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REVIEW

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Sustainable production of ectomycorrhizal fungi in the Mediterranean region to support the European Green Deal

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Societal Impact Statement

The planet faces a climate crisis with severe health, economic and environmental consequences. Political actions such as the European Green Deal aim to mitigate climate change by shifting production and consumption patterns, and the production of mycorrhizal sporocarps—the fruiting body of fungi—is no exception. The production of mycorrhizal sporocarps has a high economic, cultural and environmental impact in the Mediterranean region. With a key role in forest ecosystems, ectomycorrhizal fungi provide services and goods essential to maintain soil quality, ecosystem functions and food, contributing to the achievement of sustainable production and the European Green Deal goals—a climate-neutral Europe.

Summary

Ectomycorrhizal fungi (ECMF) cultivation is an important economic activity in the Mediterranean region. Sporocarps from ECMF species such as *Terfezia claveryi*, *Tuber melanosporum*, *Tuber aestivum* and *Lactarius delicious* have been successfully cultivated. Due to biotechnological advances, a considerable evolution in ECMF cultivation techniques was observed in the last decade. New technologies and intensified Research and Development allow for a better understanding of the physiology of the plant-fungi symbioses and how climate change affects them. Studying forest management practices is also essential to optimise the natural production of ectomycorrhizal sporocarps and help develop sustainable production practices. This knowledge revealed the importance of ECMF and their role in the rural bioeconomy and highlighted the need to establish sustainable cultivation practices. A successful example of ECMF cultivation is the production of *Terfezia* species, namely, *Terfezia claveryi* and *Terfezia boudieri*. *Terfezia* truffles are traditional delicacies with high socioeconomic relevance and numerous biotechnological applications. Furthermore, these Mediterranean native species are an important tool to develop the bioeconomy in rural areas by creating new production strategies. Furthermore, exploiting these and other native Mediterranean species can promote sustainable practices in line with new European Green Deal strategies, such as the Farm to Fork strategy, the EU Biodiversity strategy for 2030 and the Climate Law. This work reviews ECMF cultivation practices and forest management studies, presenting the case of *Terfezia* cultivation and how the

sustainable production of wild and planted ECMF may contribute to achieving the European Green Deal objectives and to a more resilient Europe.

KEYWORDS
bioeconomy, ectomycorrhiza cultivation, ectomycorrhizal fungi, European Green Deal, Mediterranean region, *Terfezia*

1 | INTRODUCTION

Over the centuries, humans have learned to harness endogenous natural resources such as fungi and their fruiting bodies, with knowledge that passed from generation to generation (Blondel, 2006). Unfortunately, much of this knowledge has been lost due to rural abandonment (Comandini & Rinaldi, 2020). Simultaneously, these and other natural resources are under pressure due to intensive agriculture (Baccar et al., 2020), abandonment of traditional forestry (Lasanta-Martínez et al., 2005), urban sprawl, pollution and climate change (European Commission, 2019). This resulted in high biodiversity loss affecting ecosystem functions, goods and services (Cardinale et al., 2012). Therefore, new solutions are needed to simultaneously protect biodiversity and make it economically productive (Pérez-Moreno et al., 2021).

Together with other soil microorganisms, ectomycorrhizal fungi (ECMF) are essential for ecosystem processes, services and functions (Bakker et al., 2019; Cohen-Shacham et al., 2016). Approximately 6,000 fungal species form ectomycorrhizae (ECM) with woody plants (Wang & Qiu, 2006). ECM are mutualistic symbioses where the fungal partner receives carbohydrates from the host plant, which are essential for mycelial growth and fruitbody production, and plants receive water and nutrients from ECMF (Agerer, 2006). ECM can also have non-nutritional effects that improve host plant fitness (e.g., protection against pathogens, toxic minerals or drought), be agents of environmental change, interact with the soil food web and contribute to soil quality (Strullu-Derrien et al., 2018).

Fungi, including ECMF, are used primarily as food but are also well-known sources of biocompounds such as enzymes, proteins, vitamins, pigments and volatile organic compounds (Culleré et al., 2010; Erjavec et al., 2012; Kalač, 2013; Wong et al., 2010; Xu et al., 2011), with many still to be discovered (Antonelli et al., 2020).

