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Review

What next for mycoprotein?

Tomas Linder

Mycoprotein is a protein-rich food ingredient derived from cultivated fungal mycelium. Mycoprotein-containing meat imitation food products were first commercialized nearly 40 years ago and have since become a safe, nutritious, and generally well-established vegetarian alternative for consumers wishing to reduce or completely avoid meat consumption. In just the past few years, there has been a notable resurgence in mycoprotein innovation with many new companies developing novel mycoprotein products while also employing a wider range of fungal species as well as cultivation methods. However, questions remain about how successful mycoprotein has been as a novel food ingredient with regard to its sustainability and resilience of production as well as its potential for further market growth globally.

Address
Department of Molecular Sciences, Swedish University of Agricultural Sciences, Uppsala, Sweden

Corresponding author: Linder, Tomas (tomas.linder@slu.se)

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Introduction

The term mycoprotein (originally spelt 'myco-protein') was originally coined in the mid-1980s to describe a protein-rich product derived from the edible mycelium of the soil-living fungus *Fusarium venenatum*, which had been developed by the British company Marlow Foods [1]. Although the first product of its kind to be commercialized for human consumption in 1985, Marlow Foods' mycoprotein (sold under the brand name Quorn) was actually not the only food (and feed) product to be developed from edible fungal mycelium at the time. The Finnish company Pekilo had developed an analogous product from the filamentous fungus *Paecilomyces variotii*, which was cultivated on organic by-products of wood pulping [2]. The protein-rich product developed from *P. variotii* mycelium (named Pekilo as well) displayed good nutritional properties but was ultimately discontinued in 1991 due in part to a shortage of cheap substrate for cultivation.

Today, fungi find an increasing number of uses in food production and processing, which can lead to some confusion of what qualifies as mycoprotein and what does not. The author recommends that the term 'mycoprotein' should only be used in reference to a protein-rich product derived from fungal mycelium after harvesting and downstream processing. As such, mycoprotein would not encompass fungal fruiting bodies (mushrooms) or fermented food products that have been inoculated with mycelium-forming (filamentous) fungi, which include such products as angkak, tempeh, koji, and oncom [3]. Nor would it include yeast-based products such as Marmite [4] — even though yeasts are also fungi. Finally, recombinant food proteins such as milk casein or chicken ovalbumin produced using genetically engineered filamentous fungi (e.g. *Trichoderma reesei* [5]) would also not qualify as mycoprotein.

Another common source of confusion regarding the nature of mycoprotein is the multiple meanings of the word fermentation. Unlike, for example, tempeh, mycoprotein is not a *fermented* product where fermentation is defined as microbially mediated transformation of an edible substrate with the aim of achieving a desirable combination of sensory properties (taste, smell, texture, and/or visual appearance) of the final food product. Instead, the production of mycoprotein is more akin to that of penicillin or recombinant insulin in that it is a *fermentation-derived* product where fermentation is defined as a biocatalytic manufacturing process employing cultured cells with the aim of achieving the highest possible process efficiency.

The choice of fungal mycelium rather than single-celled yeasts for the production of a fungal food product greatly simplifies the harvesting of the biomass from the cultivation medium [1]. Another benefit of the filamentous morphology of these fungi is the ability of the hyphae to mimic muscle fibers, although egg white protein or other binding agents must be added to cross-link the hyphae to achieve the desired texture in meat imitation products [1,6]. However, unlike yeasts, many filamentous fungi can produce highly toxic secondary metabolites known as mycotoxins [7], which necessitates very careful safety evaluation of each new fungal strain considered for mycoprotein production [1,8,9].

Mycoprotein is generally considered to be a high-quality protein source with a reported protein digestibility corrected amino acid score above 90% [1,8], which would put mycoprotein in the same range as such high-quality protein sources as soy (91%), beef (92%), egg (100%), and cow's milk (100%). Although protein does constitute the main component of mycoprotein (typically reported as 40–60% of dry weight), it also contains nonprotein components such as β-glucans, lipids, and B vitamins [8–10]. There is some debate that standard protocols used for compositional analysis may in fact overestimate the protein content in mycelial biomass somewhat due to the presence of nonprotein nitrogen-containing compounds [11]. While this review is concerned with fungal mycelium primarily as a source of dietary protein, some so-called 'oleaginous' fungi have the ability to hyperaccumulate lipids within their cells, which make them a promising source of dietary fats [12,13].

