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Review

Mycoforestry with the Saffron Milk Cap (*Lactarius deliciosus* L.:Fr. S.F. Gray) and Its Potential as a Large-Scale Food Production System

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Abstract

Mycoforestry, a farming system that produces edible fungi crops in forest plantations through controlled mycorrhizal symbiosis, has the potential to enhance biodiversity in forestry plantations and mitigate some of the negative impacts associated with modern agriculture, such as soil erosion, habitat degradation, and carbon emissions. Mycoforestry systems typically exploit a range of native fungi that can be inoculated into planting stock of commercial tree species, with biodiversity benefits delivered through expanded habitat provision for the fungi and a range of other organisms through alterations to stand structure. One mycoforestry system showing strong potential for commercial viability involves the cultivation of *Lactarius deliciosus* (L.:Fr.) S.F. Gray in Pinaceae plantations. This review aims to evaluate the benefits of mycoforestry systems with a focus on *Lactarius deliciosus* (L.:Fr.) as a case study. It will review the state of the art and discuss technical developments necessary for the successful large-scale application of mycoforestry systems.

Keywords: mycoforestry; *Lactarius deliciosus*; non-timber forest products; ectomycorrhizal fungi inoculation; ectomycorrhizal fungi *in-vitro* cultivation; fungal ecology

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1. Introduction

In this study, we evaluate the potential economic, societal and ecological benefits of large-scale applications of *Lactarius deliciosus* (L.:Fr.) S.F. Gray mycoforestry and give recommendations on how this could be achieved, with the UK as an exemplar. We explore technical aspects including inoculation success, *in-vitro* growth and long-term persistence in soils and the need to mitigate limitations that constrain the commercial viability of this food production system. Currently, large-scale application is limited by the slow *in-vitro* growth of *L. deliciosus* [1–3] and its inconsistent inoculation success and persistence in pot and plantation trials [4–8].

2. *L. deliciosus* Mycoforestry: General Overview

2.1. What Are Ectomycorrhizal Associations?

An ectomycorrhizal association is defined by the presence of three structural components: (1) a sheath or mantle that surrounds the root; (2) a Hartig net which grows inwardly and intercellularly between the epidermal and cortical cells; (3) an outwardly

growing extraradical mycelium system that forms essential connections with the soil and the fruiting bodies (basidiocarps) of the ectomycorrhizal fungus [9]. The interface where this mycorrhizal association operates (area between the fungal mantle and soil) is referred to as the mycorrhizosphere [10].

Ectomycorrhizal associations broadly function as mutualistic symbiotic biotrophy. This is because the ectomycorrhizal fungus supplies the host plant with nutrients and water that it pumps or mobilizes from the soil using its extraradical mycelial network [11–13], increasing the absorption area of the root system [9,14]. In return, the tree host provides carbohydrates to the fungal symbiont [13,15]. Apart from increasing the nutrient and water uptake capabilities of trees, ECM provide a range of other benefits to their host by increasing their resistance to environmental stressors [16–18], pests [19], pathogens and diseases [20,21].

Bacteria play a part in mycorrhizal associations, as bacteria help mobilize nutrients [22–25] and facilitate ECM growth and root colonization intensity [26–28]. Hence, ectomycorrhizal associations are tripartite (plant–fungi–bacteria). The structure of bacterial communities in the mycorrhizosphere is influenced by their associated partners, either through the supply of carbohydrates (fungi [26,29]) or through the rhizodeposition of exudates and formation of bacteria traps on root surfaces (trees [30–32]).

2.2. What Is Mycoforestry?

Mycoforestry is an approach to cultivating edible ECM in forest plantations using controlled mycorrhizal synthesis [33,34], achieved by producing an inoculum of fungal mycelium or spores and using it to confront receptive non-mycorrhized roots of a compatible host plant [12]. For this mycorrhizal synthesis to be successful, it must be conducted in an environment with favourable abiotic and biotic conditions for the coupled symbionts, as unfavourable conditions for either partner will prevent ECM development [12]. Consequently, following the establishment of the mycoforestry plantation, silvicultural practices would need to be implemented to sustain the long-term fruiting of the target fungus. Information on the optimal environmental conditions of the target fungus is required to determine the necessary management practices.

Various inoculation methods have been developed to facilitate controlled mycorrhizal synthesis such as vegetative inoculum (derived from liquid and solid pure fungal cultures), gamic inoculum (spores), natural inoculum (soil and humus) and symbiotic inoculum (mother tree planting and excised colonized roots) [35–38]. Since ectomycorrhizal fungi can become adapted to localized environmental conditions, especially *L. deliciosus* (see Sections 3.2, 3.3, 5.4 and 5.5), region-specific isolates should be used when implementing this farming system on a commercial scale. Additionally, the use of region-specific isolates should help prevent outbreeding depression and the loss of genetic variability in wild populations of *L. deliciosus*.

2.3. L. deliciosus

L. deliciosus is a basidiomycete fungus that belongs to a complex of species known as *Lactarius sect. Deliciosi* (Fr.:Fr.) Redeuilh, Verbeken and Walleyn [39]. Fungi in this complex can be differentiated by the colours of their basidiocarps (dark yellow, orange, wine red, brown and indigo) [39–41]. The basidiocarps of *L. deliciosus* are pale orange in colour (discolouring green in mature basidiocarps) and exude a bright orange latex when damaged [42]. In natural ecosystems, *L. deliciosus* forms multi-stage ectomycorrhizal associations with conifer trees from the *Pinaceae* family [8] and is characteristically associated with species in the *Pinus* genus [39,43].

L. deliciosus is naturally distributed throughout the European continent and some parts of the Middle East [8]. Moreover, because of trade and artificial introductions it can now be found in China [44], Chile [45], Australia [46,47], New Zealand [8,48] and South Africa [49]. Hence, it is broadly distributed across a variety of climatic conditions, which suggests that it is adaptable to a wide range of environmental conditions. In the UK, this fungus is more abundant in the north than in the south, where it is recorded most frequently in Scotland (Figure 1), a disparity potentially driven by Scotland having the greatest conifer forest cover [50].