Peintner et al. (2013) listed the edible sporocarps authorised for trade in 27 European countries, including 14 European Union (EU) member states. Only three species are common to all EU countries: *Cantharellus cibarius*, *Boletus edulis* and *Lactarius deliciosus*. These and other 12 ECMF species are authorised for trade-in at least 9 EU countries. However, insufficient data make it challenging to provide accurate information on ECMF production and market prices (Table 1). Because national or European official data are scarce, there are also few published studies and analyses of sporocarp production and its socioeconomic impacts, with most studies focusing on specific areas or regions (Bonet et al., 2020; Tahvanainen et al., 2016, 2019) (Table S1).

ECMF are traditionally harvested in forests, and their formation is linked to habitat characteristics and climate conditions (Parladé et al., 2014). They are an important food and income source for rural populations (de Román & Boa, 2006), and their international trade has increased in recent years (de Frutos, 2020). ECMF currently represent up to 25% of the soil expectation value (Tomao, Bonet, et al., 2017), confirming their importance as a natural resource at ecological and socioeconomic levels. However, their natural production has declined over the last century (Yun & Hall, 2004), and several species are now in danger of extinction (Arnolds, 1991; Egli, 2011; nic Lughadha et al., 2020). Among ECMF, *Terfezia* species, commonly known as desert truffles, are luxury products, being some of the most expensive products in the international market (Milanesi et al., 2020) and among the most studied (Gajos & Hilszczańska, 2013; Morte et al., 2017).

This work aims to review the current state of ECMF cultivation, focusing on the production of *Terfezia* truffles, and discuss how their exploitation can promote sustainable practices in line with the new European Green Deal (EGD) strategies and policies.

2 | FROM MYCORRHIZAL PLANT PRODUCTION TO FOREST MANAGEMENT

Several edible species from genera *Tuber*, *Lactarius* and *Terfezia* are currently successfully cultivated (Donnini et al., 2013; Karwa et al., 2011; Morte et al., 2012; Slama et al., 2010), but most commercial species are not yet cultivated. This is mainly because the mechanisms affecting ECMF production, such as mycorrhizal establishment, symbiotic processes, life cycle and ecological drivers, are not fully understood (Domínguez-Núñez et al., 2019), making their cultivation difficult to 'master'. Furthermore, because of their symbiotic relationships with plants, the fruiting conditions for those currently cultivated are complex. This led to increased research into new mycosilviculture techniques and management to improve sporocarp production (Jiang & Yanbin, 2018; Tomao, Bonet, et al., 2017). Although several mycorrhizal plant production and management methodologies are well implemented (Figure 1), the development and optimisation of techniques can still be observed, often adapted to the target host and ECM species.

2.1 | ECMF current cultivation practice

ECMF cultivation and sporocarp production require the production of ECM seedlings (Álvarez-Lafuente et al., 2018) (Figure 1). Seedlings are

TABLE 1 Several edible ECM species authorised for trade in EU countries and available data of commercialised product and market prices

ECM species	N° of EU countries[a]	Commercialized product t/year[b]	Commercialized product Period	Market prices €/kg[b]	Market prices Period	Country	References
Boletus edulis	14	25,000	2014	12	2017	Spain	Bonet et al. (2020); Baars (2017)
		400	1978–2016	7.7	1978–2016	Finland	Tahvanainen et al. (2019)
Cantharellus cibarius	14	2,500	2007	20	2003	Spain	Bonet et al. (2020); de Román and Boa (2004)
		12.6	1978–2016	13.8	1978–2016	Finland	Tahvanainen et al. (2019)
Hydnum repandum	12	700	n.a	9.9	2002	Spain	Bonet et al. (2020); de Román and Boa (2004)
Lactarius deliciosus	14	6,800	1990–1998	13	2002	Spain	Bonet et al. (2020); de Román and Bo, (2004)
		100	1978–2016	4.0	1978–2016	Finland	Tahvanainen et al. (2019)
Terfezia claveryi	2	670	2001–2015	60	n.a.	Spain	Andrino et al. (2019); Oliach et al. (2020)
Tuber aestivum	8	30	2016	50	n.a	Spain	Oliach et al. (2020)
Tuber brumale	6	0.5	2015	120	n.a	Spain	Oliach et al. (2020)
Tuber melanosporum	9	47	2013–2017	550	2016–2017	Spain	Oliach et al. (2020)

Abbreviations: €/kg, Euros per kilogramme; n.a., data not available; t/year, tonnes per year.
[a]Data from Peintner et al. (2013).
[b]Maximum values registered.