Mycoprotein is sometimes classified as a 'plant-based' ingredient although fungi are much closer relatives of animals than plants. The author has also noted some recent attempts at rebranding mycoprotein as 'fungi-based protein', which the author would strongly discourage since it is both grammatically incorrect (the correct term in this case would be either 'fungus-based protein' or 'fungal protein') and, more importantly, risks adding even more confusion.

Current state of the mycoprotein field

The impetus for developing a food product based on fungal mycelium dates back to the 1960s. At the time, fears of global protein shortages spurred researchers across the world to investigate the possibility of using bulk cellular protein of cultured micro-organism — so-called single-cell protein (SCP), as a novel source of food. This initiative included not only filamentous fungi but also yeasts, bacteria, and microalgae. By the late 1980s, Marlow Foods' Quorn mycoprotein was one of the few SCP products that remained in production. At this stage, mycoprotein products were marketed purely as vegetarian meat substitutes.

In just the last couple of years, the mycoprotein field has seen a significant resurgence. This is due in part to expiration of some of Marlow Foods' original mycoprotein patents but also due to growing interest and demand for more ethical and environmentally sustainable food alternatives to beef, pork, chicken, fish, dairy, and eggs. Consequently, such products have become collectively known as 'alternative protein' [14] and — in addition to mycoprotein, include plant-based protein, edible insects, cultivated meat, and recombinant dairy and egg proteins.

Table 1

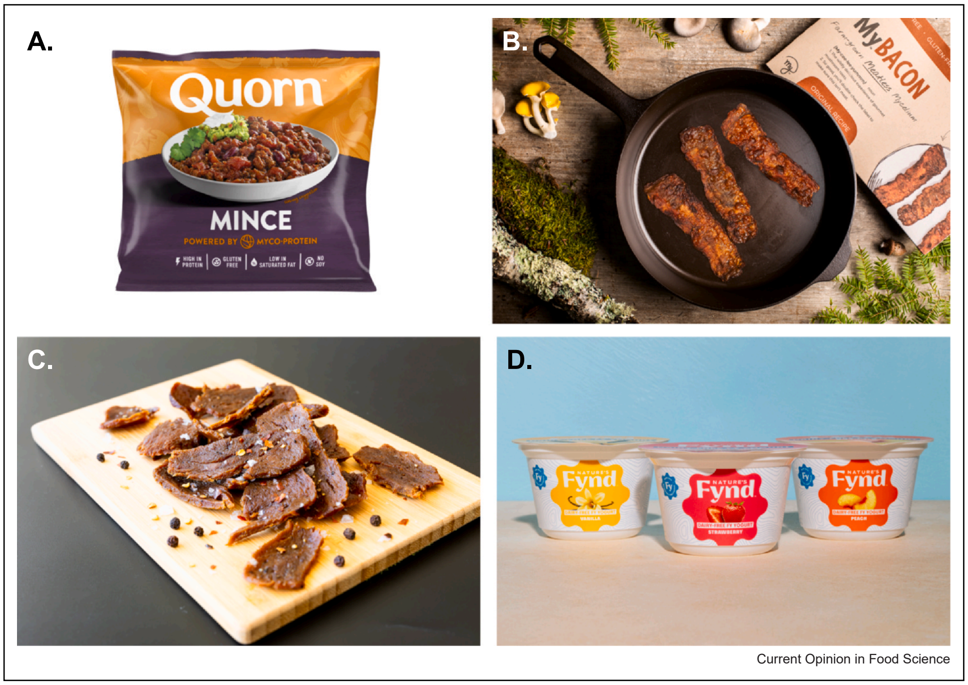
Selected producers of mycoprotein products for food (and feed, where indicated).

