological materials, while largely disregarding or evading the "living" components. Nonetheless, by leveraging microstructure design, numerous materials with novel properties have been demonstrated.

As shown in **Fig. 2a-d**, material microstructure design has become a powerful approach to improve mechanical performance, overcome property tradeoffs, and create novel functions like structural color, water repellency, and thermal regulation.[41]–[44] For example, multilayer, brick and mortar, and rotating plywood microstructures were shown as effective designs for realizing paradoxical property combinations like high strength and high toughness, soft and fast response, overcoming mechanical property tradeoffs (**Fig. 2a**).[45] Microlattices with multi-grains and dislocations were shown to make cellular materials stronger and tougher (**Fig. 2b**).[46], [47] These microstructures were now applied in 3D printed materials, ceramics, and steels for enhancing mechanical properties [48]–[50].

In addition to mechanical properties, other interesting functionalities of biological materials like the slippery surfaces of the pitcher plant[51] (**Fig. 2c**), the robust structural colors of beetle[52] (**Fig. 2d**), and the moisture-collecting insect cuticles[27], have inspired the design of self-cleaning surfaces, robust photonic crystals, and water harvesting devices, respectively. Notably, all such impressive properties of bio-inspired materials are achieved solely through the design of the material compositions and microstructures with no living components.

In the bio-inspired materials community, researchers often work hard to avoid introducing living components into bio-inspired materials. Considering living cells and microorganisms as not robust and durable, the active functions of living organisms are realized alternatively by using non-living materials. **Fig. 2e-h** showcase examples of smart, responsive, active, and programmable bio-inspired structural materials. For instance, light or temperature-sensitive materials can conduct programmed functions in response to environmental changes[53]. Shape memory materials have enabled the design of smart materials that remember and can return to their original state even after plastic deformation or micro-damages (**Fig. 2e**). Introducing structural feedback systems further allows structural materials to perform programmed functions. As shown in **Fig. 2f**, temperature rise and drop lead to two different structural configurations, which modify the heat flux, and consequently regulate temperature. Self-healing material is another example of using smart structural feedback to conduct programmed healing functions[54]. As shown in **Fig. 2g**, liquidus healing agents in the inclusions of a composite material infiltrate the cracks at the damage, which reacts with air and heals the damage. Taking a step further, by introducing external energy inputs (e.g., energy, pressure, displacement), novel bio-inspired structural materials capable of sensing and being actively tunable were created. **Fig. 2h** illustrates a metamaterial design with reconfigurable structures controlled by displacement inputs, allowing for active and continuous control of stiffness and Poisson's ratio with a single input [48]. **Fig. 2i** shows a microcracks-based displacement sensor inspired by the leg of spiders[55]. In this design, the active function of the nerve cells is realized by external power sources and voltmeters.

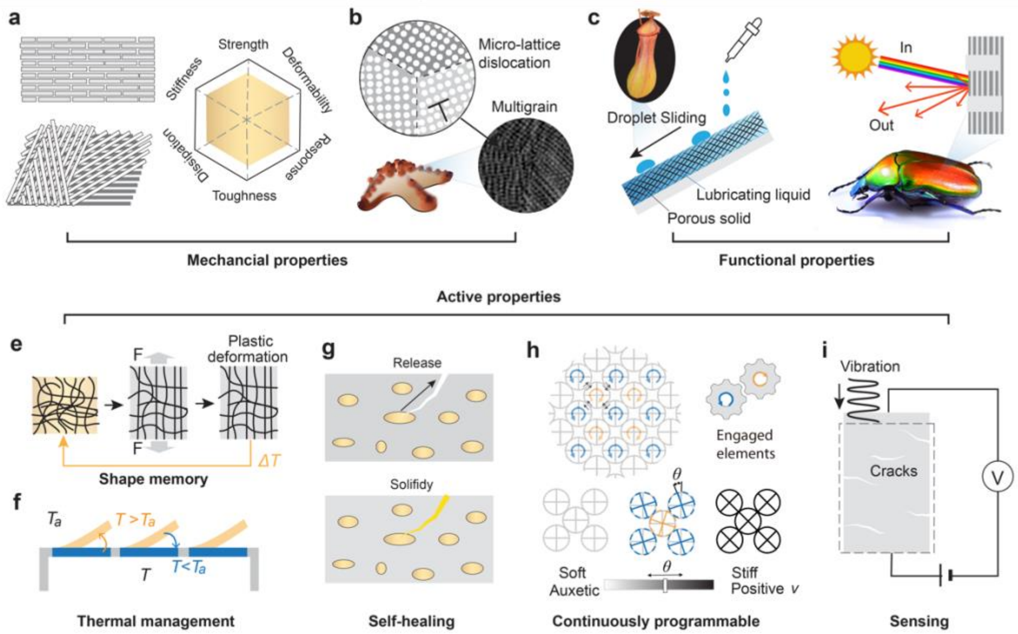

Fig. 2 Bio-inspired structural and functional material for enhanced mechanical, functional, and active properties without using living components. (a-b) Bio-inspired microstructured materials with enhanced mechanical performances. (a) Overcome performance tradeoffs and (b) with enhanced strength and damage tolerance. **(c-d)** Bio-inspired microstructured materials with self-cleaning and structural color. **(e-g)** Bio-inspired structural materials with active programmed functionality including memory, temperature regulation, self-healing, programmability, and sensing capabilities.

3. Structural engineered living materials

As discussed in the previous section, to mimic the "structural" and "living" characteristics of biological structural materials, many efforts are directed to utilize novel structural designs or "active" materials to realize responsive or active functionalities in bio-inspired materials. However, these designs, due to the absence of living components, possess some inherent limitations, such as inability to grow or self-replicate, suboptimal biocompatibility, limited "living" functions, and low sustainability. Therefore, to truly emulate the "living" attribute of natural structural materials, the integration of living cells or organisms is imperative, resonating with the principles of structural ELMs. We believe this new "path", merging abiotic structural materials with living components, enables important opportunities for developing novel structural materials, which also enhances our utilization and harmonious coexistence with nature.

3.1 Background of engineered living materials

ELMs are engineered materials composed of living cells/organisms that form or assemble the material itself and modulate the functional performance of the material post-production.[15], [18] As ELMs represent an interdisciplinary field that tightly integrates synthetic biology with material science (**Fig. 3a-b**), materials engineering for desired functionality involves two respects, i.e., editing the living components using synthetic biology approaches and tailoring abiotic components from a material science perspective.

The appeal of engineering living cells lies in their dynamic attributes, including biomass proliferation, self-adaptation, self-healing, and responsiveness to extracellular cues (**Fig. 3c**). Synthetic biology plays a pivotal role in fostering these traits through the cell-mediated synthesis of entities such as proteins and polysaccharides. This bottom-up approach allows for cellular material design and production for innovative functional materials[16]. For instance, Lu et al.[56] introduced an ingestible micro-bioelectronic device by modifying probiotic *E. coli*, enabling the interaction between bacteria and extracellular heme's outer membrane transport protein and thus facilitates heme detection. Another example is engineered biofilm composed of amyloid proteins and polysaccharides, providing a stable environment for prokaryotes. Modifying amyloid proteins such as CsgA (subunits of Curli protein) and TasA in microorganisms allows for the engineering of biofilms,[57], [58] establishing a foundation for functional living materials. Similar strategies extend to biopolymers (e.g., bacterial cellulose)[59] and enzymes. Controlled engineering of cell surface displays or surface structural proteins enables living materials to interact with environmental molecules and achieve programmability in large-scale structures[60], generating substantial interest.

Organisms in living materials benefit from the structural support and protection provided by non-living components. Typical materials for structural support include natural organics, specialized cell culture media, biocompatible polymer elastomers, and aerogel/hydrogel scaffolds, etc.[61] Regarding fabrication, while most of traditional material synthesis methods are viable, the resilience of the biological components must be considered (**Fig. 3d**). For instance, high-temperature techniques might be incompatible with precursors containing living organisms. Furthermore, processing conditions such as humidity, oxygen level, and biochemical environment should be monitored. Methods such as molding, 3D printing, dip coating, and wet spinning are frequently employed in the creation and regulation process of living materials.[62]–[64] In certain scenarios, additive abiotic parts can also act as functional materials, which enable the entire system to respond to varying stimuli.[58]

Currently, many research focuses on developing manufacturing strategies to integrate biological and non-biological components for ELMs. Moreover, there is an ongoing endeavor to broaden ELMs' application scope and utility across sectors such as therapeutics, manufacturing, electronics, construction, and devices.[18] For instance, in the domain of therapeutic, ELMs have been investigated for applications such as skin patches, drug release, internal implants, and antigen-antibody detection.[16] Additionally, the significance of biomechanics have garnered considerable interest, as it provides valuable insights into the mechanical functioning of various living organisms.[65] ELMs, wherein living organism mechanically interact with hybrid systems, present unique potential in the application of sensing and actuation[66], rehabilitation and prosthetics, etc. ELMs display an extraordinary diversity of functionalities and properties through such engineering and diverse assembly methods. However, irrespective of their use-case, many ELMs face challenges and constraints that require further development, including scalability, organisms' viability, durability, potential biological contamination, and safety concerns. A profound comprehension of various biological processes, mechanisms of biomolecules action, and the interplay between biotic and abiotic parts is crucial.

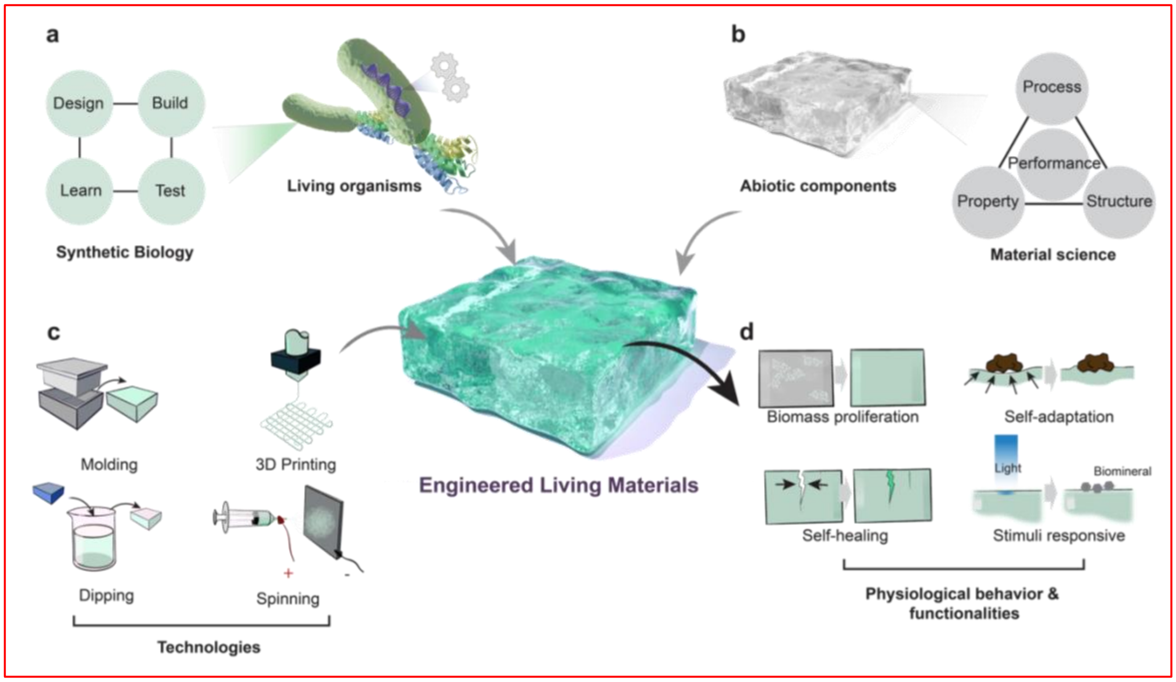

Fig. 3 Schematic of the concept of ELMs. The construction of ELMs employs (a) synthetic biology to engineer living organisms and (b) material science methodology for tailoring abiotic components. (c) Responsivity Typical technologies used in the synthesis of ELMs, including molding, 3D printing, dipping, and spinning. (d) Desired physiological behavior and functionalities for ELMs, including biomass proliferation, self-adaptation, self-healing, and stimuli.