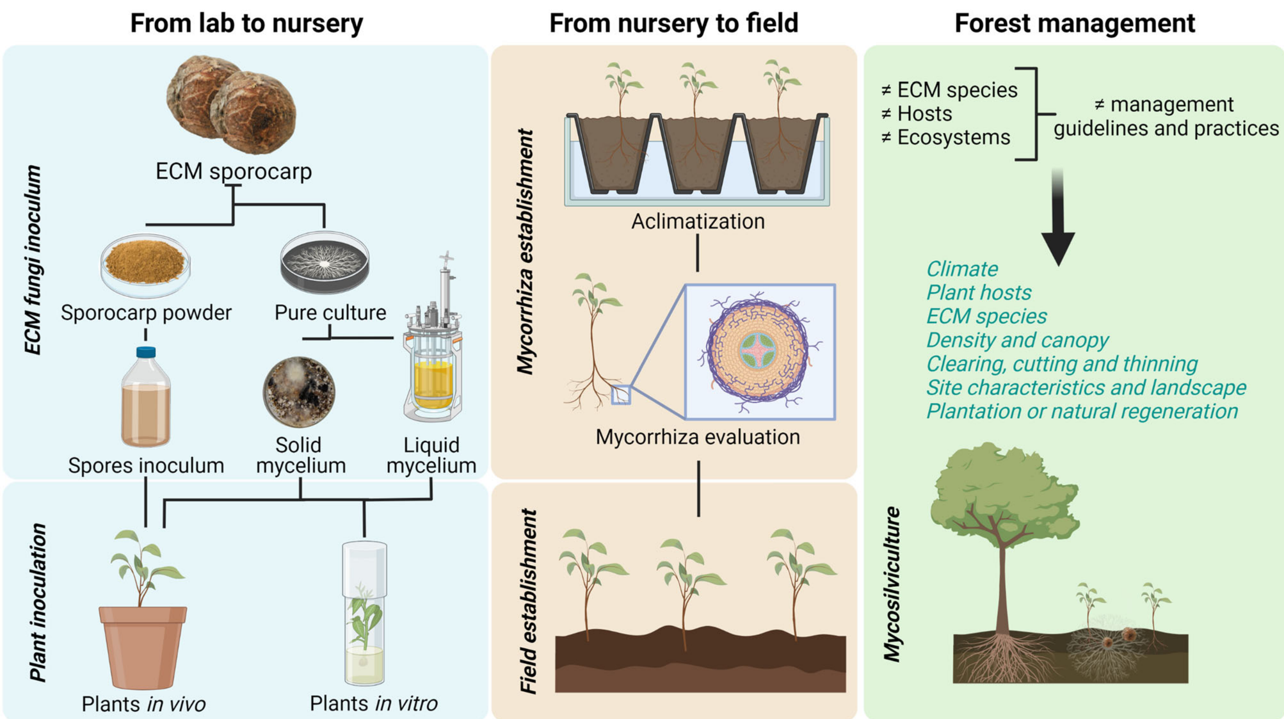

FIGURE 1 Scheme of current phases for ECM plants production and forest management criteria for their field implantation. ECM, Ectomycorrhizal. Created with BioRender.Com

usually inoculated in nurseries and later transplanted into forests, but tree inoculation in the field has also been achieved using root traps with spore inoculum (Azul et al., 2014). In addition, host plants can be inoculated in vivo using ECMF spores or in vitro using ECMF mycelium. The selected method depends on the ECMF species and the method used to obtain the host plant (seed germination or in vitro cloned plants).