Company name	Corporate headquarters	Product name
The Better Meat Co.	West Sacramento, CA, USA	Rhiza
Enifer	Espoo, Finland	Pekilo (also feed)
ENOUGH	Glasgow, UK	ABUNDA
Eternal	San Francisco, CA, US	Mycofood
Hyfé Foods	Chicago, IL, USA	(none so far)
Marlow Foods Ltd	Stokesley, UK	Quorn
Meati Foods	Boulder, CO, USA	MushroomRoot
Mush Foods	New York, NY, USA	50CUT
Mycorena	Gothenburg, Sweden	Promyc
MyForest Foods Co.	Green Island, NY, USA	MyBacon
Nature's Fynd	Chicago, IL, USA	Fy

At the time of writing, there are several mycoprotein companies in various stages of product development and commercialization (see Table 1 for selected examples). Most mycoprotein producers have focused on developing imitations of meat products (Figure 1a–c), such as mince, sausages, bacon, chicken nuggets, and jerky. However, there are also some notable examples of nonmeat imitation products, such as mycoprotein-based dairy imitation products, which have been developed and commercialized by Nature's Fynd (Figure 1d). More recently, the US mycoprotein startup company Hyfé Foods is developing mycoprotein-based pasta products [15].

A number of mycoprotein companies have chosen to employ the original *F. venenatum* A3/5 strain used in Marlow Foods' Quorn-brand products since its initial set of associated patents have now expired, and this strain already has wide-ranging regulatory approval for human consumption [16]. Nature's Fynd uses a novel *Fusarium* strain that is provisionally called '*flavolapis*' [8], while the Finnish company Enifer has chosen to resurrect the Pekilo fungal strain *P. variotii* KCL-24 [2]. US mycoprotein producer The Better Meat Co is using the ubiquitous fungus *Neurospora crassa* [9], which is a close relative of *Neurospora* species with established use in food fermentations [3]. Some mycoprotein companies, for example, Mush Foods [17] and MyForest Foods [18], have chosen to use established mushroom-forming fungi such as oyster mushroom (*Pleurotus*) for cultivation of mycelium. A number of mycoprotein producers have yet to declare the exact identity of their production strains — although some of these companies have indicated that they are using established fungal strains that already have regulatory approval for human consumption.

Figure 1



Selected examples of mycoprotein food products approved for human consumption. **(a)** Quorn®-brand imitation minced meat manufactured from the mycelium of *Fusarium venenatum*. (Image provided by Quorn Foods and used with permission.) **(b)** MyBacon-brand imitation bacon manufactured from the mycelium of oyster mushroom belonging to the genus *Pleurotus*. (Image provided by MyForest Foods and used with permission.) **(c)** Rhiza-brand imitation jerky manufactured from the mycelium of *Neurospora crassa*. (Image provided by The Better Meat Co and used with permission.) **(d)** Fy-brand imitation yogurt manufactured from the mycelium of *Fusarium* strain *flavolapis*. (Image provided by Nature's Fynd and used with permission.).

Most mycoprotein fungi are cultivated through submerged fermentation in large bioreactors containing nutrient-rich broth and are harvested continuously, typically through filtration [1]. This cultivation method allows for high productivity but requires substantial capital expenditures for bioreactor construction, operation, and maintenance. The mycoprotein startups MyForest Foods and Mush Foods employ an alternative solid-state fermentation approach where fungal mycelium is cultivated on a solid substrate such as wood chips [18] or upcycled solid food and agricultural waste [17], respectively. This solid-state fermentation strategy circumvents the need for conventional bioreactors, although the cultivation procedure still requires temperature and humidity control. While mycoprotein production through submerged fermentation has a proven four-decade record of scalability and profitability [1], it remains to be seen how well mycoprotein generated through solid-state fermentation will perform as production is scaled up.

Measuring success

With the 40th anniversary of the commercialization of the first mycoprotein products for human consumption nearly upon us [1], it would seem appropriate to take stock of what mycoprotein has achieved until now. In terms of nutritional properties and safety record, mycoprotein has performed well thus far [1,8,9], although it should be noted that the formulation of individual mycoprotein products with respect to added fats, salt, and so on will obviously influence overall nutritional quality. A number of studies have reported beneficial health effects from mycoprotein consumption, which have been reviewed previously [1].