3.2 Structural ELMs

3.2.1 Definition and classifications

Structural ELMs constitute an emerging subset among ELMs, characterized by the modification of material structure and/or composition through the involvement of living organisms, particularly tailored for load-bearing applications. This category emphasizes crucial features such as the material's structural composition, mechanical properties, and additional biological attributes such as biomineralization and self-healing mechanisms, etc.

While this broad definition of structural ELMs seems straightforward, a point of contention arises concerning the necessity for these materials to retain their biological activity during use. It is a prevalent notion that ELMs require a living component to confer material growth and responsiveness attributes absent in traditional structural materials. This forms the foundational principle of ELMs, driving the field's advancement. However, the distinct nature and competitive edge of ELMs lie in the regulatory influence of the biological component over the entire material's structure or composition, primarily achieved via synthetic biological methods.[17] Thus, the temporal aspect of the biotic component's role, whether it functions during pre-material preparation or during material use, should not be the defining essence. The critical factor is the influence of the organism's biochemical processes on the material's structure or other characteristics.

Materials derived from biological sources, commonly known as bio-derived materials, have a long-standing history and notable successes, particularly in fields such as architecture and energy.[67]–[69] For instance, 'super wood', achieved by delignifying and densifying wood with unidirectionally arranged lumens, exhibit specific strength rivaling steels and holds promise for the construction industry.[70] Another example involves hierarchically porous materials derived from pomelo peels after carbonization and structural modification, find applications in energy storage[71] and photothermal seawater desalination[72]. Numerous similar examples abound.

It is important to note that these bio-derived materials should not be classified as ELMs or Structural ELMs. This distinction arises because biological materials are directly used without prior engineering by living organisms. Therefore, here we propose a criterion: if the structures or composition of raw materials undergo pre-regulation through synthetic biology or similar methods before further processing, the resulting material can be considered as an ELM. To support this argument, an example is drawn from the field of art and furniture design. Pioneers such as Alice and Gavin Munro have ingeniously directed the growth of trees into chair shapes, cutting the chairs directly from the living plant.[73] They conceptualize each tree as a 'carbon sink 3D printer', and the resulting chair as a 'growth material'. We believe this innovative approach aligns with the principles of Structural ELMs, illustrating how intentional manipulation of living organisms contributes to the final material. Nonetheless, the complexity of this topic warrants further discussion. As a nascent field, many standards within this domain await refinement.

Building on this proposed definition, we suggest a classification scheme for structural ELMs, following Srubar's classification of ELM[18], and divide them into five categories: bacteria-based, fungi-based, plant-based, animal cell-based, and consortia-based structural ELMs (**Fig. 4**). While the classification can also pivot on mechanical properties, application fields, structural or pattern characteristics, and so forth, given the diverse capabilities of living organisms in shaping structure and controlling corresponding properties, it seems both logical and appropriate to use living organisms as a classification criterion.

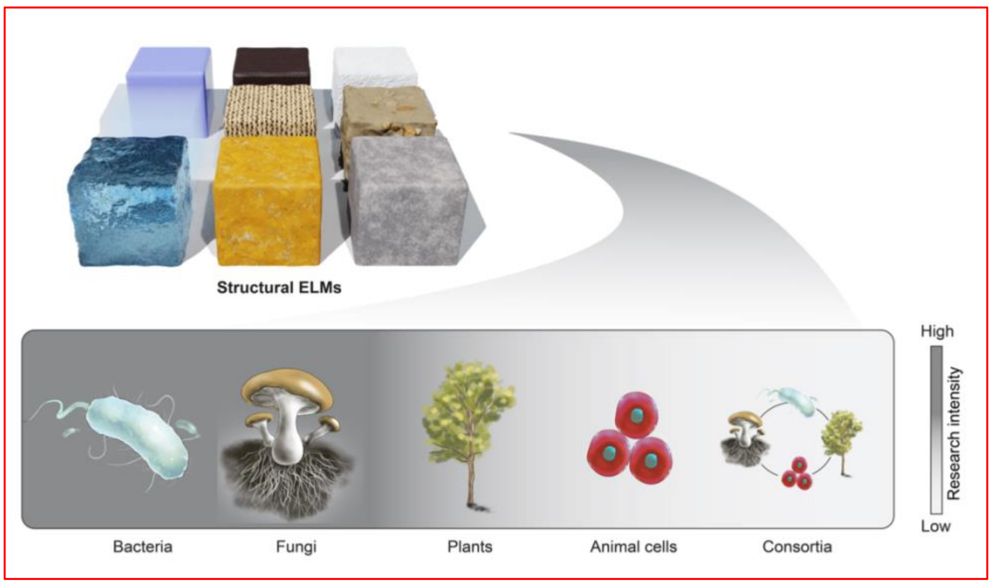

Fig. 4. **Classification of structural ELMs.** Using living organisms as taxon, structural ELMs can be classified into five categories: bacteria-based, fungi-based, plant-based, animal cell-based, and consortia-based structural ELMs.

3.2.1.1 Bacteria-based structural EMLs. Bacteria, among the most primitive life forms, have proliferated across the planet with the identification of 42 phyla over billions of years of evolution[74]. With their ability to convert carbon or nitrogen sources into a variety of compounds and biopolymers through biochemical process, bacteria, being prokaryotes with a simple structure and diminutive size (typically only a tenth that of eukaryotes[75]), become an ideal platform for constructing structural ELMs. Common forms of bacterial structural EMLs include bacterial living building materials (LBMs) such as bacterial concrete/soil, biofilm-based composite materials, and bacterial cellulose (BC)-based materials.

LBMs represent a significant subset of structural ELMs. Bacterial concrete, for instance, combines specific bacterial strains with concrete, leveraging microbially induced mineralization or, in most of cases, microbially induced calcite precipitation (MICP) to bestow self-healing properties (**Fig. 5a1**). The *Bacillus* genus is a commonly utilized bacteria, as their spores can remain viable within concrete. Several enterprises have pioneered bacterial cultures for cultivating strains that produce carbonates. For example, in Belie et al.'s report[76], a mixed ureolytic culture (MUC) developed by Avecom was employed to culture anaerobic granular bacteria, which were subsequently amalgamated with concrete, demonstrating the feasibility for potential large-scale applications. Furthermore, bacteria-inoculated "scaffolds" can assemble sand grains without cement, and the resultant structure is toughened via MICP. Notably, LBMs, by eliminating cement, can reduce 5-8% of CO_2 emissions[77]. Two types of bacteria, *Synechococcus sp.* PC7002 and E. coli HB101:pBU11 had been selected to build LBMs by Hubler et al.[78], in which they can induce MICP via urea hydrolysis (**Fig. 5d**). Given the water-soluble nature of these scaffolds, once the material is fixed by the precipitation, the bacteria can be recovered and reused.

Bacterial biofilms, in line with other ELMs studies, have emerged as primary materials for structural ELMs, (**Fig. 5a2**). Joshi et al.[79] introduced a biodegradable aquaplastic, utilizing curli cellulose as the structural matrix, with genetically engineered *E. coli* producing extracellular protein hydrogels. This biofilm composite aquagel can be processed into structured plastic through template casting and natural drying (**Fig. 5e**). Owing to the viability of *E. coli*, the as-obtained plastic exhibited self-healing properties. Their subsequent work further reported the manufacture of stiff and robust materials solely reliant on living cells (without structural support material), which displayed advantages such as lightness, durability, and self-healing properties[80].

Bacterial cellulose (BC) is polysaccharide produced by bacteria, serving as a constituent for biofilm or structural support (**Fig. 5a3**). Compared to plant cellulose, BC exhibits a nanoscale diameter, higher crystallinity (70-80%), and exceptional purity, thereby demonstrating superior mechanical robustness.[81] It has been reported that BC film possesses an elastic modulus within the range of 15-35 GPa[82]. Various bacteria species, particularly those belonging to the *Komagaeibacter* and *Gluconacetobacter* genera, have been identified as proficient producers of BC with both high yield[83] and quality[84]. This makes BC a highly promising candidate for the development of structural ELMs. For instance, Schaffner et al.[85] demonstrated an approach to construct intricate structures embedded with bacteria using 3D printing (**Fig. 5f**). In this process, in situ formation of BC occurred within the hydrogel scaffold, which can potentially serve as skin transplants in the future. More recently, Ellis et al.[86] have also verified the feasibility of crafting BC spheroids to build 3D structures, demonstrating promise for structural ELMs applications (**Fig. 5g**). Additionally, Binelli et al.[87] demonstrated a manufacturing platform capable of generating cellulose structures with complex shapes and living functionality by utilizing 3D printing with bacteria-laden inks in a granular gel (**Fig. 5h**).

In **Table 1**, we summarize some representative works on bacterial structural ELMs. In light of their exceptional versatility and mechanical properties, bacteria-based ELMs are poised to remain a pivotal category within the structural ELMs domain.