The greatest challenge for spore and mycelium inoculation methods is producing high-quality mycorrhizal plants colonised with only the desired ECMF (Murat & Martin, 2008). Contamination can happen during mycorrhizal establishment in nurseries or following seedling transplantation into the field, imperilling the persistence and spread of the inoculated ECMF (Domínguez-Núñez et al., 2019). In addition, several aspects of fungal physiology and ecology may affect mycorrhisation and sporocarp production, namely, interactions with mycorrhiza helper bacteria (MHB). MHB improve mycorrhisation, plant survival in nursery conditions and sporocarp production (Azul et al., 2014; Navarro-Ródenas et al., 2016); reduce environmental and pathogen impacts on ECM hosts; fix nitrogen and improve nutrient acquisition (Domínguez-Núñez et al., 2019). MHB include *Bacillus*, *Pseudomonas*, *Burkholderia* and *Streptomyces* (Choudhary et al., 2017; Mello et al., 2010). Our knowledge of ECMF interactions with other microorganisms is still limited but may be key to improve their commercial production.

After mycorrhizal establishment and acclimatisation in the nursery, the mycorrhizal plants ate transferred to the field. At this stage, it is crucial to select an area with the best possible conditions for plant and mycorrhiza development, such as the landscape, soil proprieties and climatic characteristics (Oliach et al., 2020). These vary with the selected plant host and ECM and the cultivation practices to apply. The cultivation of ECMF is still recent compared with other horticultural practices, and further research and full-scale experiments are needed to develop practices that guarantee and increase ECMF production (Guerin-Laguette, 2021). The current cultivation practices for ECMF sporocarp production include maintenance of the plantations by performing weed control and clearing (with or without mechanisation), irrigation systems, among others (Guerin-Laguette, 2021; Oliach et al., 2020; Olivera et al., 2014). After the mycorrhizal plants have been established in the field, it is important to monitor the persistence and development of the introduced ECMF species, which is usually performed using microscopy and molecular tools (Guerin-Laguette, 2021).

2.2 | Forest management

Climate conditions have been considered the main factor promoting variability in sporocarp production (Olano et al., 2020). Dry seasons were observed to affect sporocarp production, especially in Mediterranean regions. However, climate cannot be dissociated from other variables. Because of their relationship with plants, ECMF communities are sensitive to shifts in vegetation (Lauber et al., 2008). Appropriate forest management practices are, therefore, key for both preserving fungal diversity (Tomao, Bonet, et al., 2017) and increasing fungal productivity.

Recent studies suggest that forest stand structure (including plant species, age and density, landscape, canopy cover and the relationship between tree and sporocarp production) and forest management practices (e.g., understory thinning and clearing, regulation of edible sporocarp harvest and mycorrhizal plant regeneration and use) also play an essential role (Suz et al., 2015; Tomao, Bonet, et al., 2017) (see Table S1). For example, Collado et al. (2019) found that sporocarp yield was correlated with tree growth (seasonal wood production) and mediated by summer and autumn precipitation, indicating that tree growth and sporocarp biomass are sensitive to precipitation events under water-limited conditions. Olano et al. (2020) observed that *Boletus edulis* and *Lactarius deliciosus* sporocarp yields were correlated with previous year normalised difference vegetation index (NDVI), indicating that higher carbon availability favours ECMF development.

Several studies show that ECMF are more abundant in younger stands, which can be related to higher tree growth rates (Ágreda et al., 2014; Bonet et al., 2008; Egli et al., 2010; Martínez-Peña, Ágreda, et al., 2012; Tahvanainen et al., 2016). Martínez-Peña, Ágreda, et al. (2012) also observed a second yield peak of *Lactarius deliciosus* sporocarp production in stands over 70 years old, suggesting a relationship with the more open canopies and more intensive management in older stands. Accordingly, forest management practices such as thinning and clearing have positively affected sporocarp production, with higher sporocarp yields observed immediately after thinning (Bonet et al., 2012; Collado et al., 2018; Tahvanainen et al., 2016). Tree radial growth following thinning has also led to increased ECMF sporocarp production (e.g., *Boletus edulis*) (Egli et al., 2010).

Predictive models can be developed to facilitate management decisions (Table S1). These should be as many variables as possible in order to predict the impacts of management strategies and climate on sporocarp seasonal production (de Frutos et al., 2019a, 2019b). The published models were based on studies conducted in native and planted forests, and many of them address the production of both mycorrhizal and saprotrophic fungi (Table S1). Some models focused only on ECMF production, with special attention to the productivity of edible marketable species (Martínez-Peña, Ágreda, et al., 2012; Martínez-Peña, de-Miguel, et al., 2012; Olano et al., 2020; Ortega-Martínez et al., 2011; Salerni & Perini, 2004; Tahvanainen et al., 2016). Most models include precipitation, temperature and forest management as main variables. Still they do not consider how ECMF production affects soil quality and contributes to improved water-saving and quality, which are main factors for sustainable production and halting climate change. The influence of forest management practices on ECMF sporocarp yields reflects the importance of host trees for fungal biomass production and reinforces the importance of forest management to increase sporocarp production. However, it needs to be better understood and analysed with other variables, such as soil and water quality (Bonet et al., 2020; Tomao, Antonio, et al., 2017).