Mycoprotein products are generally marketed as more sustainable alternatives to conventional meat and dairy. Animal agriculture is notorious for its high impacts on the environment in terms of greenhouse gas (GHG) emissions, fresh water use, and the destruction of natural ecosystems [19]. However, the environmental benefits of replacing all kinds of animal-derived protein (meat, eggs, and dairy) with mycoprotein are not always clear-cut when considering the 'classical' method of producing mycoprotein through submerged fermentation using a glucose feedstock [20]. The electricity requirements for large-scale cultivation and downstream processing are a key factor in the environmental footprint, which means that the individual environmental footprint of any one mycoprotein production facility is highly dependent on the local energy mix. It should also be noted that the ammonia commonly used as nitrogen feedstock for cultivation of fungal mycelium is generally manufactured using natural gas [21].

Results are less ambiguous when comparing mycoprotein to beef specifically since beef is especially costly in terms of environmental impact [19]. A recent modeling study predicted that replacing just 20% of global beef consumption with mycoprotein by the year 2050 would have a disproportionate effect on reducing land use change and its associated GHG emissions [22]. In this context, it is worth noting that a number of mycoprotein producers such as Mush Foods and Mycorena are exploring mycoprotein/meat hybrid products [17,23]. Mycorena are developing their own range of ready-made hybrid products [23], while Mush Foods are developing mycoprotein ingredients ('mycelium blends') that are sold to other food companies for final product development [17].

Resilience is another factor worth considering. How resistant are current mycoprotein production methods to system-level shocks such as supply chain disruptions caused by pandemics, extreme weather events, social conflicts, and so on? The overwhelming reliance on glucose as a carbon feedstock for fungal cultivation among most mycoprotein producers is probably the largest source of vulnerability [21,24]. The production of Quorn mycoprotein, which is dependent on glucose, already has a documented vulnerability to supply chain disruptions [1]. Climate change is expected to adversely affect sugar yields going forward, which can lead to downstream effects such as export controls and price spikes. It is therefore encouraging that a number of mycoprotein producers have proactively chosen to use nonglucose feedstocks such as food industry side streams (Enifer, Hyfé Foods), agricultural residues (Mush Foods), and wood chips (MyForest Foods) [2,15,17,18].

In terms of consumer acceptance, older mycoprotein brands such as Quorn are firmly established in countries such as the United Kingdom and the United States. Nevertheless, mycoprotein products remain a niche market in those countries where they have received regulatory approval, which is currently limited to the United States, a number of European countries, Australia, New Zealand, the Philippines, and Singapore. The limited accessibility to mycoprotein products worldwide is in part due to regulatory hurdles. A less well-understood factor in countries with no prior history of mycoprotein consumption is how food neophobia would impact consumer acceptance and how mycoprotein fits in with local food culture and tradition as well as religious practices. Two additional factors that pertain to accessibility of mycoprotein products in developing nations are affordability and adequate infrastructure for transport and storage of mycoprotein products. This latter aspect derives from the fact that nearly all current mycoprotein products require either cold or frozen storage. This requirement becomes an issue in countries that lack stable cold chains and reliable electricity supply overall [21].