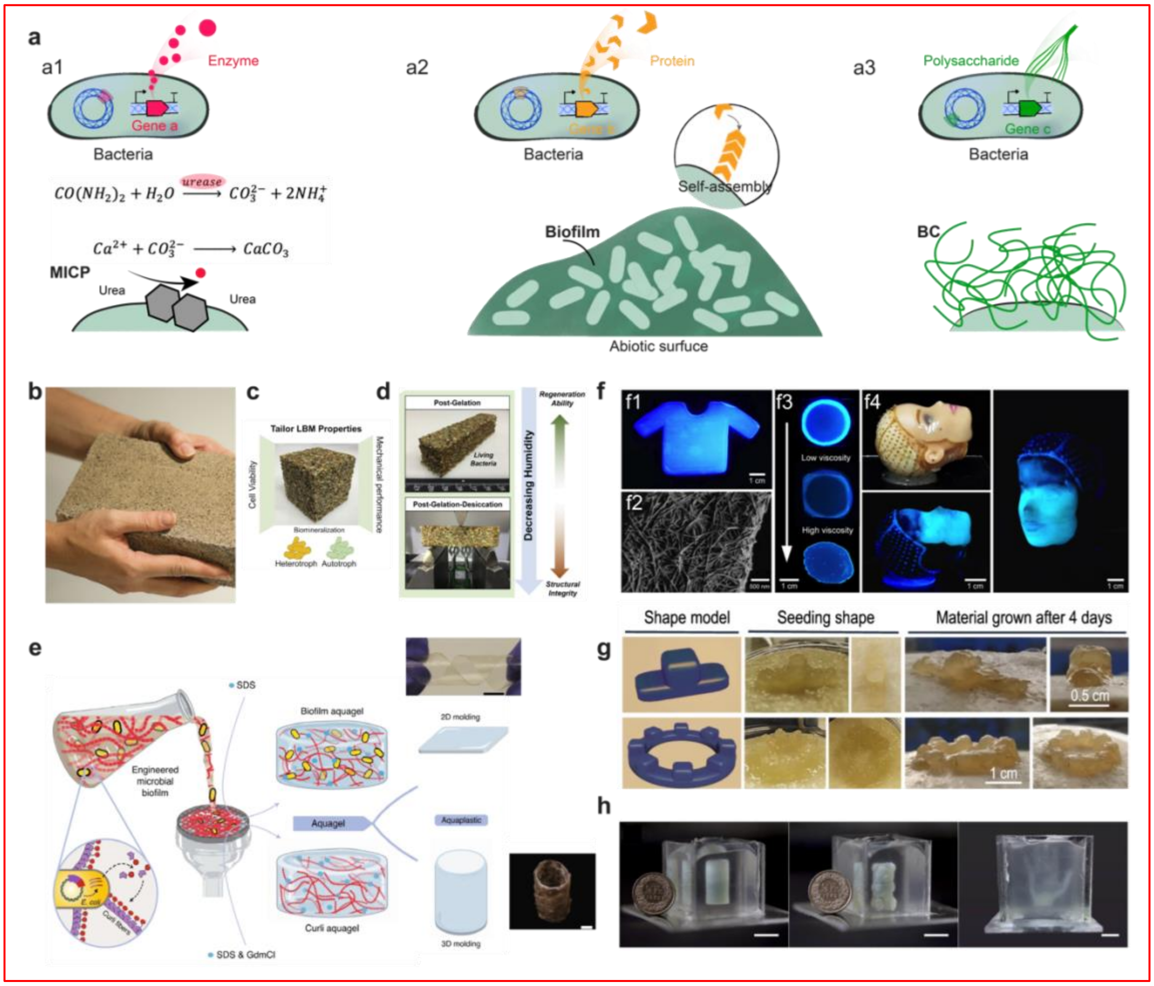

Fig. 5 Bacteria-based structural ELMs. (a) Schematic of attractive features of bacteria platform, including a1) MICP, a2) amyloid protein in the biofilm, and a3) BC. (b) Photo of a biomanufactured brick. Reproduced with permission from Ref.[88] . © John Wiley & Sons, Ltd 2013. (c) Idea of tailoring LBM properties by different MICP pathway. Reproduced with permission from Ref.[78] . © Elsevier Ltd. 2021. (d) Influence of humidity for LBM. Reproduced with permission from Ref.[89] . © Elsevier Ltd. 2019. (e) Schematics of aquaplastic fabrication from genetically engineered bacteria programmed to produce a functional curli fiber-based aquagel that can be molded into two- (2D) and three-dimensional (3D) architectures. Inserts are photos of corresponding aquaplastic samples. Reproduced with permission from Ref.[79] © Springer Nature 2021. (f) 3D-printed bacteria-functionalized structures with complex shapes for bioremediation and biomedical applications. f1) In situ formation of bacterial cellulose is used to generate a 3D-printed scaffold. Bacterial cellulose is visualized with a specific fluorescent dye at 365 nm. f2) SEM image of bacterial cellulose nanofibril network. f3) Growth of bacterial cellulose depends on oxygen availability and the viscosity of the Flink. f4) A doll face was scanned, and Flink containing A. xylinum was deposited onto the face using a custom-built 3D printer. In situ cellulose growth leads to the formation of a cellulose-reinforced hydrogel that, after removal of all biological residues, can serve as a skin transplant. Reproduced with permission from Ref.[85] . © American Association for the Advancement of Science 2017. (g) Growth of two example 3D shapes constructed using BC. Model of desired structure (left), the seeded spheroid shape assembled manually (middle) and the resultant material structure produced after 4 days of further growth (right). Reproduced with permission from Ref.[86] . © Springer Nature 2021. (h) Three-dimensional cellulose structures obtained from bacteria-laden inks printed in granular gels. Reproduced with permission from Ref.[87]. © Elsevier Ltd. 2022.

Structural ELMs	Biotic components		Abiotic components		Methods	Strength (MPa)		Young's modulus (MPa)	Dry density (g/cm3)	Applications	Ref
	Organisms	Species	Type	Materials		Tensile	Compressive				
Bacterial -based	Bacteria (MICP)	Sporosarcina pasteurii	Mixture	Resin+culture medium	3D printing	-	-	1990 ± 400	2.25	Not specified	Ref.[94]
Living Building	Bacteria (MICP)	Synechococcus sp. PCC 7002	Mixture	Hydrogel+sand +biomineral	Moulding	-	3.60 ± 0.327	293.9 ± 11.0	1.2*	Construction	Ref.[89]
Living Building	Bacteria (MICP)	E. coli	Mixture	Hydrogel+sand +biomineral	Moulding	-	2.59 ± 0.22	-	1.5*	Construction	Ref.[78]
Living Building	Bacteria (MICP)	Synechococcus	Mixture	Hydrogel+sand +biomineral	Moulding	-	3.77 ± 0.1	-	1.5*	Construction	Ref.[78]
Gradient mineraliz	Bacteria (Biofil	E. coli MG1655 PRO	Mineral	Biomineral	Direct culture	-	-	2.59	-	Not specified	Ref.[93]
Bacterial -based	Bacteria (Biofil	E. coli MG1655 PRO	-	-	Direct culture	-	-	10200 ± 3600	0.057 ± 0.11	Not specified	Ref.[92]
Curli Aquaplas	Bacteria (Biofil	-	Mixture	Hydrogel+protein	Moulding	29 ± 5	-	1200 ± 200	0.13*	Platic substituti	Ref.[79]
Biofilem Aquaplas	Bacteria (Biofil	E. coli PQN4	Mixture	Hydrogel+protein	Moulding	18 ± 5	-	1000 ± 200	0.1*	Platic substituti	Ref.[79]
Bacterial -based	Bacteria （BC）	Komagataeibacter	Mixture	Xanthan gum, D-mannitiol,	3D printing	-	-	-	-	Not specified	Ref.[87]
Bacterial -based	Bacteria （BC）	Komagataeibacter rhaeticus	-	-	Manually assemble	5.13	-	700	-	Not specified	Ref.[86]
Bacterial -based	Bacteria （BC）	Pseudomonas putia+acetobac	Mixture	Hyaluronic acid+K-	3D printing	-	-	~0.05	-	Biomedical	Ref.[85]
Bacterial -based	Bacteria （BC）	Komagataeibacter rhaeticus	-	-	Direct culture	0.49	-	235.91 ± 30.83	1.13	Not specified	Ref.[91]
Bacterial -based	Bacteria （BC）	Komagataeibacter rhaeticus	-	-	Direct culture	0.823	-	386.54 ± 87.43	1.26	Not specified	Ref.[91]
Bacterial -based	Bacteria （BC）	Komagataeibacter rhaeticus	-	-	Direct culture	0.009	-	3.14 ± 0.35	1	Not specified	Ref.[91]
Bacterial -based	Bacteria （BC）	Acetobacter xylinum FF-89	Plastic	Epoxy	Moulding (heat-	325	-	20,000-21,000	2.7	Optical applicati	Ref.[90]

Table 1. Summary of biotic/abiotic components, mechanical property, as well as application of typical bacteria-based structural ELMs. Density with * was calculated by mass over volume presented in the corresponding reference.

3.2.1.2 Fungi-based structural ELMs. Similar to bacteria, fungi are frequently utilized as microbial living organisms in the development of structural ELMs. Unlike single-celled yeast used in alcohol and bread production, most fungi exhibit filamentous growth. As shown in **Fig. 6a**, the mycelium, which constitutes the vegetative lower part of the fungus, can proliferate indefinitely under suitable conditions, making fungi the largest known organism, with some fungal mycelia covering several square kilometers[95]. The growth unit of the mycelium is hypha, and its form is determined by the assembly of cell wall.[96] While the hypha cell wall varies slightly depending on the fungal species, its general structure remain consistent, featuring a fibrous, gel-like carbohydrate polymer scaffold enveloped by an outer layer containing a variety of proteins and surface modifications. More specifically, the inner cell wall is composed of a covalently bonded, branched β-(1,3) glucan/β-(1,6) glucan core and chitin around the cell, providing the primary structural framework that withstands mechanical loading. The outer components comprise gel-like or hydrophobic proteins and often exhibit significant variations among species. This multilayered configuration contributes to mechanical support and protection for the cells against environmental cues. The mycelium's vigorous growth, complex three-dimensional fibrous structure, and superior mechanical properties, along with diverse surface characteristics of the hypha cell wall, collectively present promising opportunities for structural ELMs.

Fungi can be inoculated into various abiotic components through different techniques, with molding being a representative method. This involves blending raw feedstock with the fungal inoculum, which is then shaped within a mold (**Fig. 6a**). Mycelium-based bricks and slabs crafted from agricultural waste such as straw, cotton, wood, and hemp husk have been reported and are entering commercial applications.[97]–[105] For example, McBee et al.[106] developed fungal composite blocks with potential for large structure and fusion between different units (**Fig. 6b**). Additionally, molding can yield products like "fungal leather".[107] Elsacker et al.[108] introduced a pure mycelium material as a leather substitute (**Fig. 6c**), which exhibits a Young's modulus of approximately 20 MPa and self-healing properties. Interestingly, the mechanical performance was even improved after healing. These studies either underscore the mechanical role of mycelium in composite materials or take advantage of its growth and self-healing properties. Additionally, mycelium induced biomineralization has also been employed in structural ELMs. It has been reported that the three-dimensional structure of fungal mycelium serves as an excellent site for mineralization, offering superior control over calcium ions.[109] Moreover, fungi is capable of adsorbing and removing heavy metal ions from pollutants[110], suggesting potential applications for LBMs like pollutant-cleaning concrete.