3 | A CASE OF SUCCESS: *TERFEZIA* SPECIES CULTIVATION

Terfezia species, known as desert truffles, are adapted to various soil types and edaphoclimatic conditions throughout the Mediterranean region and are both a source of valuable sporocarps and biocompounds (Díez et al., 2002). Desert truffles have been used since the Bronze Age in the Middle Euphrates (Shavit, 2014) and remain very popular due to their high nutritional and gastronomic value and profitable sporocarps (Khalifa et al., 2019; Mandeel & Al-Laith, 2007). They are important for local traditions and economy, but native traditions related to desert truffles are disappearing, and their habitats and natural abundance are decreasing due to excessive harvesting, climate changes, rural abandonment and natural disturbances, among other factors (Boa, 2004; Morte et al., 2012).

Desert truffles are hypogeous fungi that form *ectendomycorrhizae* with Cistaceae plants and are mainly distributed throughout the Mediterranean basin (Marqués-Gálvez, Miyauchi, et al., 2020; Navarro-Ródenas et al., 2012; Sitrit et al., 2014). *Terfezia* truffle production is seasonal and takes place in spring, in arid and semiarid regions (Morte et al., 2012). *Terfezia claveryi* and *Terfezia boudieri* have been successfully cultivated (Morte et al., 2017, 2020), and *Terfezia arenaria* cultivation in acid soils is currently under development (Louro, 2020; Louro et al., 2021). In addition, 16 other *Terfezia* species were found in the Iberian Peninsula (Table S2), opening new possibilities for *Terfezia* cultivation and exploitation. However, much is still unknown about their edibility, properties and associated economic value.

Terfezia species are an example of successful cultivation of mycorrhizal fungi, achieved through a combination of biotechnology, for optimisation of fungal inoculum production, and forest management techniques (Louro et al., 2021; Morte et al., 2009; Morte & Andrino, 2014; Morte & Honrubia, 1992). Knowledge by local collectors and producers has been fundamental in understanding plant phenology as a key factor affecting desert truffle production, for example, the coincidence of the production season with flower blooming (Marqués-Gálvez, Morte, & Navarro-Ródenas, 2020).

Similarly to most ECMF, *Terfezia* breeding programmes are based on the plantation of inoculated plants (Arenas et al., 2018; Louro et al., 2021; Morte et al., 2009, 2020; Morte & Andrino, 2014). *Terfezia* mycorrhization (in vitro and ex vitro) and maintenance have been studied (Gutiérrez et al., 2003; Jamali & Banihashemi, 2013; Navarro-Ródenas et al., 2012; Turgeman et al., 2016; Zaretsky et al., 2006; Zitouni-Haouar et al., 2014), and one method patented (Andrino et al., 2013).

Management protocols for establishing desert truffle plantations have been developed over the last two decades (Andrino et al., 2019; Morte et al., 2009, 2017). These protocols need to consider that precipitation is critical for desert truffle production (Morte et al., 2012). Therefore, agroclimatic parameters such as evapotranspiration, soil water potential (SWP), relative air humidity, aridity index (AI) and air vapour pressure deficit (VPD) are essential to understand truffle production. SWP and AI were the main agroclimatic parameters determining annual truffle yields in a 15-year old *Helianthemum almeriense* × *Terfezia claveryi* plantation (Andrino et al., 2019) and can be managed using irrigation during autumn and spring to maximise desert truffle production (Andrino et al., 2019). Marqués-Gálvez, Miyauchi, et al. (2020) reported a switch in the phenology of *H. almeriense* × *T. claveryi* mycorrhizal plants during the spring–summer transition, namely, a sigmoidal relationship between stomatal conductance and VPD, which was correlated with total truffle production; that is, truffle yield was observed to decrease in years with early summers and early VPD threshold. This indicates that the VPD–stomatal conductance relationship can be used as a marker for truffle production and, together with VPD control, be a tool for desert truffle production management (Marqués-Gálvez, Miyauchi, et al., 2020).