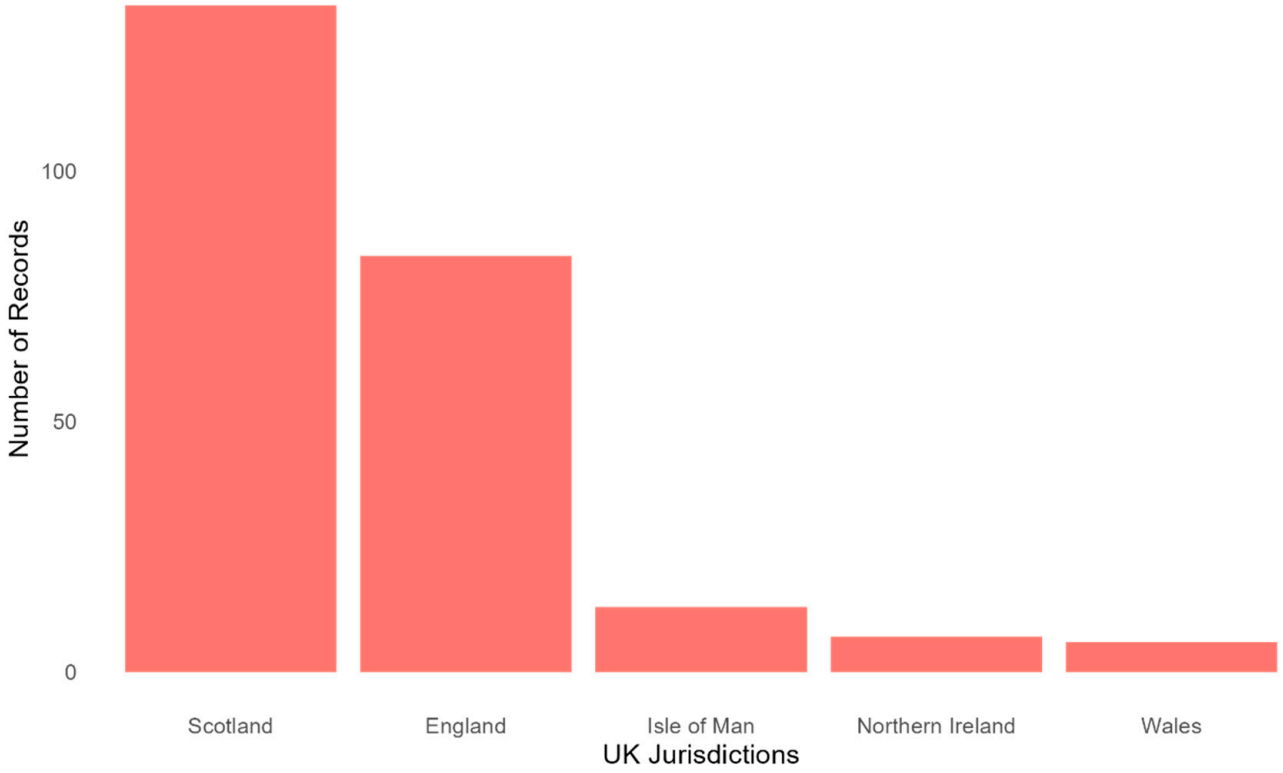

Figure 1. Number of accepted *L. deliciosus* basidiocarp records per jurisdiction in the United Kingdom from 2000–2024. *L. deliciosus* presence records were downloaded from NBN Atlas [51] on 4 September 2025.

2.4. *L. deliciosus* Mycoforestry and Its Potential in the UK

L. deliciosus produces edible basidiocarps that are consumed and sold internationally, in areas such as Europe [52,53], Guatemala [54], Nigeria [55], Turkey [56] and China [57]. The cultivation of *L. deliciosus* basidiocarps was pioneered in France by Poitou et al. [58] using laboratory-inoculated *Pinus pinaster* Aiton seedlings planted in a former vineyard near Bordeaux. After 3 years, the inoculated stands in this plantation began to produce basidiocarps [59]. Since then, *L. deliciosus* has been successfully used to inoculate a range of different *Pinus* species such as *P. halepensis* Miller [4], *P. sylvestris* L. [6,60], *P. radiata* [48], *P. nigra* J.F.Arnold [61], *P. pinaster* [5], *P. massoniana* Lamb. [62], *P. pinea* L. and *P. armandii* Franch. [63]. However, this practice is still in its infancy and further research is needed to overcome the substantial knowledge gaps and limitations (see Sections 3–5) preventing the large-scale application of this mycoforestry practice.

This mycoforestry system has not been commercially implemented in the UK. Nevertheless, results from plantations in New Zealand can offer insights into their economic potential, where small-scale *P. sylvestris* plantations recorded an annual yield equating to >1 T/ha [12]. Consequently, if *L. deliciosus* plantations in the UK produce similar yields, this would generate a minimum annual income of €17,010 €/ha from mushroom produc-

tion alone (based on the current market price advertised by online retailers in Spain [64]). Additionally, if these yields could be sustained throughout an entire optimal *P. sylvestris* forest plantation rotation period of 50 years [65], this would result in a minimum total income generation of 782,460 €/ha (excluding first four years to allow for *L. deliciosus* establishment [6]). However, reservations should be made towards the value stated above, as increases in the supply of *L. deliciosus* would likely result in a price decrease due to greater availability, as observed in *L. deliciosus* markets in Spain [66].

2.5. Benefits of Upscaling L. deliciosus Mycoforestry

Presently, *L. deliciosus* markets are dependent on the harvesting of wild populations to meet consumer demands [53,66]. However, basidiocarp productivity from wild fungi populations is currently declining due to habitat loss [67–69], forest floor trampling [70], climate change [71,72] and air pollution [73], which could lead to inflated basidiocarp prices if market demand exceeds supply [66]. Hence, the upscaling of this mycoforestry practice should mitigate price inflations, making *L. deliciosus* a more accessible and economically viable food source for lower-income households. Large-scale *L. deliciosus* mycoforestry plantations should also reduce anthropogenic foraging pressures in natural ecosystems, increasing the amount of available food for wildlife (especially for rodent and marsupial species, [74–77]) and mitigating the detrimental effects of mushroom foraging such as forest floor trampling [70] or disturbance to wildlife [78].

Studies demonstrate that trees inoculated with *L. deliciosus* exhibit enhanced resistance to plant pathogens (though not always significant) [61,79], accelerated growth rates [80], and improved survival in adverse soil conditions [81]. Hence, large-scale inoculation of *P. sylvestris* trees with *L. deliciosus* in forestry offers ecological and economic advantages through faster timber production, reduced tree mortality, and decreased fungicide applications—thereby minimizing detrimental effects on non-target native wildlife [82–86]. Since *L. deliciosus* can increase tree seedling survival in adverse environmental conditions, development of large-scale *L. deliciosus* inoculation protocols would also benefit forest restoration and ectomycoremediation projects. This includes revegetation or decontamination of polluted lands, as *L. deliciosus* has been recorded to degrade pollutants such as triphenylmethane dyes [87] and polycyclic aromatic hydrocarbons [88]. Additionally, Thomas and Jump [33] analysed the carbon sequestration potential of *L. deliciosus* mycoforestry compared to the nine most important food production systems and concluded that this is the only system to sequester carbon, suggesting it could aid countries meet their legally binding Paris Agreement [89] targets.

L. deliciosus has been reported to harbour anti-inflammatory [90], antimicrobial [91], immunomodulatory [92], antiproliferative and anticancer [93–95], antioxidant and anti-hyperglycemic properties [96]. Hence, commercial scale production systems could have significant benefits for the pharmacological industry. Since wild basidiocarp production in natural ecosystems is currently declining, these plantations could help maintain an adequate supply and serve as living repositories of pharmacologically active chemicals.