Beyond molding, 3D printing is widely adopted to fabricate ELMs due to its capability of customizing complex structures (**Fig. 6a**). Gantenbein et al.[111] proposed a 3D printing approach to fabricate various structural materials constituted of mycelium-laden hydrogel, showcasing appealing properties such as mechanical robustness, self-cleaning, and self-healing after sufficient fungal growth (**Fig. 6d**). Shen et al.[112] reported another fungi-based structural material made by an indirect inoculation method, where hemp, inoculated with fungi, serve as a base for 3D printing (**Fig. 6e**). On top of the it, biocomposite was printed by utilizing an ink incorporating coffee grounds, chitosan hydrogel and commercial cellulose microfibers. Interestingly, the orientation of microfibers during extrusion establishes a hierarchical anisotropy, impacting the mechanical performance. With controlled toolpathing, the resulting material with mycelium inoculated from the base achieves the highest tensile strength (4.88 MPa) reported so far in fungal composites. This platform is expected to offer versatility across various application domains such as self-assemble containers and textiles.

Considerable efforts are underway to explore the morphology and mechanical property control of fungi-based structural ELMs.[97], [113] By altering the culture medium composition, both the morphology of the mycelium and the mechanical properties can be manipulated. Sağlam and Özgünler[114] investigated the effects of five commonly used fillers on the growth of mycelium and the mechanical properties of resultant bricks. It was found that a high filler to mycelium ratio will hamper the growth of mycelium, and an elevated cellulose content in the fillers might adversely affect both growth and mechanical performance.

Athanassiou et al. reported that when the mycelia grow on a substrate with hard-to-digest nutrition, chitin production increased, resulting in BLMs of a higher Young's modulus.[115] Chang et al. incorporated glycogen synthase kinase-3 (GSK-3) inhibitors into the culture substrate, leading to suppressed growth of the fruiting bodies. These results provide further insights for tailoring the stability of fungi-based structural ELMs.[116]

In **Table 2**, representative mycelium composites reported in literature was summarized. They typically show low density and relatively weak mechanical property. However, owing to their facile manipulation, swift proliferation, and robust compatibility with non-living components, mycelium composite materials not only persist as a focal point within the realm of structural ELMs but also exhibit substantial potential for expedited transition into application and commercialization stage.

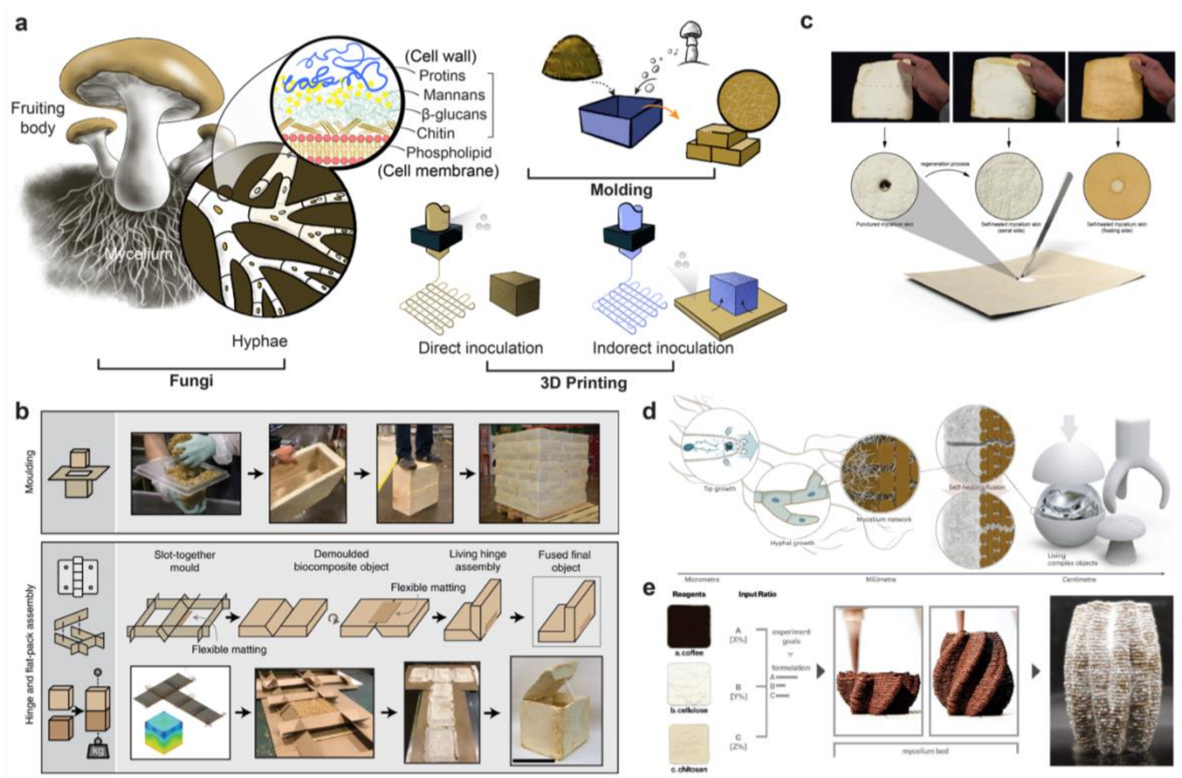

Fig. 6 Fungi-based structural ELMs. (a) Schematic of fungi structure at different scales and typical processing methods of molding (up) and 3D printing (down) for fungi-based ELMs. (b) The fungal mycelium of *Ganoderma sp.* is mixed with raw feedstock and placed in plastic precast vacuform molds made from wax-coated cardboard to produce lightweight yet strong biocomposite blocks that can be assembled into larger structures. Flexible connectors made from cloth or matting enable the joining of biocomposite block units, yielding 'living hinges' that can be used to build more sophisticated structures by kinematic and origami-inspired assembly paradigms. Reproduced with permission from Ref.[106] . © Springer Nature 2021. (c) Regeneration process of "fungal leather". Reproduced with permission from Ref.[108] . © Wiley - VCH GmbH 2023. (d) Hierarchical structure of the resulting mycelium-based objects, highlighting (from left to right) the cell-level growth through self-organization processes, the hyphal cells that form the mycelial network, the growth of the mycelial network between printed hydrogel filaments, the self-healing and regeneration processes across large air gaps and the macroscopic geometry of the complex material according to the shapes that are relevant for the final applications. Reproduced with permission from Ref.[111] . © Springer Nature 2022. (e) Overview of the design and fabrication process, including biocomposite design, additive manufacturing fabrication, and indirect inoculation of mycelium. Reproduced with permission from Ref.[112]. © Author(s) 2023. CC BY-NC-ND 4.0.

Structural ELMs	Biotic components		Abiotic components		Methods	Strength (MPa)		Young's modulus (MPa)	Dry density (g/cm3)	Applications	Ref
	Organ	Species	Type	Materials		Tensile	Compressi				
Mycelium Biocomposites	Fungi	Ganoderma	Mixture	Malt	3D printing	0.06-0.07	-	0.5-0.6	-	Device	Ref.[1
Mycelium Leather	Fungi	Ganoderma	-	-	Moulding	0.92 ± 0.19	-	22.56 ± 1,91	0.3-0.5	Leather	Ref.[1
Mycelium Biocomposites	Fungi	Ecovative	Biowaste	Chitosan+c	3D printing	0.72	-	160.27	0.466	Not specified	Ref.[1
Mycelium Biofoam	Fungi	Irpex lacteus	Biowaste	Mixture	Moulding	-	0.35-0.57	50-30	0.24	Construction	Ref.[1
Mycelium Biocomposites	Fungi	Trametes	Biowaste	wood (pine	Moulding	-	-	0.14	0.0874 ± 0.0052	Not specified	Ref.[1
Mycelium Biocomposites	Fungi	Trametes	Biowaste	flax	Moulding	-	-	1.32	0.0685 ± 0.0022	Not specified	Ref.[1
Mycelium Biocomposites	Fungi	Trametes	Biowaste	flax	Moulding	-	-	1.18	0.0658 ± 0.0042	Not specified	Ref.[1
Mycelium Biocomposites	Fungi	Trametes	Biowaste	flax (loose)	Moulding	-	-	0.28	0.0598 ± 0.0117	Not specified	Ref.[1
Mycelium Biocomposites	Fungi	Trametes	Biowaste	hemp	Moulding	-	-	1.19	0.00721 ±	Not specified	Ref.[1
Mycelium Biocomposites	Fungi	Trametes	Biowaste	hemp	Moulding	-	-	0.77	0.0974 ± 0.0032	Not specified	Ref.[1
Mycelium Biocomposites	Fungi	Trametes	Biowaste	hemp	Moulding	-	-	0.51	0.0886 ± 0.0014	Not specified	Ref.[1
Mycelium Biocomposites	Fungi	Trametes	Biowaste	wood	Moulding	-	0.52 ± 0.08	-	0.179	Construction	Ref.[1
Mycelium Biocomposites	Fungi	Trametes	Biowaste	hemp	Moulding	-	0.36 ± 0.05	-	0.134	Construction	Ref.[1
Mycelium Biocomposites	Fungi	Pleurotus	Mixture	wheat +	Moulding	0.096	0.035	-	0.029	Platic	Ref.[1
Mycelium Biocomposites	Fungi	Pleurotus	Biowaste	cotton	Moulding	0.24 ± 0.03	-	97 ± 9.0	0.39 ± 0.01	Not specified	Ref.[9
Mycelium Biocomposites	Fungi	Pleurotus	Biowaste	cotton	Moulding	0.13 ± 0.02	-	35 ± 6.5	0.35 ± 0.02	Not specified	Ref.[9
Mycelium Biocomposites	Fungi	Trametes	Biowaste	cotton	Moulding	0.15 ± 0.01	-	59 ± 6.8	0.35 ± 0.02	Not specified	Ref.[9
Mycelium Biocomposites	Fungi	Pleurotus	Biowaste	raspeseed	Moulding	0.03 ± 0.00	-	9 ± 1.2	0.35 ± 0.01	Not specified	Ref.[9
Mycelium Biocomposites	Fungi	Pleurotus	Biowaste	raspeseed	Moulding	0.03 ± 0.00	-	6 ± 0.3	0.24 ± 0.01	Not specified	Ref.[9
Mycelium Biocomposites	Fungi	Pleurotus	Biowaste	raspeseed	Moulding	0.01 ± 0.00	-	2 ± 0.3	0.13 ± 0.01	Not specified	Ref.[9
Mycelium Biocomposites	Fungi	Pleurotus	Biowaste	raspeseed	Moulding	-	-	-	0.13 ± 0.01	Not specified	Ref.[9
Mycelium Biocomposites	Fungi	Trametes	Biowaste	beech	Moulding	0.05 ± 0.01	-	13 ± 0.5	0.17 ± 0.01	Not specified	Ref.[9
Mycelium Biocomposites	Fungi	Trametes	Biowaste	raspeseed	Moulding	0.04 ± 0.01	-	4 ± 0.4	0.1 ± 0.01	Not specified	Ref.[9
Mycelium Biocomposites	Fungi	Ecovative	Biowaste	hemp fiber	Moulding	0.1	-	7.13	0.1	Not specified	Ref.[1
Mycelium Biocomposites	Fungi	Ecovative	Biowaste	hemp pith	Moulding	0.13	0.23	6.14	0.12	Not specified	Ref.[1
Mycelium Biocomposites	Fungi	Ecovative	Biowaste	cotton	Moulding	0.2	-	3.65	0.14	Not specified	Ref.[1

Table 2. Summary of biotic/abiotic components, mechanical property, as well as application of mycelium-based structural ELMs.