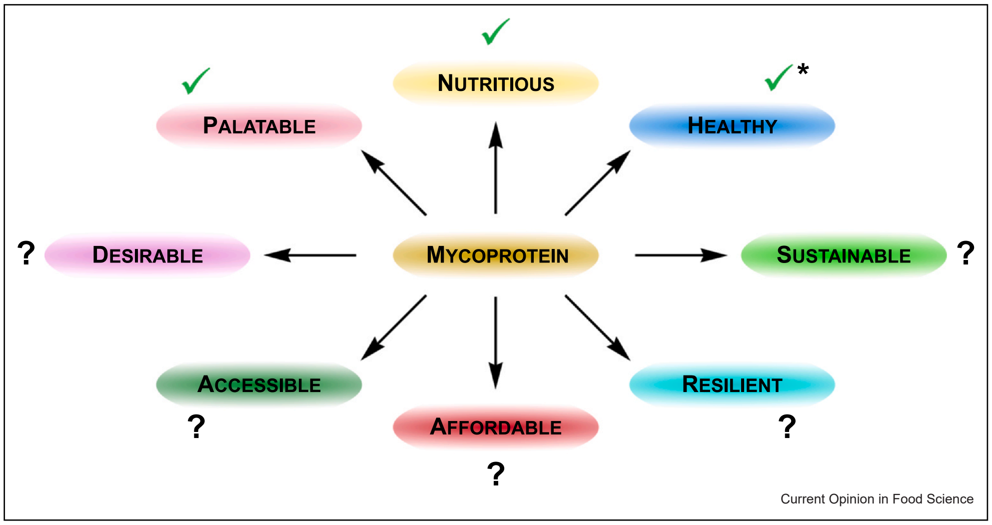
A final dilemma that concerns both consumer preference and sustainability is the very real potential for competition between different categories of alternative protein such as between mycoprotein and plant-based products. In fact, by competing directly with plant-based products rather than animal-derived protein, mycoprotein actually risk increasing overall environmental impacts by displacing food products with a lower environmental footprint than its own [25].

Untapped potential of novel carbon feedstocks for increasing sustainability and resilience of mycoprotein production

From the previous section, it is clear that mycoprotein still has some ways to go in order to achieve success with regard to factors such as sustainability and resilience (Figure 2). The choice of carbon feedstock is one of the most important determinants of process sustainability [20] and resilience [21,24], which should motivate a transition away from food-grade carbon feedstocks such as glucose. The use of side streams from food industry, agriculture and forestry is a step in the right direction — although committing a particular mycoprotein process to a specific side stream can itself become a vulnerability if the side stream disappears, which was the case with the original Pekilo process [2].

One exciting category of carbon feedstocks that has yet to be employed in commercial mycoprotein production is noncarbohydrate organic compounds such as methanol, ethanol, and acetic acid. Such compounds can be synthesized directly from captured CO_2 either through direct chemical catalytic conversion or biocatalytic conversion (e.g. syngas fermentation) — a concept the author has termed 'carbon capture, conversion and cultivation' (CCCC) [26]. This process concept is attractive because it decouples food production entirely from photosynthetic carbon fixation and its associated biophysical requirements such as access to arable land and favorable climate conditions. This effectively 'climate-proofs' food production provided that electricity can be provided reliably to power CO_2 capture, catalytic conversion into organic feedstocks, cultivation of the fungal mycelium, and subsequent downstream processing. Theoretical modeling of an analogous process in bacteria powered by photovoltaics has shown that the predicted geographical footprint of a CCCC-type process could shrink land use requirements by 10-fold compared to soy cultivation [27]. The author is unaware of any published studies that have investigated the land

Figure 2



Has mycoprotein reached its full potential? This review argues that mycoprotein products have established themselves as safe, nutritious, and palatable in the nearly 40 years since they were first commercialized [1]. (The health benefits of mycoprotein will obviously depend on the overall formulation of the mycoprotein-containing product, such as salt and fat content.) However, the full potential of mycoprotein has yet to be realized in terms of such properties as sustainability, resilience, accessibility, affordability, and desirability. With regard to sustainability and resilience, the prevailing use of glucose as a carbon feedstock for mycoprotein production not only entails a noticeable environmental footprint in terms of land use and its associated GHG emissions [20] but also leaves the process vulnerable to disruptions in the feedstock supply chain [1,24], especially in light of the effects climate change is expected to have on agricultural yields [21]. At present, mycoprotein products are only commercially available in selected countries, predominantly in Europe and North America. Improving accessibility to mycoprotein products to consumers globally will involve not only achieving widespread regulatory approval but also accounting for areas that do not possess stable cold chains or electricity supply in general. This precludes the distribution of mycoprotein products that require cold or frozen storage. To facilitate access to mycoprotein products for consumers in electricity insecure areas, mycoprotein producers need to diversify their product range to include dry mycoprotein products that can be stored at ambient temperature [21], for example, mycoprotein-containing flour and pasta products [15]. Improving desirability of mycoprotein products to achieve greater consumer adoption is perhaps one of the greatest challenges. Will improved sensory properties of mycoprotein products (taste, appearance, and mouthfeel) as well as achieving price parity with conventional meat products be enough to drive greater market penetration, considering that the consumption of meat and other forms of animal protein have deep cultural significance in many societies [31]?

use requirements for the use of CO_2-derived organic feedstocks for mycoprotein production and should be a priority going forward.