3. *In-Vitro* Growth Requirements of *L. deliciosus*

Here we focus on the abiotic and biotic factors that affect the growth of this fungus in liquid culture, given that liquid fermentation and mycelial slurry inoculation have been identified as the optimal methods for cultivating *L. deliciosus* and inoculating root systems of host plants (see Section 4.1) [4,97].

3.1. Liquid Media

Gomes et al. [98] observed the greatest *in-vitro* growth of *L. deliciosus* in biotin–aneurin–folic acid (BAF) [99], compared to potato dextrose broth (PDB), modified Melin-Norkans (MMN) with added glucose of 2% [100], malt extract, and Oddoux [101]. Evidence of BAF being the optimal medium for the *in-vitro* growth of *L. deliciosus* has also been reported in solid culture studies [60,102–104]. BAF contains higher concentrations of glucose, amino acids and vitamins compared to the other media tested, and increases in *L. deliciosus* growth have been attributed to these three components in *in-vitro* studies [60,105–109]. Two of the nitrogen (N) sources BAF contains (peptone and yeast extract) have also been recorded as the optimal N sources for *L. deliciosus* in a multitude of liquid culture studies [110–113].

While glucose has been recorded as the optimal C source in liquid culture [106] and hypothesized to be a key ingredient stimulating *L. deliciosus* growth in BAF, research from China presents conflicting results. Seven Chinese studies optimizing C sources in liquid culture (Table A1) identified soluble starch most frequently as the optimal C source. This regional discrepancy may reflect the greater volume of research conducted in China compared to the West, where only one study [106] has examined this question. The variation could also stem from intraspecific differences in carbon utilization capabilities among *L. deliciosus* isolates, as observed with other ECM [114]. Applications of different carbohydrates at equal weight in these studies might also have caused these results. Since 1 g of starch yields 1.11 grams of glucose upon complete hydrolysis, greater amounts of free glucose may have been available in soluble starch treatments compared to glucose treatments [115–117]. Differences in optimal C source results could also be due to taxonomic confusion, as *Lactarius* spp. in the *Lactarius sect. Deliciosi* (especially *L. hatsudake* Nobuj. Tanaka) complex have often been mistaken as *L. deliciosus* in China [118,119]. Evidence of this misidentification can be observed in scientific articles [120,121], as *L. deliciosus* is often referred to as the "purple pine fungus". Reinforcingly, Dong et al. [122] genetically identified the purple pine fungus in China as *L. hatsudake* and *L. vividus* X.H. Wang, Nuytinck & Verbeken. The mistaking of *L. deliciosus* for other fungi in the same complex may be more widespread [123].

Since BAF has been identified as the optimal growth medium for the *in-vitro* growth of *L. deliciosus* [60,98,102,103,124], this medium should be used as a base recipe for *in-vitro* growth optimization experiments. To clarify the differences in optimal C results between China and western countries, the growth promoting effects of different C sources should be tested in BAF. Studies should also test different combinations of C sources, as Zhan and Wei [125] recorded increased *L. deliciosus* growth when C sources were added in combination. Furthermore, the effects of other potential growth promoting compounds should be tested in BAF (root exudates, growth regulator hormones, plant materials and plant material filtrates, see Section 3.5). Any growth-stimulating compound identified in these trials should then be tested at different concentrations in BAF, in a multifactorial manner, to optimize their concentrations and subsequent growth-promoting effects. To avoid nutrient saturation of the medium from the addition of multiple novel compounds, one of the treatment levels in the multifactorial experiment should be absence (0%) of each novel compound, solution, filtrate or plant material. Identifying the optimal concentrations and compound mixtures would provide a targeted medium for the *in-vitro* growth of *L. deliciosus*, increasing its growth rate and avoiding problems associated with prolonged ECM culture times such as decreases in inoculum viability [126]. Once optimal compound concentrations have been identified, further optimization of *L. deliciosus* growth in liquid culture could be carried out by manipulating the pH, temperature and oxygen concentration (see Sections 3.2–3.4).

3.2. pH

The pH of the medium greatly influences the *in-vitro* growth of fungi, with growth increasing under optimal pH conditions [127]. Research into the optimal pH for the *in-vitro* growth of *L. deliciosus* in BAF liquid media has been scant. However, Pereira et al. [124] reported the optimal *in-vitro* growth of an *L. aff. deliciosus* isolate in BAF at a pH of 5.5 and 6.5 in static and agitated conditions, respectively. These results are consistent with those obtained in different media and in solid BAF culture (Table A2), as most of these studies have either recorded a weakly acidic or basic pH as the optimum. Variability in optimal pH can also occur because of the isolate used, as Chung [103] and Flores et al. [128] reported differences in optimal pH among *L. deliciosus* isolates tested in BAF solid medium. Variation in pH preference between isolates of the same species could be due to genetic variability or localized adaptation to certain environmental conditions. The four studies that tested the optimal pH for their *L. deliciosus* isolates and recorded the pH of the source site [129–132] showed that the in-vitro optimal pH aligned with source site conditions, suggesting adaptation to localised pH conditions. However, Hung and Trappe [127] caution that this relationship is not universal, and that a multitude of factors can influence the optimal *in-vitro* pH. Consequently, testing for the optimal pH of an *L. deliciosus* isolate prior to large-scale culturing is a necessity, as the optimal pH can also differ because of the media used [2]. These optimization experiments can also identify isolates with broader pH tolerance ranges; a valuable trait for mycoforestry applications given the variability of soil pH conditions in field settings [133–136]. Hence, inoculating trees with an isolate that can grow well in a range of pH conditions would be better for long-term plantations than a counterpart that can only thrive in one.

3.3. Temperature

Experiments which have analysed the effects of temperature on the *in-vitro* growth of *L. deliciosus* have recorded differences in optimal temperature depending on where the isolate was sourced. For Chinese *L. deliciosus* isolates an optimal *in-vitro* temperature range of 25–28 °C has been recorded (Table A3), whilst for European isolates an optimal range of 22–23 °C has been reported [129,130]. Differences in optimal temperature between these two regions could be a result of localized adaptation to in-situ climatic conditions. The two isolates used in the European studies were from mountainous areas [129,130], whereas, the isolates used in the two Chinese studies that recorded in-situ conditions [109,132], were sourced from a semiarid region were soil temperatures reach >45 °C. These two Chinese isolates had higher *in-vitro* temperature tolerances, as they could grow at 30 °C, a temperature that recorded no growth in the one European isolate tested at this temperature [129]. However, even with these differing results, some universal trends can be observed between isolates from these two regions, as temperatures <20 °C and >30 °C impeded the growth of every isolate tested [109,129,132].