3.2.1.3 Plant-based structural ELMs. The use of plants by humans likely dates back to prehistoric times, encompassing materials such as branches, sticks, leaves, and vines. Today, while we have continually innovated in our exploitation of plant-based resources, from the development of super wood to plant-inspired slippery surfaces, research utilizing plants or plant cells as living components within structural ELMs or the broader ELMs field remains relatively limited. This limitation can be attributed to the intricate biological structure of plants compared to microbial organisms. The growth of a plant involves the coordination of numerous tissues, and plants are more susceptible to environment stresses with typically longer growth cycles, posing significant challenges to the development of plant-based structural ELMs.

Historically, notable endeavors in architecture and furniture have leveraged plant's capability of environmental adaptation, employing techniques such as guiding growth tips along predetermined paths or directly bending saplings to shape trees. [122](**Fig. 7a**). Architectural example includes plant bridges, such as the Vine bridges in Japan's Iya Valley[123] (**Fig. 7b**), and structures built using the Baubotanik method, which employs living plants as the load-bearing materials[124], [125] (**Fig. 7c**). These built structures depend on the interplay of joints and plant growth (**Fig. 7c1**). Storz et al.[124] manipulated trees to achieve desired shapes using industrial structures, and eventually constructed an eight-meter tower (**Fig. 7c2-c3**). In the furniture sector, Krubsack explored the concept of "living chairs" in early 20th century by guiding the growth of saplings (**Fig. 7d**).[122]

While these works have contributed to the concept, well-established examples of structural ELMs directly utilizing living plants are relatively rare. However, recent work by Chiara et al. introduced a novel approach, focusing on developing plant-based structural ELMs using incubated and dehydrated plant cells.[126] This method involves culturing and harvesting cells, mixing them with abiotic material, and compressing into structure-controlled biocomposite. The resulting material exhibits notable elastic modulus and strength, benefiting from the highly oriented microstructure of plant cells. This methodology, resembling strategies employed in other structural ELMs, may provide insights for developing multiscale structural ELMs with bottom-up design tactics.

In our opinion, advancing in this area necessitates the collaboration with modern fields such as synthetic biology and genetic engineering of plants to provide more feasible conditions. Potential avenues for progress include engineering plants morphology via genetic editing, manipulating biopolymer composition, adjusting growth rate, and other approaches., facilitating their integration with non-biological scaffolds.

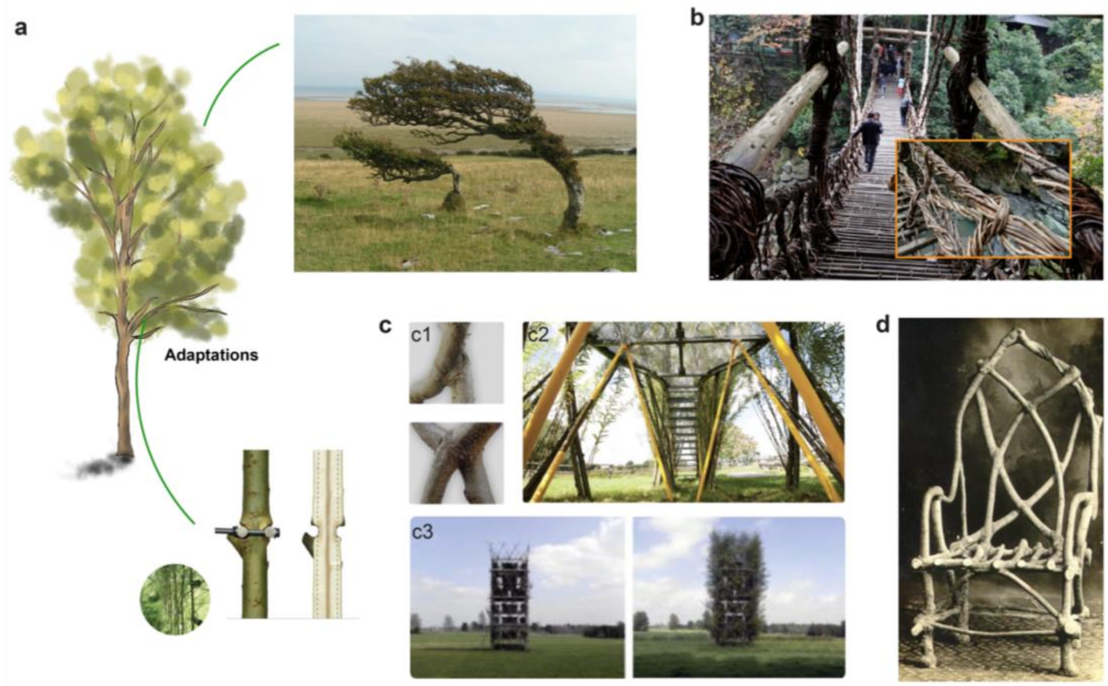

Fig. 7 Plant-based structural ELMs. (a) Schematic of tree's capability of adaptation, in nature, the shape the trees adapt to the wind [By Dave Dunford, CC BY-SA 2.0, https://commons.wikimedia.org/w/index.php?curid=9191364], and the plant adapt to technical element after 3 years growth Reproduced with permission from Ref.[124]. © John Wiley & Sons, Ltd. 2012. (b) Photo of vine bridge in Japan's Iya Valley, insert is the detail of the woven vine. [By Kimon Berlin - Flickr: Iya vine bridge, CC BY-SA 2.0, https://commons.wikimedia.org/w/index.php?curid=19347885, insert: By KimonBerlin - https://www.flickr.com/photos/kimon/6551509515/, CC BY-SA 2.0, https://commons.wikimedia.org/w/index.php?curid=57574388] (c) Baubotanical architechture. c1) samples of junction between plants, c2) Baubotanical platform, c3) Development of the Baubotanical Tower in the first growing season. Reproduced with permission from Ref.[124]. © John Wiley & Sons, Ltd. 2012. (d) Krubsack chair. [Public Domain, https://commons.wikimedia.org/w/index.php?curid=106324387]

3.2.1.4 Animal cell-based and consortia-based structural ELMs. Despite extensive investigation in various fields, the utilization of animal cells in structural ELMs has been relatively limited. A notable application involves the development of living biomaterials, such as engineered living blood vessels generated from human cells seeded on abiotic vascular scaffolds via polymer fabrication.[127] Additionally, the advent of 3D bioprinting, which combines traditional additive manufacturing with live animal cells, emerges as a promising technique for printing replaceable tissues and organs, addressing numerous medical challenges (**Fig. 8a**). Bioprinting strategies include structural biomimicry (printing the structure, cell types, and component gradients of tissues and organs), autonomous self-assembly (mimicking the process of early organ development or relying on cellular tissues undergoing self-assembly to construct structures), and mini-tissues (printing minimal structural or functional units for subsequent self-assembly).[128] While these studies primarily focus on cell viability and the physiological functionality, the mechanical properties, equally critical, often receive less attention. As a platform incorporating animal cells, non-living substrate and structure construction, the significance of 3D bioprinting need to be emphasized in the field of structural ELMs.

For structural materials, material selection is crucial. Considering the need for cell growth and function, a limited range of matrix materials in 3D bioprinting have been used so far, including collagen, hyaluronic acid, diatomaceous earth, and photo-curable acrylates. The interaction between tissue cells and the matrix is also a major determinant in material selection.[129] For example, Kang et al.[130] integrated graphene oxide (GO) with a 3D collagen scaffold to facilitate the osteogenic differentiation of Mesenchymal Stem Cells (MSCs). In this system, the GO promoted the expression of osteogenesis-related genes and proteins, making it a promising platform for bone regeneration (**Fig. 8b**). Subsequent research corroborated the interplay between the abiotic components and the osteogenic development of MSCs[131] (**Fig. 8c**). Compared to other organisms introduced earlier, the use of animal cells for structural ELMs comes with more limitations and requirements. However, developing structural ELMs for scenarios without physiological function requirements is simpler than fabricating fully functional artificial organs, making the emergence of 3D bioprinted animal cell based structural ELMs highly plausible in the near future.

In addition to animal cells, structural ELMs that incorporate diverse living organisms, known as consortia, present an intriguing approach. Functionalities can be achieved through inter-organismal communication via biomolecule exchanges. A notable example is McBee et al.'s fungal-bacterial system[106], where composite bricks were constructed from the mycelium of *Ganoderma sp.* fungi and particles of hemp husk as organic feedstock. Moreover, the inclusion of two engineered bacteria strains (*Pantoea agglomerans*) as information sender and receiver endows the living material system with more potential of message exchanges (**Fig. 8d1**). Specifically, upon contact between bricks with different strains, a "message" (expression of mCherry) was left on the contact position due to the response to the information molecule AHL (**Fig. 8d2**). These composites decent mechanical strength as well as features like self-healing and forming stable structures by natural fusion of contacted surfaces.

Consortium systems can leverage the metabolic division of labor (DOL), enabling different populations to undertake distinct yet complementary metabolic tasks, thus easing the burden to manipulate a single population.[132] For instance, Gilbert et al.[133] established a platform for generating Bacterial Cellulose (BC) materials employing a symbiotic culture of *Saccharomyces cerevisiae* yeast and *Komagataeibacter rgaeticus* bacteria (**Fig. 8e1**). In this system, yeast acts as an environmental sensor and enzyme secreter, modifying the surrounding BC produced by bacteria (**Fig. 8e2**). This gives the resulting material remarkable mechanical property and the ability to respond to chemical or optical stimuli. These innovations underscore the potential of consortia systems in advancing structural ELMs.