Climate changes are predicted to lead to future increases in temperature and decreases in precipitation and relative humidity in Mediterranean regions (Dubrovský et al., 2014), which would result in lower VPD (Andrino et al., 2019). Future decreases in truffle production due to climate changes may therefore arise. Climate changes are also predicted to lead to increased atmospheric CO_2 concentrations. Because high CO_2 concentrations induce partial stomatal closure, decreasing water loss by transpiration (Lindner et al., 2010), it is important to understand how this increase can affect ECMF. For example, high atmospheric CO_2 concentrations coupled with drought and high VPD (water stress) were observed to improve net C assimilation and water use efficiency in *H. almeriense* × *T. claveryi* and lead to increased flowering events (Marqués-Gálvez, Navarro-Ródenas, et al., 2020).

Andrino et al. (2019) showed that the production of *T. claveryi* is conditioned by many climatic factors, leading to production fluctuations that directly affect the final product yields and economic revenue. So future management practices for desert truffle production should consider these and other questions related to climate change effects.

Desert truffle life strategies may also be important for their cultivation. For example, *Terfezia* species were recently found to be heterothallic; that is, they have two mating-type idiomorphs (MAT1-1 and MAT1-2), and only strains with differing MAT are sexually compatible (Marqués-Gálvez, Miyauchi, et al., 2020; Martin et al., 2010). However, in *T. borchii*, which is also heterothallic, strains with the same matting type were found to produce truffles (Iotti et al., 2016). Therefore, improved knowledge of fungal life cycles and reproduction is needed to master their cultivation.

A better understanding of the effects of soil type and rhizosphere bacteria on plants mycorrhizal with desert truffles can also be essential to develop novel techniques to improve plant fitness and survival and mycorrhizal establishment (Navarro-Ródenas et al., 2016).

3.1 | Terfezia truffles as functional foods and new applications

Desert truffles are considered functional foods because of their high protein (20% of dry weight) and carbohydrate contents. They also have high fibre and lipid contents (Ahmed et al., 1981; Hamza et al., 2016; Kıvrak, 2015; Tejedor-Calvo et al., 2020). *Terfezia* species are rich in saturated (Tejedor-Calvo et al., 2020), monosaturated and polyunsaturated fatty acids, namely oleic and linoleic acids (Murcia et al., 2003; Tejedor-Calvo et al., 2020). They have an interesting aromatic profile and flavour. Several volatile compounds have been identified (e.g., 1-octen-3-ol; hexanal, 2-octenal; Kamle et al., 2017), especially in *Tuber* species (Mauriello et al., 2004; Splivallo et al., 2011).

Among the most interesting properties of *Terfezia* species are their antioxidant (Dahham et al., 2018; Dundar et al., 2012), enzymatic (Benaceur et al., 2020; Pérez-Gilabert et al., 2005, 2014), antibiotic (Harir et al., 2019; Janakat et al., 2004, 2005; Neggaz et al., 2018), anti-proliferative and anti-cancer activities (Table S3) (Al Obaydi et al., 2020; Dahham et al., 2018; Tejedor-Calvo et al., 2020). Several species of *Terfezia* produce common food antioxidants, such as tocopherol (α and δ), butylated hydroxyanisole (BHA), butylated hydroxytoluene (BHT) and propyl gallate (Martínez-Tomé et al., 2014; Tejedor-Calvo et al., 2020). They also have an advantage over other food products since preservation and freezing do not affect their properties (Martínez-Tomé et al., 2014; Murcia et al., 2003). Their addition can improve food nutritional quality and antioxidant activity, allowing its consumption at any time of the year (Gadallah & Ashoush, 2016). Their nutritional and aromatic profile together with their biological activities make them a potential resource for new plant-based meat products, as can be seen by the number of patents involving *Terfezia* species. Their proprieties also make them an important resource for cosmetic and pharmaceutical industries.