3.4. Oxygen Concentration

In submerged conditions, oxygen availability is one of the most important factors controlling fungal growth [97,137,138]. To date, research optimizing the oxygen concentration for *L. deliciosus* in Western journals has been scant. However, in China two studies have attempted to discover the *in-vitro* optimal oxygen concentration for *L. deliciosus* in conical flask culture, observing optimal growth at liquid-to-flask volume ratios of 75/250 ml [112] and 90/250 ml [121]. Additionally, Li et al. [112] fully optimized the *in-vitro* oxygen concentration for their isolate by optimizing the rotation speed, reporting an optimal rotation per minute (RPM) speed of 210, which suggests that this fungus prefers well oxygenated conditions. Since intraspecific variation has been recorded with other abiotic factors (see

Sections 3.2 and 3.3), and only one study has fully optimized the *in-vitro* oxygen concentration of *L. deliciosus* [112], further research into this matter is needed. It is worth noting that Wang et al. [121] referred to *L. deliciosus* as the "purple pine fungus", which suggests that they may have been experimenting with a different species (see Section 3.1).

3.5. Effects of Root Exudates, Plant Material and Plant Growth Regulators on the In-Vitro Growth of L. deliciosus

3.5.1. Root Exudates

Root exudates are compounds secreted by plants into soils, consisting of organic soluble substances such as carbohydrates, amino acids, organic acids, lipids, flavonoids, cytokinins and enzymes. [139–141]. These compounds once exuded by the root can act as signal mechanisms [142,143] and growth stimulators for ECM [144–146]. The only experiment to analyse the effects of root exudates and root materials on the *in-vitro* growth of *L. deliciosus* was undertaken by Melin [147]. In their experiment, they recorded a growth increase of 160% when *P. sylvestris* roots were added to the medium. However, further tests conducted by this author on other ECM weren't always positive, as growth inhibition and decreases in growth promotion were recorded because of the sterilization and root processing methods used, high root exudate concentrations, and root maturation. Consequently, careful consideration of the root processing methods and their physical state is necessary when undertaking these experiments. Since no experiments have tested the effects of root material and their exudates in BAF, further experiments should repeat this study in this medium, as media type can influence the growth promoting effects of a compound [145]. Additionally, when Melin [147] tested the effects of root exudates and materials, some of the species in the same complex as *L. deliciosus* (deliciosi complex) were not considered separate species [43]. Possible taxonomic confusion can be noted in Melin's work, as they stated that *Picea* spp. are a host of *L. deliciosus* [105], whereas modern taxonomic literature reports the species forming natural mycorrhizal associations with *Pinus* spp. [148,149]. While these results are informative given testing on a species within the deliciosi complex, verification of these results is needed with a genetically confirmed *L. deliciosus* isolates. Exudates from non-mycorrhizal plants species such as *Brassica rapa subsp. rapa* L. could also be tested as they have been reported to significantly increase the *in-vitro* growth of *Paxillus involutus* (Batsch) Fr. [144] (see Section 5.2). If these experiments are successful, they could offer practitioners a low-tech and cheap method for improving the *in-vitro* growth of *L. deliciosus*.

Plants alter the exudates they release based on their environmental conditions [139,150,151]. To optimize the potential benefits of root exudate solutions, experiments should test the root exudates from plants with different nutritional statuses, as this has never been considered in *L. deliciosus in-vitro* growth optimization experiments. Evidence of the nutritional status of plants influencing the degree of fungal growth stimulation by root exudates has been recorded with arbuscular mycorrhizal fungi, with growth-promoting effects by root exudates increasing in low phosphorus conditions [152]. Consequently, further studies should test the growth stimulating effects of aseptically cultured phosphorus deficient *Pinus* spp. and see if the exudate from their roots stimulate growth better than non-deficient counterparts.

Compounds found in root exudates should also be tested singularly in BAF, without root exudate solutions. This is because Sun and Freis [145] recorded higher growth rates for some ECM (*S. granulatus*, *S. variegatus* (Sw.) Kuntze *Thelephora terrestris* Ehrh. and *Pisolithus tinctorius* (Pers.) Coker and Couch) when exudate compounds (palmitic, stearic acid and 2-Isopentenyl-aminopurine) were tested separately (compared to the root exudate solution tested). Testing exudate compounds in this manner should allow practitioners to better customize BAF medium for *L. deliciosus* growth, as the results from these single factor experiments would identify the exudates that best promote growth, and the compound

concentrations needed to facilitate this. Additionally, some *P. sylvestris* root exudates such as jasmonic acid have been recorded to inhibit the growth of ECM [153]. Hence, bypassing root exudate solutions and individually adding exudate compounds to the medium should result in greater growth through the mitigation of these inhibitors. Root exudate compounds which record the greatest growth promoting effects should then be tested in a multifactorial manner, in BAF, in different combinations, as Gogala and Pohleven [154] further increased the growth stimulation effects of Kinetin by adding it to the medium with β-indolylacetic acid.

3.5.2. Effect of Plant Material and Filtrates Not Derived from Roots

The addition of pine plant material filtrates have been reported to increase the growth of *L. deliciosus* [155]. Additionally, Melin [156] recorded *L. deliciosus in-vitro* growth increases of 5900% and 2475% in 20 ml of Lindeberg [157] nutrient medium after the addition of 0.8 ml of a *Populus tremula* L. leaf extract and ash solution, respectively. Greater *in-vitro* growth of *L. deliciosus* with the addition of leaf and pine filtrates in these studies could be due to its saprotrophic capabilities, which enable it to scavenge its own nutrients from plant matter. Evidence of *L. deliciosus* saprotrophic capabilities have already been recorded, as Gramss et al. [88] found that *L. deliciosus* was the one of the best ECM (out of 22) at degrading polycyclic aromatic hydrocarbons. Given that the type of media used has a significant effect on growth-promoting effects by root exudates [145], and none of the above-mentioned experiments were conducted in BAF, further experiments should test the effects of pine needle and leaf filtrates on the growth of *L. deliciosus* in this medium. However, when adding plant materials to media, the condition of the needles or leaves must be taken into consideration, as decreases in *L. deliciosus* growth have been recorded when filtrates from fresh pine needles were added to media [155,158]. Decreases in growth from the fresh needle filtrates could have occurred because of the antibiotic properties or tannins contained in pine needles [159,160]. Hence, fresh pine needles may contain greater amounts of these inhibitor compounds.

4. Nursey Stage and the Production of Inoculated Plants

4.1. Different Types of Inoculation Methods That Have Been Used and Their Success

In *L. deliciosus* pot experiments, five inoculation methods have been used: mycelial slurry and plugs, solid-state fermentation (SSF), spores and alginate beads [4,5,60,79–81,124,132,161–168]. Mycelium entrapped in alginate beads has been reported as the most ineffective inoculation method due to the low or absent fungal colonization post inoculation [4,161]. Poor success using this method in these studies was attributed to the mycelial fragmentation processes and chemicals used in the fabrication of the beads. Spore inoculations have recorded slightly more success, as González-Ochoa et al. [5] recorded some of their highest inoculation rates using this technique. However, success using spore inoculum hasn't been consistently reported across all studies [12]. Additionally, the disadvantages associated with this method (variations in colonization abilities; high chance of contamination; slower colonization rate compared to vegetative inoculum) make it unsuitable for *L. deliciosus* mycoforestry [37,38].