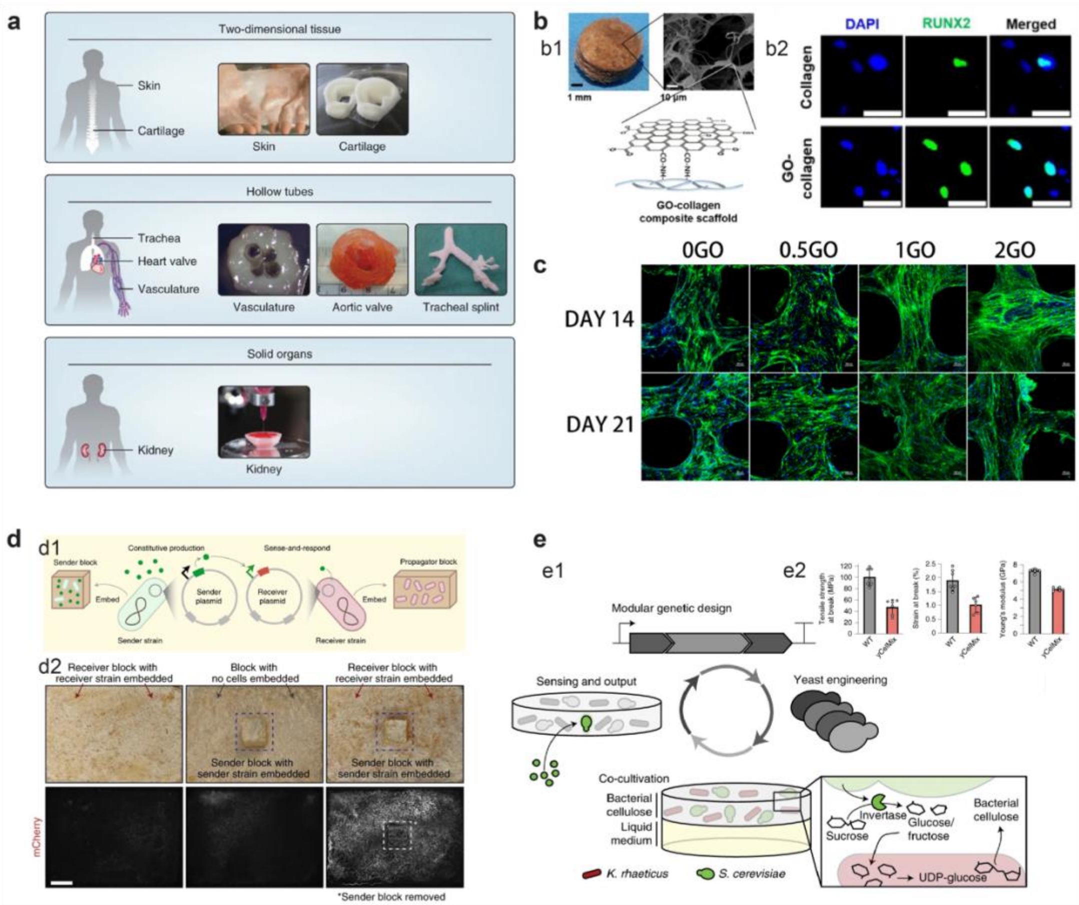

Fig. 8 Animal cell-based and consortia-based structural ELMs. (a) Examples of human-scale bioprinted tissues. Reproduced with permission from Ref.[128] . © Springer Nature 2014. (b) GO-collagen scaffold, b1) photo and SEM image, b2) Immunocytochemical staining of RUNX2 (green) in hMSCs cultured on collagen scaffolds and GO-collagen scaffolds at 3 weeks. Cell nuclei were stained with DAPI (blue). Scale bars: 50 μm. Reproduced with permission from Ref.[130]. © Elsevier Ltd. 2014. (c) Assessment of the overall presence of MSCs in the scaffolds. (a) Immunofluorescence images of the scaffolds on days 14 and 21 after printing. Green and blue signals indicate F-actin and the nuclei, respectively. The results showed that MSCs secrete more F-actin fibers during the differentiation process in response to GO, thus promoting osteogenesis. Reproduced with permission from Ref.[131]. © SAGE Publications 2022. (d) Developing a stimuli-responsive ELM by consortia system. d1) A schematic of the functionalization of a stimuli-responsive ELM with engineered sender and propagator strains. d2) 'sender' strain is embedded in a sender block and produces a signal molecule, AHL. When the sender block is placed in contact with a block containing a 'receiver' strain and rehydrated, the receiver block produces mCherry in response to the AHL signal. Scale bar: 5 cm. Reproduced with permission from Ref.[106]. © Springer Nature 2021. (e) Consortia system of bacteria and yeast. e1) Schematic summary of synthetic symbiotic culture of bacteria and yeast (Syn-SCOBY) ELMs (UDP = uridine diphosphate). e2) Tensile strength at break, strain at break and Young's modulus of the material. Reproduced with permission from Ref.[133]. © Springer Nature 2021.

3.2.2 Mechanical performance and physiological behaviors

Structural ELMs display notable variability in their mechanical properties, influenced by living organisms, matrix composition, and reinforcement structures at different length scales. The emphasis on mechanical properties also varies across different fields. As shown in **Fig. 9**, mycelium-based structural ELMs primarily occupy in the lower left part in the specific strength-specific stiffness Ashby plot, displaying mechanical properties similar to natural cork and many foam materials. This characteristic is particularly pronounced in mycelium and organic biowaste composite, attributed to their loosely bonded nature. Notably, while mycelium-derived faux leather may not match the strength of genuine leather, its Young's modulus is comparable, suggesting promising application potential.

In contrast, bacterial-based structural ELMs typically demonstrate a more robust mechanical performance, akin to cancellous bone, wood, and certain polymers. Plant-based ELMs, with limited samples often comprising large wood and vine segments combined with non-biological components, are expected to perform like natural wood. Some microbial stiff ELMs exhibit exceptional stiffness comparable to natural structural materials such as compact bone and bamboo, although achieving scalable and large-size fabrication of these materials remains challenging. Clearly, compared to traditional non-living structural materials such as steel, ceramics, leather, and plastics, the mechanical performance of many current structural ELMs is less competitive.

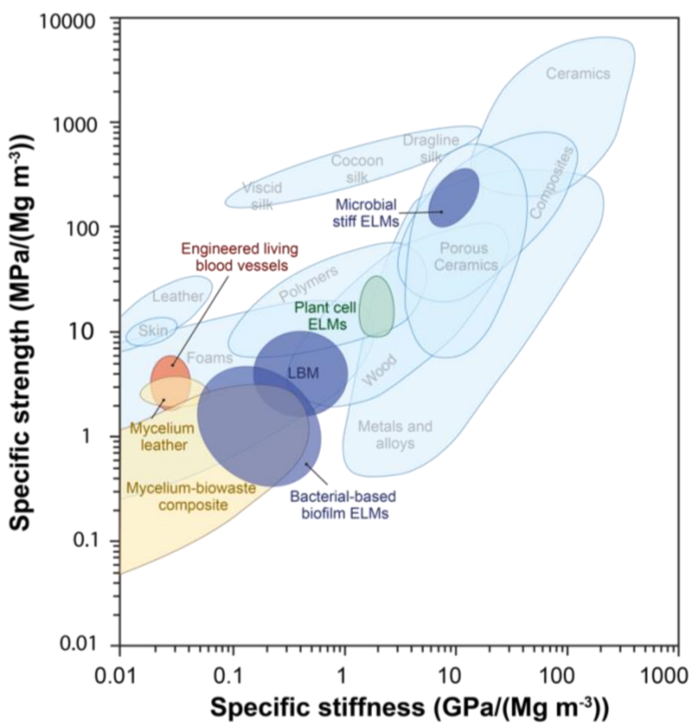

Fig. 9 Ashby plot of specific values (that is, normalized by density) of strength and stiffness (or Young's modulus) of representative structural ELMs summarized in the precent review and typical natural and synthetic materials (plotted in light blue). Adapted with permission from Ref.[6]. © Springer Nature 2014.

To enhance the mechanical performance of structural ELMs and make them suitable for practical applications, researchers have invested significant efforts. A key focus area involves harnessing the biofunctions of living organisms to improve mechanical strength. Consequently, strategies such as biomineralization, biofilm engineering, and fiber reinforcement have been employed. Many structural ELMs developed through these strategies can exhibit mechanical characteristics approaching their non-living counterparts.[80], [134]

Biomineralization is the study of mineral formation mechanisms by organisms, where biological macromolecules often play a crucial role in this process[135]. Synthetic biology enables the modification of microbes to express specific enzyme, functional proteins, polysaccharides, or peptide, thereby promoting biomineralization and strengthening structural ELMs (**Fig. 10a**). For instance, bacteria can be engineered and screened to induce the formation of various minerals, including calcium carbonate, hydroxyapatite (HA), and silica. MICP is essential in constructing many structural ELMs, given calcite's high stiffness, compressive strength, efficient adhesion to gels, and excellent compatibility.[15], [136] Xin et al.[94] proposed a strategy involving pre-designed 3D printed polymer skeletal structures that guide bacteria (*Sporosarcina Pasterurii*) to trigger urease-induced biomineralization (**Fig. 10b**). The polymer scaffold's intricate design, such as lattice and Bouligand structures, utilizes MICP to achieve a mineral content of up to 90%, rendering the composite material's specific strength and fracture toughness comparable to natural composites.

For calcium carbonate formation in bacteria, two metabolic pathways, ureolysis and non-ureolysis, have been identified. In ureolysis, catalyzed by bacteria-produced urease, urea decomposes to produce CO_3^{2-} ions, which then combine with Ca^{2+} ions in the medium, enabling calcium carbonate formation. Alternatively, the non-ureolysis process involves the generation of CO_2 through bacterial respiration, followed by water dissolution, ultimately form calcium carbonate[137]. This urease-free pathway avoids introducing additional nitrogen into the environment.

Biomineralization of HA, induced by specific biomolecules secreted through bacterial editing, has been employed in the construction of structural ELMs. Wang et al. devised a light-responsive *E. coli* that guides HA mineralization, using the CsgA-Mfp3S-pep fusion protein as a functional element with its expression regulated by blue light irradiation (**Fig. 10c**).[93] This was achieved by fusing the coding sequences of the CsgA protein and Mfp3S-pep, both positioned downstream of the light-sensitive pDawn transcriptional control element. Varying the intensities of blue light induced a gradient biofilm, resulting in in-situ HA mineralization and the formation of a thickness-gradient HA minerals. The light-controlled mineralization feature can also be used in localized damage repair applications. Similar material design approaches have been used to create intricately shaped silica nanomaterials.[138], [139] For instance, drawing inspiration from the mechanism diatoms use to generate complex silica patterns, Wallace et al. utilized *E. coli* to express silaffin R5 peptides and selected eight modifying enzymes from a pool of 38 to modify the R5 peptides.[138] By modifying the R5 peptides that induce silica mineralization, the authors were able to control the size, shape, and dispersion of the resultant silica nanoparticles. This study provides valuable insights into using bacterial expression to control biomineralization products, thereby constructing performance-controllable structural ELMs.