3.2 | Socioeconomic relevance

Terfezia truffles are a natural resource with promising cultural and economic potential. Their cultivation can be a source of revenue for rural populations through truffle commercialisation or mycotourism (truffle hunting) and other leisure and well-being activities (Honrubia et al., 2014; Serra et al., 2017). Furthermore, their cultivation is sustainable and can be combined with other agroforestry activities (Morte et al., 2009), similarly to true truffle (Tuber spp.) production (Sourzat, 2020). Because of their ability to grow in dry environments, *Terfezia* species can be potentially cultivated in new areas as climate changes progress, as predicted for *Tuber* species (Čejka et al., 2020). They can also be a solution to rehabilitate unproductive or disturbed lands, since they can decrease soil erosion and promote soil biological activity (Morte et al., 2008).

Consortia of stakeholders with different expertise, namely, producers, technological developers, research institutions and restaurateurs, such as the Asociación Española de Turmicultura2017 (https://trufadeldesierto.com/), have started to promote cultivation and consumption of desert truffles. However, to ensure rural development, the ecosystem management must follow three fundamental principles: (i) production through the exploitation of endogenous natural resources; (ii) conservation by pursuing sustainable criteria and (iii) taking into account local biodiversity and multifunctionality (Honrubia et al., 2014).

Terfezia is therefore an important sustainable crop that profits from the sustainable exploitation of endogenous resources and simultaneously contributes to environmental awareness and climate change mitigation.

4 | IMPORTANCE OF ECMF WITHIN EUROPEAN POLICIES

European rural areas have suffered from land abandonment during the latter 20th century, with environmental, socioeconomic and landscape repercussions (Lasanta et al., 2017), such as loss of traditional knowledge and changes in land-use patterns (Hummel & Smith, 2017).

Sporocarps have been in the past and still are in certain European regions, an essential resource in rural areas, providing food, medicines and substantial income to some rural families and small companies, and are part of an increasing economic and cultural interest in the use of non-timber forest products (Miina et al., 2020). Creating new sustainable methodologies that value these endogenous resources can bring economic value to rural populations and be a strategy for sustainability, ecosystem conservation and decreasing the exodus from rural areas (Martínez-Ibarra et al., 2019; Serra et al., 2017). These activities are supported by national and European policies and financial strategies integrated into the European agricultural fund for rural development (European Commission, 2021), created by the European Union as a Common Agriculture Policy (CAP) funding instrument to support rural development strategies and projects. Sporocarp-related economic activities fit into the priorities of this fund because of their environmental, economic and social aspects. The impacts of *Terfezia* truffle sustainable cultivation (Figure 2) illustrate how sporocarps can contribute to achieving the European Green Deal (EGD) aim of climate neutrality by 2050 (European Commission, 2019). Plantations of *Terfezia claveryi* can reach a production of 400 kg/ha per year, while natural areas only produce between 50 and 170 kg/ha (Oliach et al., 2020). The low production rates in natural areas are mainly due to climate change disturbances, such as low precipitation, and anthropogenic factors. The implementation of measures that promote sustainable production is crucial to mitigate climate change and loss of biodiversity and optimising the cultivation of these species and maintaining natural production. Investing in R&D will contribute to the development of nature-based solutions and new sustainable production techniques, which are crucial tools for rural development and the EGD goals.

4.1 | Within European Green Deal strategies

The European Union (EU) recently developed new efforts to meet the goals defined in the 2015 Paris Agreement (United Nations, 2015a) and the United Nations 2030 Agenda for Sustainable Development (United Nations, 2015b), adopting a robust agenda, the European Green Deal (EGD) (European Commission, 2019). These measures meet the current public demands derived from increased awareness of environmental questions, mostly those concerning climate change, natural disturbances, biodiversity loss and human welfare implications (Fisher, 2019).

Currently, the legislation within the EU regarding wild and edible ECM sporocarps is still scarce, and only a few EU member countries have lists or guidelines of edible sporocarps authorised for trade (Peintner et al., 2013). Moreover, there is a lack of uniformity between EU and country levels regarding (i) legislation for trade and food safety; (ii) management and conservation; (iii) creation of protected zones and a list of protected species and (iv) specific areas and authorisations for collecting and harvesting, among others. Supportive legislation and regulation of activities are essential to support rural development, namely, small businesses, farmers and forest owners. Moreover, understanding how economic activities associated with ECMF cultivation meet the EGD strategies and contribute to sustainable rural development is essential.