Most studies which have conducted *L. deliciosus* pot experiments have used SSF [79,80,162–165] or mycelial slurry [4,5,124,161,166–168]. In inoculation studies that have compared the success of these two methods, conflicting results have been reported. Diaz et al. [4] recorded higher growth rates using mycelial slurry compared to SSF, contradicting findings by Parladé et al. [161]. Diaz et al. [4] injected the root system of older trees (4 months, compared with seedling emergence at 15 days post sowing) with double the amount of mycelial slurry (10 ml/plant). Consequently, the lower mycorrhization results recorded by Parladé et al. [161] are most likely due to their plants having a reduced

infectivity potential caused by a combination of these two factors. Even with these conflicting inoculation results, mycelial slurry seems to be the superior inoculation method for commercial production systems, given the potential for cultivating *L. deliciosus* on a large scale using bioreactors [4,169]. SSF inoculum has also been stated to be a more time consuming and laborious plant inoculation method compared to mycelial slurry [4].

Future studies should aim to optimize the mycelial slurry inoculation method. Optimization of this method can be achieved through various ways, such as increasing the mycelial dose given per plant (g/L), the placement of the inoculum within the root system (direct root placement rather than indirect), the fragmentation method used (blending time and power or the machinery used to fragment mycelium), or through the addition of novel compounds, nutrient solutions or mycorrhizal helper bacteria (MHB) to the mycelial slurry. Increases in mycorrhization of plants by *L. deliciosus* or other ECM have already been recorded by some of the recommendations mentioned above [4,60,170,171]. The only above-mentioned recommendations that remain unexplored are the fragmentation method used, or the placement of the mycelium within the root system. To minimize energy expenditure in the production of *L. deliciosus* inoculum, efforts should focus on optimizing the placement of the inoculum, fragmentation of the mycelium and the addition of novel compounds and MHB prior to analysing the effects of higher mycelial doses per plant.

4.2. Effect of Potting Media on the Inoculation Success and Colonization Intensity of L. deliciosus

For a potting medium to be suitable for mycoforestry, it must facilitate high colonization intensity (the percentage of the root system which has been colonized) and mycorrhization rates (number of plants that were successfully colonized) by the target fungus [37]. A colonization intensity rate of ≥33% has been deemed necessary for plants to be suitable for outplanting [172]. Having a high *L. deliciosus* colonization intensity rate prior to out planting is important as the persistence of this fungus in introduced soils has been positively correlated with colonization intensity [7]. However, Guerin-laguette et al. [48] recorded greater basidiocarp production from some of their initially low colonized trees. Hence, having a high mycorrhization rate seems to be the more important factor. Additionally, having a greater amount of inoculated plants for out planting should make the system more cost effective for practitioners.

In *L. deliciosus* pot trials conducted under greenhouse or nursery conditions, the highest colonization intensity results (>70%) were obtained using peat and vermiculite in a ratio of 1:10 [173], whereas the highest mycorrhization results (100%) were recorded by Wang et al. [162] using a potting mixture consisting of vermiculite, perlite, peat, and pine bark (4:2:1:1 by volume). However, colonization results using peat and vermiculite have not been consistent across experiments, with some researchers reporting low colonization intensity (<33%) [4,5,79,161] and mycorrhization (<40%) [4,79]. Variations in colonization and mycorrhization results could be due to a multitude of factors such as intraspecific variation in the colonization abilities of isolates [7,161,167,174], the host plant species used [79,174,175], potting medium [4,5], contamination from non-target ECM (see Section 5.1), the amount of inoculum applied and inoculation method used (see Section 4.1), high fertilizer applications [4,60,166] and domestication of the isolate [174].

Even if consistently high colonization intensity and mycorrhization results using peat and vermiculite based potting mixtures were recorded across all studies, the requirement for peat in potting mixtures poses a significant threat to the commercial viability and sustainability of this mycoforestry system. Drying of peatlands for the subsequent harvesting of peat results in detrimental effects to the environment such as the production of greenhouse gas emissions [176], release of toxic metals [177], eutrophication of wetlands [178], loss of peatland habitats [179] and the decline of peatland specialist species [180]. Conse-

quently, international governments are seeking to phase out the sale of peat [181,182] or implement legislation that will prohibit its sale [183]. Hence, there is a need to identify a peat-free alternative that facilitates adequate mycorrhization and colonization intensity by *L. deliciosus*.

Published research into peat-free potting media alternatives for *L. deliciosus* mycoforestry has been scant, although González-Ochoa et al. [5] used a peat-free medium (composted pine bark) in their *P. pinaster* pot trial and recorded greater root colonization intensities compared to the peat and vermiculite medium used. However, lower colonization intensities were recorded compared to some other studies using peat and vermiculite potting media [80,163,164,173]. Even with the lower colonization rates, this study showcases the potential of using non-peat composted plant material in potting media. Furthermore, *L. deliciosus* has been successfully grown using plant materials such as pine wood chips and sawdust, wheat bran and cotton seed hulls [184]. However, when experimenting with plant products, careful consideration must be taken, as polyphenol-rich residues such as tannins can be toxic to microbial populations [185]. Toxic effects from the addition of plant materials to media have been recorded in *L. deliciosus in-vitro* studies [155,158], as filtrates from fresh pine needles resulted in decreased *L. deliciosus* growth. Guerin-Laguette et al. [48] also recorded initial decreases in *L. deliciosus* fructification and root colonization intensity in trees that had been mulched using pine bark, indicating that bark impeded growth and establishment of the fungus. Hence, studies using plant materials should opt for decomposed materials, as tannins are biodegraded [186] or leached out over time through rainwater due to their water solubility [187].

Given the lack of research into peat alternatives, more pot inoculation trials should be carried out using a range of peat-free mixtures. Since high colonization intensity and mycorrhization rates are essential in *L. deliciosus* mycoforestry, future experiments should aim to achieve this with peat-free potting media. In these experiments, different combinations of minerals and non-peat composted organic matter should be tested using a high mineral to organic matter ratio (as the highest colonization intensity rates were recorded using this mineral to organic matter ratio) [173]. Careful consideration must be taken when trialing novel potting media to ensure that the factors recorded to adversely affect colonization are avoided in the potting mixtures. To further facilitate mycorrhization and colonization intensity by the fungus in these peat free potting mixtures, ameliorants such as MHB, Tween 80 (non-ionic surfactant and emulsifier) and vegetable oil should also be tested, as they have improved colonization for other ECM [170,171].