Numerous bacteria-based structural ELMs have leveraged the properties of bacterial biofilms (**Fig. 10d**). This strategy not only underscores the environmental responsiveness of biofilms but also strengthens the resulting composite by engineering the mechanical properties of the biofilm. Park et al.[92] report a highly stiff *E. coli* biofilm with inducible CsgA curli nanofibrils, indicating a superior mechanical performance (**Fig. 10e**). Biofilm also facilitate bacteria assembly to enable high stiffness. In a demonstration by Joshi et al.[80], a self-regeneratable and extremely stiff living materials was created, where microbial cells served as building block. The Young's modulus was exceptionally high (**Fig. 10f1**) due to the tight packing structure of the microbe cells (**Fig. 10f2-f3).**

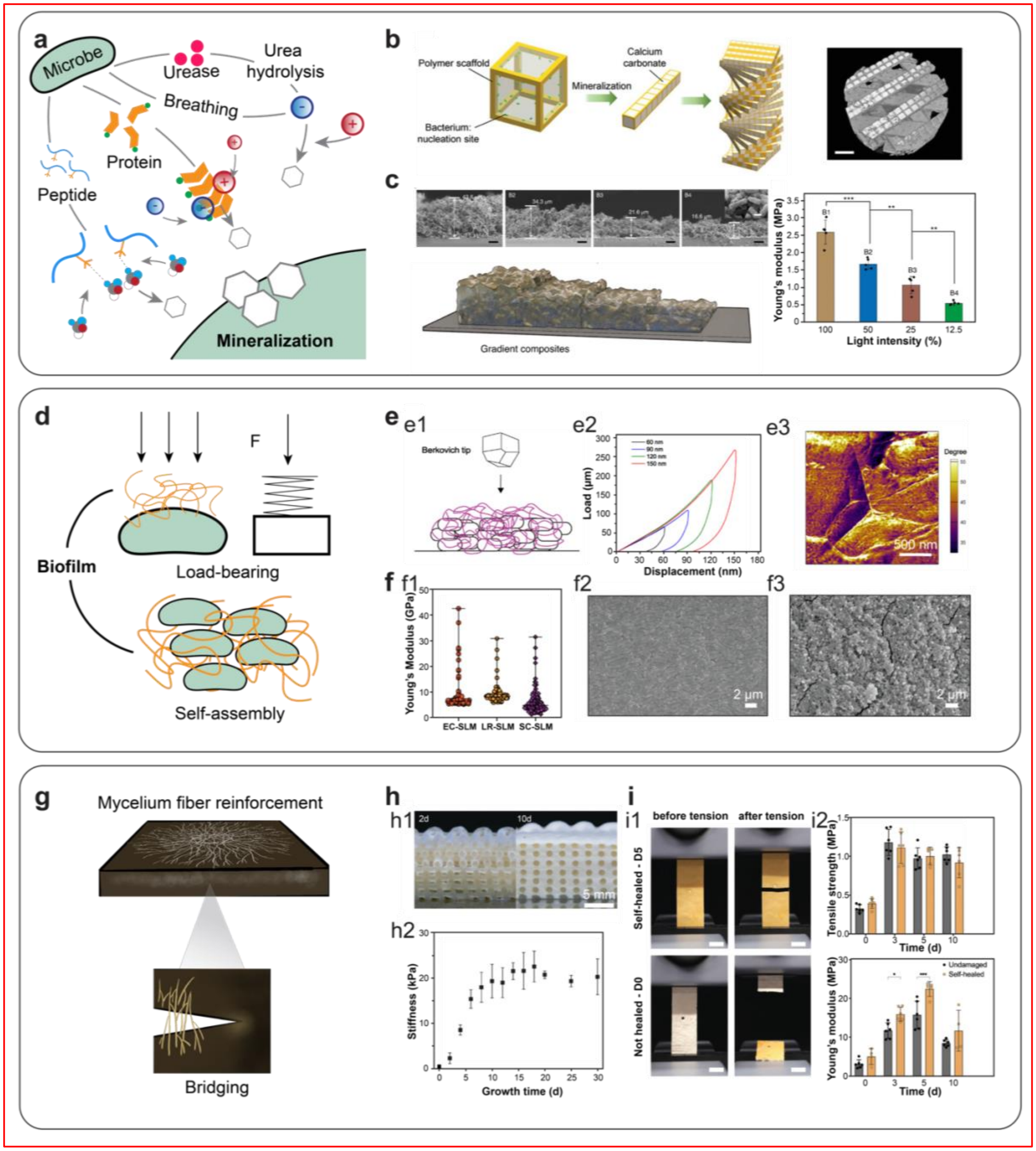

Fig. 10 Mechanical properties improving strategies: Biomineralization, biofilm engineering, and fiber reinforcement. (a) Schematic of different microbe-induced mineralization pathways: urea hydrolysis/bacteria breathing produce carbonate ion, which will combine with the calcium ion in water; functional proteins promote the nucleation, growth and adhesion of mineral; peptide aggregation also facilitates the mineral nucleation. (b) Schematics to show bacteria-assisted mineral growth within a 3D-printed bouligand scaffold (left), and micro-CT scanned images of the mineral phases (right). Reproduced with permission from Ref.[94]. © Wiley - VCH GmbH 2021. (c) Schematic illustration showing the generation of living gradient composites through in situ mineralization of biofilms with gradient biomass densities (left). Inserts are sectional SEM micrographs showing the morphologies of different regions. The gradient biofilms were formed by projecting light with varying intensities and precise spatial control onto the Petri dish containing the lightreceiver-CsgA–Mfp3S-pep strain suspended in medium. Macroscale indentation

analysis for estimating the Young's modulus of the different regions in the gradient composites (right). Reproduced with permission from Ref.[93]. © Springer Nature 2020. (d) Schematic of the roles of biofilm played in improving mechanical properties. (e) e1) Schematic of a biofilm with inducible CsgA curli nanofibrils and stiffness characterization with instrumented indentation using a Berkovich probe tip, e2) mean load-displacement curves on the static medium biofilm with multiple indenting depths. e3) Atomic force microscopy (AFM) phase image showing an indented area after a 150 nm indentation. Reproduced with permission from Ref.[92]. © Elsevier Ltd. 2022. (f) Example of bacteria with biofilm assembling into a robust matrix. f1) Young's modulus obtained from nano-indentation, f2-f3) SEM images show the top view and cross sections of the material. Reproduced with permission from Ref.[80]. © Wiley-VCH GmbH 2021. (g) Schematic of mycelium fiber reinforcement and fiber bridging behind cracks. (h) 3D printed mycelium composite grid. h1) Cross-section of the grid after two and ten days of incubation. h2) Apparent stiffness as a function of growth time. Reproduced with permission from Ref.[111]. © Springer Nature 2022. (i) i1) Photographs of self-healed and unhealed sample before and after tension, i2) tensile strength and Young's modulus of the samples. Reproduced with permission from Ref.[108]. © Wiley-VCH GmbH 2023.

Regarding the mechanical properties of biofilms, they display characteristics of both solids and liquids, exhibiting mechanical responses resembling those of viscoelastic fluids.[140]–[142] Factors influencing the stiffness and rheological properties of biofilms include environmental elements (e.g., extracellular matrix, pH, temperature, etc.) and the composition/structure of the biopolymer in biofilm. The macromolecules constituting the biofilm form stress-bearing structures through intermolecular interactions, such as entanglement and cross-linking. Under shear forces or other mechanical loads, structural rearrangements and molecular cross-linking can modify the mechanical properties of biofilms. Synthetic biology tools, including chemical induction, quorum sensing (QS)-based control, and spatiotemporal control, enable the control of biopolymer expression level and structures.[141]

While fungal biofilms share similar functionalities with bacterial biofilms, research into the rheology of fungal biofilms is somewhat limited. Consequently, fungal-based structural ELMs often employ the strategy of fiber reinforcement to enhance their mechanical properties. This approach involves controlling the interfacial properties between the mycelium and feedstock materials, akin to conventional fiber-reinforced composites. Mycelium serves as a reinforcing network for composite materials and fiber bridging for constraining cracks propagation (**Fig. 10g**). The chitin structures in the cell walls of hyphae, along with the flexible beta-glucans, provide impressive mechanical strength to the mycelium. Mycelium-derived chitin nanopapers exhibit exceptional tensile strength, reaching up to 200 MPa.[143] It has been reported that the higher mycelium network density improves the mechanical properties of the structural ELMs. For instance, the stiffness of mycelium-filled 3D lattice increases with biomass growing (**Fig. 10h**).[111] Self-healed mycelium-based leather, with a denser mycelium mesh, exhibits higher strength (**Fig. 10i**).[108] The type, network density, and structure of hyphae directly influence the mechanical properties of the composite material.

In addition to enhancing mechanical performance, structural ELMs prevent damage from environmental degradation and can self-heal. The term 'self-healing' encompasses two distinct mechanisms. One involves the overall damage repair of the composite material, often including the growth of living organisms or the reconstruction of the biological structure itself (**Fig. 11a**). Examples include the fusion of mycelium-based brick cross-sections, the patching of holes in fungal leather, or the repair of a crack on a vine bridge. The other form of self-healing refers to the repair of cracks in the abiotic part of the material, mainly utilizing the products of biological expression and the induced chemical reactions, such as biomineralization reactions initiated by microorganisms (**Fig. 11b**). For instance, in bacteria-based self-healing concrete, microbially induced calcium carbonate precipitation (MICP) can be induced at crack sites and fill the gaps. Fungi can be also employed for self-healing concrete, which may have the potential to repair larger cracks due to the high growth rate of fungi.[144] While some types of fungi have demonstrated such traits, further in-depth investigations are needed.

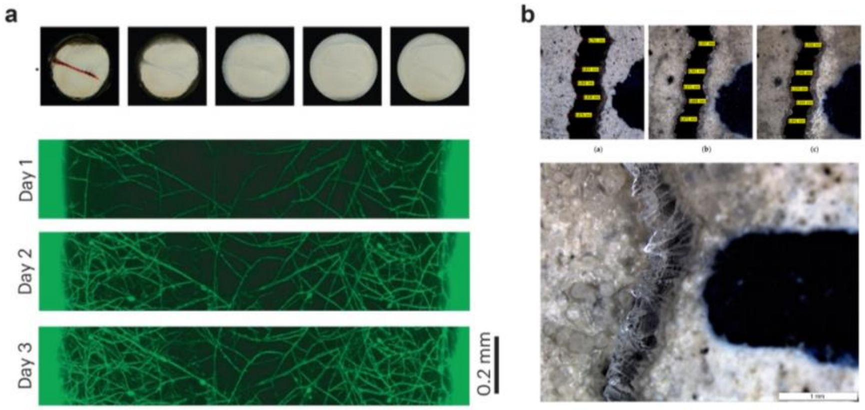

Fig. 11 **Two types of self-healing of structural ELMs.** (a) Self-healing relying on living organisms' growth. The photos show the healing process of cut on a mycelium composite (Reproduced with permission from Ref.[108]. © Wiley-VCH GmbH 2023.) and Laser confocal microscopy images of dyed mycelia (green) growing between two hydrogel filaments printed 1.2 mm apart. Reproduced with permission from Ref.[111]. © Springer Nature 2022. (b) crack healing in abiotic parts achieved by microbes induced mineralization. The photos show the healing process in bacterial concrete. Reproduced with permission from Ref.[76]. © Author(s) 2020, CC BY 4.0.