In the near term, the expanded use of nonglucose feedstocks for mycoprotein production is a promising approach to not only decrease the environmental footprint of mycoprotein but also increase its resilience. While side streams from the food industry provide a relatively nonproblematic source of feedstock, it is unclear how much can be made available for mycoprotein production on a global scale, especially since some of these side streams (e.g. organic waste from dairy processing) could face eventual elimination by production of alternative protein such as dairy imitations.

Inedible plant biomass such as straw and wood is another potential source of carbon feedstock that has the potential to improve the sustainability and resilience of mycoprotein production. MyForest Foods have already demonstrated the feasibility of small-scale cultivation of oyster mushroom mycelium on wood chips [18], but it remains to be determined to what extent such a process can be scaled up. However, as there is no requirement for large bioreactors, this approach is particularly attractive in areas of the world where there is no capital for fermentation infrastructure, electricity supply is unreliable, and there is a lack of skilled labor in bioprocess engineering. While oyster mushroom is a naturally wood-degrading fungus, mycoprotein production from inedible plant biomass using fungi that lack the ability to degrade the inedible carbohydrates in wood requires a combination of thermochemical pretreatment of the feedstock followed by enzymatic digestion of the carbohydrate chains into shorter fragments that can easily be assimilated by the fungus. Pilot experiments using *F. venenatum* have shown some promise [28]. An alternative approach for fungi that do not naturally degrade wood or straw involve thermochemical gasification of the plant feedstock into syngas, which is a mixture of hydrogen gas, carbon monoxide, and CO_2. This syngas can then be chemically converted into simple organic feedstocks including methanol and acetic acid [29], which can then be used to cultivate fungal mycelium [26]. This last approach has not yet been applied in commercial mycoprotein as far as the author is aware.

Algal biomass is another interesting candidate feedstock for mycoprotein production. Macroalgae such as kelp grow rapidly and do not require freshwater. However, the carbohydrate composition of macroalgae differs significantly from that of land-living plants, and therefore, the direct utilization of algal biomass as a carbon feedstock will likely require fungal species specialized at degrading this type of substrate [30]. Alternatively, algal biomass can be subjected to thermochemical gasification as described above and converted into generic organic feedstocks for already established mycoprotein production strains.

In summary, there are clearly many promising alternative carbon feedstocks that have the potential to improve process sustainability and resilience. However, it should be noted that global mycoprotein production capacity would have to increase substantially before any tangible effects on food system sustainability and resilience would manifest themselves.

Conclusion

The mycoprotein field is seeing an exciting revitalization nearly four decades after the first mycoprotein-containing food product appeared in store freezers. On the one hand, mycoprotein has been a success in establishing itself as safe, nutritious and palatable alternative to meat products. On the other hand, mycoprotein still has potential to go much further (Figure 2). This review has focused mostly on how the choice of carbon feedstock can greatly decrease the environmental footprint of mycoprotein product while at the same time improving the resilience of the mycoprotein production process from sudden shocks to global supply chains. An increased frequency of extreme weather events caused by climate change is the most obvious threat to global food production. The possibility of using novel carbon feedstocks to decouple mycoprotein production from agricultural yields — either by using nonedible biomass (wood, straw, macroalgae) [28,30] or direct catalytic conversion of captured CO_2 into simple organic compounds [26], would turn mycoprotein into an invaluable instrument in securing global food security in an otherwise increasingly volatile future.

Data Availability

No data were used for the research described in the article.

Declaration of Competing Interest

The author currently serves as an unpaid advisor to the company Arkeon, which is developing microbial food products based on an archaeal production organism rather than filamentous fungi. The present article is solely the work of the author. Arkeon was not involved in authoring or editing the article text in any way.

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- •• of outstanding interest

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