5. Long-Term Persistence and Fructification of *L. deliciosus* in Mycoforestry Plantations

5.1. Impacts of ECM Communities on the Persistence of L. deliciosus in Soils

ECM communities naturally co-exist within the root system of a single tree [188–190] and their composition changes over time [191]. In *L. deliciosus* experiments, contamination from non-target ECM has resulted in conflicting results. In some studies non-target ECM have outcompeted and displaced *L. deliciosus* from the inoculated tree, resulting in the disappearance or gradual decline of this fungus in introduced soils [7,163], whereas in other studies, contamination from non-target ECM has been reported to have no effect on the basidiocarp productivity or persistence of this fungus [44,48,59]. Non-antagonistic results reported in some of these experiments could have been due to niche partitioning, as Taylor and Bruns [192] recorded the co-existence of ECM within *P. muricata* D.Don stands because of this mechanism. However, a multitude of factors could have caused these contrasting results, as the persistence of ECM in soil ecosystems are influenced by soil temperature [193,194], nutrient availability [195,196], number of competitors [197],

species pairings and inter- and intraspecific competition [198–200], pH [195,201,202] and soil moisture [203,204]. Hence, future research should aim to better understand the effects of indigenous ECM communities on the persistence of *L. deliciosus* under different environmental conditions, as this could help facilitate the establishment of this fungus in field sites through the co-inoculation or promotion of symbiotic fungal communities. For example, increased mycorrhiza formation has already been recorded in *Tuber borchii* Vittad. inoculated plants when co-inoculated with *Arthrinium phaeospermum* (Corda) M.B. Ellis strain [205].

5.2. Intercropping with Brassicaceae Plants in L. deliciosus Mycoforestry Plantations

Intercropping *L. deliciosus* plantations with *Brassicaceae* flora (*B. rapa subsp. rapa*.) has the potential to increase the persistence of *L. deliciosus* in soils and the economic value of these plantations. This is because root exudates from *Brassica* spp. have been recorded to significantly increase the *in-vitro* growth of *P. involutus* [144]. Consequently, if similar effects are recorded with *L. deliciosus*, increases in mycelial growth should increase the productivity of these plantations and subsequently the revenue gained, as the basidiocarp productivity of *L. deliciosus* has been recorded to be positively correlated with mycelial biomass [206] and colonization of host root systems [48]. Additionally, the sale of *Brassica* crop would further increase the income generated through these plantations. However, to ensure the intercropping of these plantations doesn't adversely affect the persistence of *L. deliciosus* through the growth stimulation of antagonistic ECM, the effects of exudates from *Brassica* spp. on indigenous ECM communities should also be recorded. In addition, the nutrient removal effects of this intercropping treatment should be monitored alongside fungal growth stimulation, as *B. rapa subsp. rapa* has been reported to have a very high phosphorus (P) requirement [207] and this demand could reduce tree growth overtime through the depletion of P in soils. On the other hand, the high phosphorus requirements of *B. rapa subsp. rapa* could result in further growth stimulation, as mycorrhizal symbiosis can be stimulated in low phosphorus conditions [152]. Since no research has tested the effects of *Brassica* spp. exudates on *L. deliciosus*, further *in-vitro* and in situ research is needed to verify if these also stimulate the growth of this fungus.

5.3. Applications of Mycorrhizal Helper Bacteria (MHB)

No published research has tested the effects of MHB on the colonization intensity and persistence of *L. deliciosus*. This is surprising, given that MHB extracted from the rhizosphere of *P. pinea* have been recorded to increase the colonization of host root systems by other ECM [208]. Hence, further research should test the effects of MHB at different concentrations in pot and field trials. Since the objective of this research is to improve the commercial viability of this food production system, further studies should focus on testing commercially available MHB, as successful results with MHB that can't be cultivated on a large scale would be of limited practical value. One commercially available MHB that justifies further experimentation is *Psedomonas fluorescens Migula*, as this MHB has been recorded to increase the colonization intensity of *Boletus edulis* Bull in host root systems [171].

5.4. Effects of Soil Type on the Persistence of L. deliciosus

The type of soil in the field site has been recorded by Hortal et al. [173] and Parlade et al. [163] to significantly affect the persistence of *L. deliciosus*, with unfavourable physical-chemical and biotic soil characteristics resulting in the disappearance of poorly suited isolates overtime. In Scotland, the predominant soil types in which *L. deliciosus* basidiocarps have been recorded are mineral podzols (Figure 2). The proliferation of *L. deliciosus* in mineral podzols could be due to the low nutrient content of these soils [209], as these

conditions facilitate mycorrhization by *L. deliciosus* [4,166]. Moreover, *L deliciosus* has an affinity for sandy soils in Northern Europe [148], and pine trees, their plant hosts, facilitate the podzolization of sandy soils over time [210]. The proliferation of this fungus in soils with a high mineral content has also been recorded in other regions [211,212]. In pot trials the highest colonization rates were obtained in potting mixtures with a high mineral content (see Section 4.2). These findings suggest that soils with a high mineral ratio are the optimal soil type for the persistence of *L. deliciosus*, especially in Scotland, as basidiocarp productivity has been positively correlated with mycelial biomass [206] and colonization of host root systems [48]. However, no research has been conducted in the UK on the effects of soil types on the persistence of *L. deliciosus*.