3.2.3 Applications

The potential applications of structural ELMs are vast and fascinating, spanning various sectors, including construction, home furnishing, textiles, electronic devices, packaging, and more.

In the construction industry (**Fig. 12a**), living building materials put forward an environmental-friendly and reusable concept. Their capabilities, such as growth fusion, self-repair, and adaptation to environmental changes, have the potential to revolutionize building and civil engineering materials. For example, bio-concrete consistently repairs internal micro-cracks, significantly extending the lifespan of buildings, reducing maintenance and replacement needs, and lessening the ecological footprint of the construction sector. Large-scale construction feasibility using self-healing concrete and biological cementation has already been demonstrated (**Fig. 12b-c**).[76], [145] Several organizations are actively constructing living buildings entirely using structural ELMs, such as the 13-meter-tall Hy-Fi tower (**Fig. 12d**) made from fungal bricks[146] and the Auerworld Palace (**Fig. 12e**) constructed from trees[122].

In industrial manufacturing, structural ELMs present a green, sustainable strategy, replacing a variety of petroleum derivatives, textiles and leathers (**Fig. 12f**). Examples include plastics based on bacteria[79] (**Fig. 12h**) and "fabrics" with various patterns based on plant roots[147]. Some enterprises, such as Ecovative Design LLC and Grown.bio, focus on applying mycelium to packaging products (**Fig. 12g**), aiming to reduce carbon emissions and sequester carbon through the use of biological materials.

In furniture and art, creations such as chairs and wall decorations made through structural ELMs epitomize the symbiotic relationship between humans and nature (**Fig. 12i**). In the biomedical field, structural ELMs could make breakthroughs in biocompatible and reactive medical implants or devices. For example, living bone implant materials created by 3D bioprinting, promoting cellular osteogenic differentiation, could offer better biocompatibility compared to currently used artificial counterparts. Finally, structural ELMs hold prospective utility in defense and disaster management. Certain fungi tiles with excellent insulation properties could emerge as fire retardants. As structural ELMs continue to evolve, their application spectrum is poised for expansion.

In essence, the application of structural ELMs provides abundant opportunities across existing fields. By harnessing insights from historical material explorations and leveraging the toolbox of synthetic biology and materials science, the creation of genuinely sustainable structural ELMs for human society becomes an attainable vision.

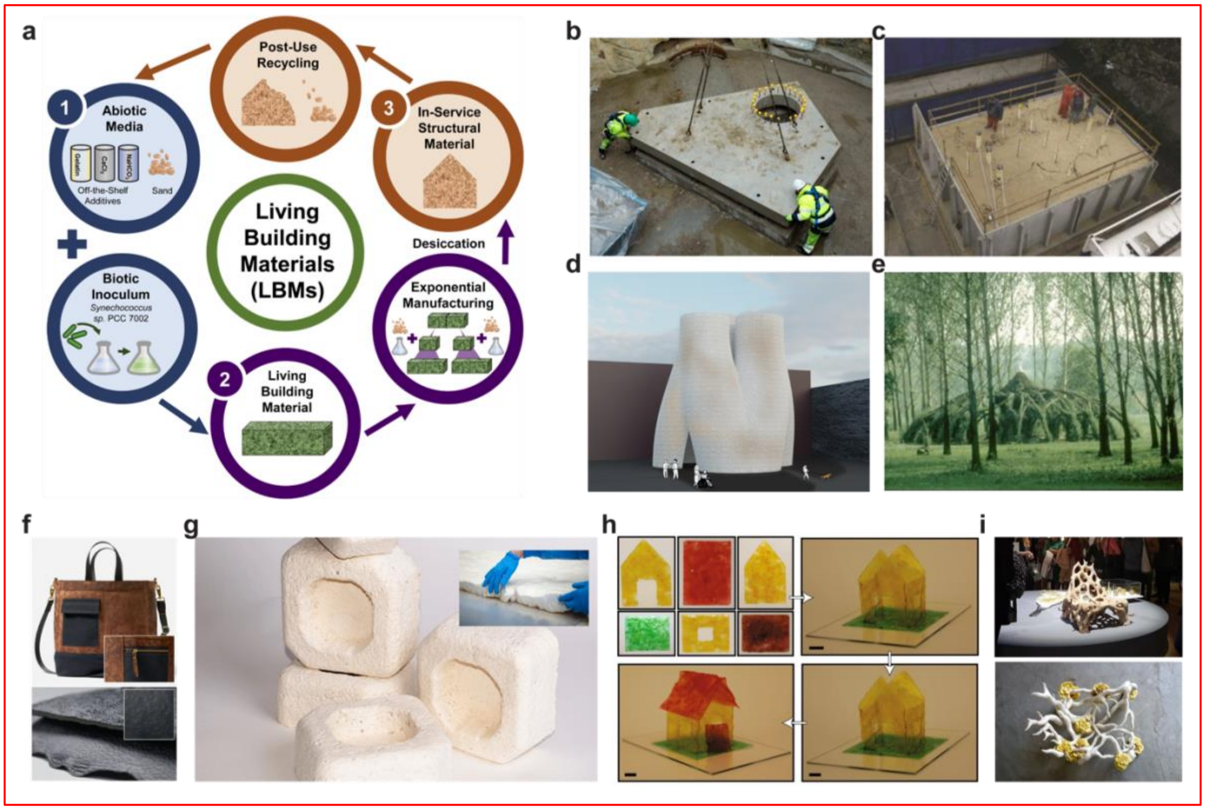

Fig. 12 Typical applications of structural ELMs. (a) The Life Cycle of Living Building Materials. Reprinted with permission from Ref.[89]. © Elsevier Ltd. 2019. (b) Installation of the roof slab made of bacteria-based self healing-concrete on the inspection chamber inside the construction pit. Reproduced with permission from Ref.[76]. © Author(s) 2020, CC BY 4.0. (c) Experimental device for biological cementation in large scale of 100 m^3 (VAN PAASSEN LA 2009). Reproduced with permission from Ref.[145]. © Authors 2021. (d) A concept drawing of Hy-Fi tower made by mycelium-based bricks. (e) Auerworld Palace in Germany. Reproduced with permission from Ref.[122]. © Elsevier 2017. (f) Fungi-derived leather substitutes. Reproduced with permission from Ref.[107]. © Springer Nature 2020. (g) Photo of the Mushroom Packaging produced by Ecovative Design LLC. Insert is the photo shows the mycelium growth. [Photo source: https://www.ecovative.com/] (h) Bacterial plastic products. Reproduced with permission from Ref.[79]. © Springer Nature 2021. (i) The Mycelium Chair (up) which is acquired for being the permanent collection in Centre Pompidou, and one other mycelium art collection (down). [Photo source: https://www.ericklarenbeek.com/]

4. Challenges & prospects

Structural ELMs exhibit distinctive attributes absent in traditional structural materials, including adaptability, self-healing, environmental friendliness, sustainability, and carbon sequestration, underscoring significant engineering potential. Nevertheless, several challenges persist：

Mechanical Limitations: Despite various reinforcement techniques, the mechanical properties of current structural ELMs often lag behind traditional engineering materials. Contributing factors include the inherent mechanical constraints of the biological material, low density of the reinforcement structure, weak bonding between phases, uncontrolled microstructures leading to defects, and growth-related limitations that make techniques like high-temperature calcination challenging.

Application Constraints: Given the mechanical fragility of living organisms relative to non-living materials, integrating living components introduces a potential compromise in mechanical robustness.

Structural ELMs may not completely replace traditional structural materials and could even fall short of natural material strengths, making their optimal integration into practical scenarios a formidable challenge

Viability of Living Components and System Durability: Despite resilience in controlled lab environments, living organisms face challenges in harsh real-world conditions, such as lack of moisture, direct sunlight exposure, or low temperatures. The hygroscopic nature of biotic components may lead to catastrophic damage in high humidity, questioning the long-term durability and functionality of the system.

Scalability: While attempts have been made to construct large-scale structural ELMs, such as self-healing concrete and soil, achieving scalable production faces challenges, such as the long growth cycles of many living organisms, limited culture success rates, and other factors.

Biological contamination and Safety: Genetically engineered microorganisms may pose unforeseen risks despite selective breeding. Controlling biological contamination while maintaining organism vitality in the material to ensure safety is an issue that needs resolution.

To address these challenges and facilitate the transition of structural ELMs from laboratories to daily life, several future avenues warrant exploration. Firstly, a fundamental understanding of the interplay between various factors and mechanical properties is essential to establishing design principles for these materials. Secondly, emphasis should be placed on studying the material's response characteristics under mechanical loads, i.e., the influence of stress on the biological and non-biological components. Additionally, there is a need to develop environmentally friendly, low-cost substrates with high survival rates for large-scale applications of structural ELMs. Significant development space remains for plant-based, animal cell-based, and consortia system-based structural ELMs. Leveraging technologies like 3D bioprinting according to specific application requirements and environmental conditions represents a promising direction. For instance, it is foreseeable to design implants and medical devices that match individual physiological needs using structural ELMs. Lastly, as biosecurity gains prominence, ensuring environmental and public health safety will be pivotal

In conclusion, while optimism surrounds the future of structural ELMs due to their demonstrated potential, it is essential to recognize their inherent limitations. Our ability to engineer materials falls short of the biological organism's manipulation of natural materials, and the mechanical upper limit of structural ELMs' may hardly exceed that of natural structural materials, even with optimal design. Consequently, their applicability in sectors demanding extreme material performance might be limited. Identifying niches that align with the unique characteristics of structural ELMs is a pressing task, and a prudent approach is necessary, avoiding undue optimism in this emerging field.

5. Conclusions

In this paper, we presented the first comprehensive review of structural ELMs. We first highlight two key features of biological structural materials, i.e., the living nature and hierarchical structure. We then explicate the intricate correlations between living components, hierarchical structures, and materials properties in these materials. We then review prevalent biomimetic strategies which involve replicating biological structures, and emphasize their limitations in achieving true living attributes to environmental cues. Thus, the superiority of structural ELMs— truly emulate the "living" aspect of natural materials — was then underscored. We then proceed to define and classify these materials into four categories based on living organisms: bacterial, fungal, plant-based, and other structural ELMs. We next systematically discuss mechanisms of mechanical property enhancement, including biomineralization, engineering biological membranes, and fiber reinforcement, as well as the principal feature of self-healing. Finally, we synthesize the pressing challenges confronting structural ELMs, spanning inferior mechanical properties, concerns regarding viability and system durability, scalability issues, and potential biocontamination risk. Finally, we provide a forward-looking perspective on future directions in this field. We believe that this review serves as a valuable reference for the future development of structural ELMs.

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Declaration of Interests:

The authors declare no conflict of interests.

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