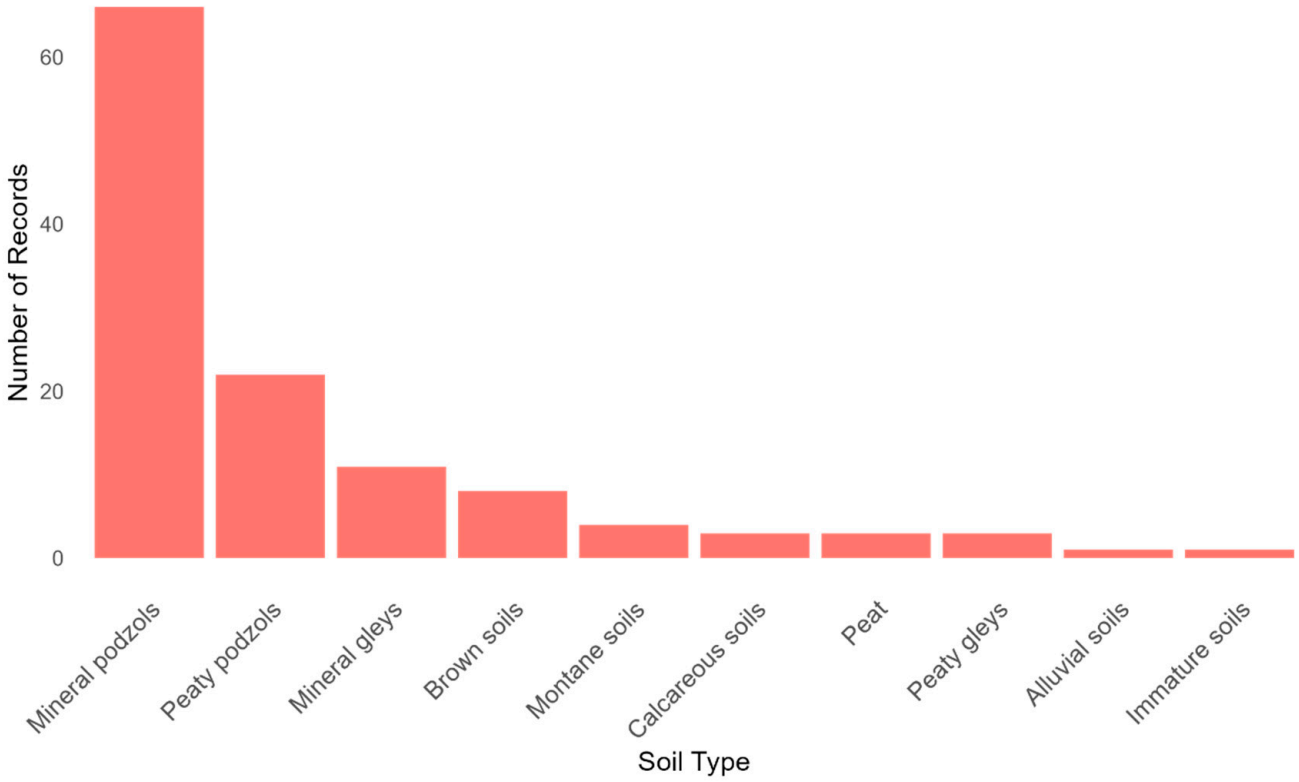

Figure 2. *L. deliciosus* records in Scotland from 2000–2024 in different soil types. *L. deliciosus* presence records and soil type data were downloaded from NBN Atlas [51] on 4 September 2025. Soil type data was derived from the National Soil Map of Scotland [213].

Globally, successful field applications of this mycoforestry system have been undertaken in various soil types such as sandy clay [58], clayey loam [7], silt loam [6,48] and clay soils [44]. The successful persistence of *L. deliciosus* in these soil types indicates its preference for clay and loam based soils. However, these prior experiments were predominantly undertaken in areas with contrasting meteorological conditions to each other, as they were undertaken in the Mediterranean [7,58], New Zealand [6,48] and Southwest China [44]. Hence, it is difficult to discern general trends in *L. deliciosus* persistence from these results. Geographical differences in optimal soil type can already be seen from the literature, as *L. deliciosus* is attributed to sandy soils in Northern Europe (Figure 2) [148], contradicting the findings of Hortal et al. [7], as they recorded poor *L. deliciosus* persistence in sandy loam and good persistence in clayey loam. Contrasting results between these two regions could be due to the soil moisture tolerances of *L. deliciosus*, as water availability may be a key factor limiting the persistence of this fungus in arid climates. Evidence of reductions in water availability having a negative impact on this fungus has already been recorded,

with drought and reduced rainfall resulting in decreased basidiocarp productivity [6]. Consequently, the greater persistence of this fungus in clay soils in arid regions could be due to the greater water holding capacities of clay soils compared to sandy soils [214,215].

To better understand the performance of *L. deliciosus* mycoforestry in different soil types. Further in situ plantation trials are needed in areas with soils of different texture classes and similar meteorological conditions. Controlled pot trials manipulating the physical and chemical properties of these soils should also be undertaken alongside to better understand the effects of these soil factors. The results from these experiments, along with meteorological data, should help identify where and under what conditions this mycoforestry system would be economically profitable. This information should also give insights into the treatments required to maintain the long-term basidiocarp productivity in these plantations. To optimize the selection of suitable plantation sites and symbionts, the influence of the source site's soil conditions on the persistence of *L. deliciosus* isolates post out-planting should also be evaluated using isolates sourced from different soil types and climates, as evidence of localized adaption to source site conditions has been reported [174].

5.5. Impacts of Climate on the Persistence of L. deliciosus

Decreases in basidiocarp productivity have been attributed to climatic factors such as reduced annual rainfall (especially in summer) and high wind intensity [6,48,216]. Since basidiocarp productivity has been positively correlated with extraradical mycelium [206] and colonization of host root systems [48], results from these studies offer insights into the effects of climate on the proliferation of *L. deliciosus*. However, none of these studies identified the optimal meteorological conditions for *L. deliciosus* or conducted controlled experiments that manipulated these factors. Further studies analysing the effects of climate on the persistence of *L. deliciosus* need to be undertaken to determine the optimal climatic conditions for both international populations and those in the UK. Results from these studies should be coupled with those of persistence in different soil texture classes to map and identify regions where this food production system would be the most productive. Additionally, land managers could use the climatic data generated from these experiments to understand the maintenance required for the persistence of *L. deliciosus* within their plantations. Since localized adaptation to different climatic conditions has been recorded with *L. deliciosus* [174], experiments analysing the effects of meteorological conditions on the proliferation and fructification of this fungus should aim to use multiple isolates sourced from areas with different climates. Using isolates sourced from different climates should help better distinguish general species trends from those of localized adaptation.

5.6. Effects of Mycophagous Invertebrate Communities on Basidiocarp Productivity

One important under studied factor that could affect the basidiocarp productivity of *L. deliciosus* plantations is the impact of mycophagous invertebrates. A plethora of invertebrates are reported to feed on the basidiocarps of *L. deliciosus* such as Gastropoda species [217], Collembola species [218] and Diptera larvae [219]. In China, severe greenhouse infestations of Diptera larvae resulted in the disappearance of *L. deliciosus* from the root systems of inoculated plants [162]. Heavy infestations of Diptera larvae have also been reported in Europe in basidiocarps of wild *L. deliciosus* populations [219]. Justifications for the heavy infestations of *L. deliciosus* by Diptera larvae are attributed to the mild-tasting latex they produce being relatively ineffective at dissuading mycophagous organisms [47]. On the other hand, the consumption of *L. deliciosus* basidiocarp by mycophagous invertebrates could have some positive impacts, as *Deroceras invadens* Reise, Hutchinson, Schunack & Schlitt, 2011 has been recorded to act as a vector of spore dispersal for *T. aestivum* Vittad [220]. Hence, mycophagous organisms could help maintain the persistence of

L. deliciosus in introduced soils. Since the impact of mycophagous invertebrates have never been monitored in a plantation setting, further research should evaluate the impacts of these communities on the persistence of *L. deliciosus* and its basidiocarp production.

5.7. L. deliciosus Basidiocarp Productivity Within Mycoforestry Plantations

Currently, no economic modelling has been conducted on the long-term productivity of *L. deliciosus* plantations. The lack of a viable economic model is likely due to substantial knowledge gaps in the long-term persistence and productivity of this mycoforestry system under varying environmental conditions (see Sections 5.1 and 5.4–5.6). However, basidiocarp productivity of *L. deliciosus* in natural forest ecosystems has been successfully modelled [221], indicating that it should be possible to model the economic potential of these plantations under a variety of environmental scenarios once these limitations have been overcome. Better demonstrating the economic potential of these plantations could entice interested stakeholders to adopt this practice, as these models would offer key insights into the profitability of this food production system under different environmental conditions and over a full forest rotation period. To accurately portray the long-term economic potential of these plantations over the next 50 years (length of an optimal *P. sylvestris* forest rotation period [65]), these models should incorporate different climate change scenarios, as Kauserud et al. [222] concluded that climate change should result in longer ECM growth periods and fruiting seasons in the UK.

6. Conclusions and Future Directions

L. deliciosus mycoforestry has significant potential as a sustainable food production system and a resource for the pharmaceutical industry, with markets for this fungus already established in many countries around the world (see Sections 2.4 and 2.5). However, there are many knowledge gaps (see Sections 3–5) that need to be explored before *L. deliciosus* mycoforestry can become a commercially viable and widespread food production system. Hence, further research and development is needed across all technical aspects of this system.

Better understanding how soil and meteorological factors affect the growth and persistence of this fungus should be of the highest priority. Knowing how environmental factors affect the persistence of *L. deliciosus* should aid in identifying suitable sites for this mycoforestry system and the silvicultural practices needed to maximize productivity. Since information on the optimal environmental conditions for *L. deliciosus* is currently unavailable (see Sections 5.4 and 5.5), the silvicultural practices required to maintain the long-term fruiting of this fungus in these plantations weren't discussed due to the uncertainty surrounding this subject. Greater information on how soil factors affect *L. deliciosus* should also help identify a sustainable peat free potting medium that reliably provides adequate mycorrhization and colonization intensity by this fungus.

Since localized adaptation to different environmental conditions has been recorded by *L. deliciosus* populations, studies analysing the effects of environmental factors on the persistence of *L. deliciosus* should incorporate multiple isolates sourced from different environmental conditions. Being able to distinguish general species trends from those of localized adaptations should help facilitate the selection and breeding of efficient symbionts through the creation of a library of isolates targeted to different regions and environmental conditions. Moreover, having a library of targeted isolates for specific areas would minimise any potential negative impacts of *L. deliciosus* mycoforestry on natural *L. deliciosus* populations.

Greater transnational *L. deliciosus* research collaboration is needed between North America and Europe and their east Asian counterparts, as acknowledgement of research endeavours between these regions is lacking. Having greater collaboration and

acknowledgement of research between these regions could significantly advance the field of mycoforestry, especially since China is the world's largest producer and exporter of edible mushrooms [223] and the second largest global investor into research and development [224].

The knowledge gained through the upscaling of *L. deliciosus* mycoforestry should help expand the field, potentially aiding establishment of plantations with other ectomycorrhizal fungi and tree hosts. Through the expansion of this field, the ecological benefits of this practice should increase, particularly through the diversification of forest plantation and management practices. Given the plethora of benefits mycoforestry can provide, research must continue to unlock the potential of this promising food production system.

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Abbreviations

The following abbreviations are used in this manuscript:

ECM	Ectomycorrhizal fungi
C	Carbon
MHB	Mycorrhizal helper bacteria
SSF	Solid-state fermentation
BAF	Biotin–aneurin–folic acid
PDB	Potato dextrose broth
N	Nitrogen
RPM	Rotations per minute
P	Phosphorus
PDA	Potato dextrose agar

Appendix A

Table A1. Carbon source which yielded optimal growth in Chinese liquid culture in vitro studies.

Article	Optimal Carbon Source
Fu et al. [110]	Sucrose
Han et al. [111]	Soluble Starch
Hu et al. [225]	Soluble starch
Li et al. [112]	Maltose
Lin and Chen [113]	Soluble starch
Su et al. [226]	Soluble starch
Wang et al. [121]	Glucose

Table A2. Temperature at which optimal growth was recorded for Chinese *L. deliciosus* isolates.

Article	Temperature Range Tested (°C)	Optimal Temperature (°C)
Xu et al. [109]	5, 10, 20, 25, 28, 30, 37 and 40	25
Zhu et al. [132]	5, 10, 20, 25, 28, 30, 37 and 40	28
Hu et al. [225]	23, 25, 27, 29 and 31	27
Li et al. [158]	20, 25, 28, 30 and 32	28
Wang et al. [227]	18, 20, 22, 24, 26 and 28	26
Xue et al. [228]	15, 22, 27 and 32	27
Zhan and Wei [125]	15, 20, 25, 30 and 35	25
Zhou et al. [229]	18, 20, 24, 26, 28 and 30	26
Zhou et al. [230]	5, 7, 10, 12, 15, 17, 20, 22, 25, 27, 30, 32, 35, 37 and 40	27

Table A3. pH level at which optimal growth was recorded for *L. deliciosus* isolates.

Article	Number of Isolates Tested	Media Used	Optimal pH
Chung [103]	4	Solid MMN, PDA and BAF	IF 725004 (BAF = 6.8; MMN = 6.8; PDA = 5.8) IF 1608006 (BAF = 6.3; MMN = 6.8; PDA = 5.8) IF 914002 (BAF = 6.3; MMN = 6.8; PDA = 5.8) IF 936001 (BAF = 5.3; MMN = 5.8; PDA = 5.8)
Flores et al. [128]	4	Solid BAF	*L. deliciosus* SM 63.00 (6.5) *L. deliciosus* PX 252.01 (4.5) *L. deliciosus* SO.10 (5.5) *L. deliciosus* Rp.01 (7.0)
Guerin-Laguette et al. [60]	1	Solid BAF	6
Han et al. [111]	1	Custom PDB	7
Hu et al. [225]	1	Custom PDB	7
Lazarević et al. [130]	1	Liquid MMN	5.8
Li et al. [158]	1	PDA	5
Li et al. [112]	1	Liquid modified Martin's medium	Single factor experiment = 6 Multifactorial experiment = 8

Table A3. *Cont.*

Article	Number of Isolates Tested	Media Used	Optimal pH
Olaizola et al. [131]	1	Liquid MMN	8.5
Sanchez et al. [129]	1	Solid MMN	6.5
Torres and honrubia [2]	1	Solid Raper, Hagem, MMN, PDA, MMN (+10 g glucose) and 2% malt extract agar	Raper (7.5); Hagem (7–7.5); MMN (6.5); PDA (5.5), MMN (+10 g glucose) (7.5); 2% MEA (7.5)
Wang et al. [227]	1	PDA	6
Xu et al. [109]	1	Solid and Liquid MMN	6
Xue et al. [228]	1	Custom PDA	6
Zhou et al. [229]	1	3 different modified PDB media	8
Zhou et al. [230]	1	PDB	6.5
Zhu et al. [132]	1	Solid and liquid MMN	6.0

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