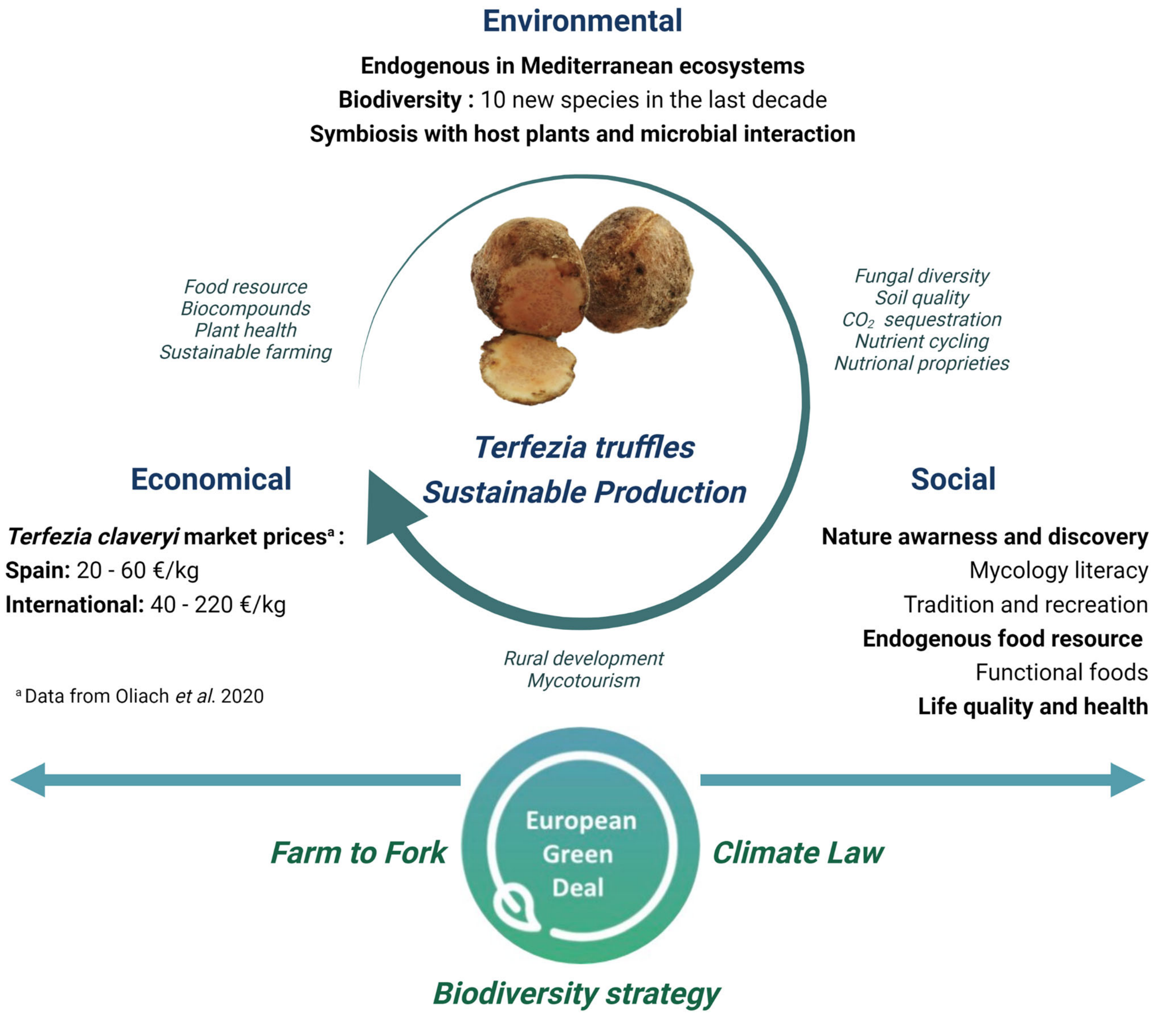

FIGURE 2 Conceptual model for the sustainable cultivation and exploitation of Terfezia truffles and how this can contribute to the European Green Deal goals (green text) and strategies (blue arrows). Created with BioRender.Com

The EGD agenda aims to reinforce Europe's resilience by halting biodiversity loss and building a healthy and sustainable food system. To achieve these goals, the EU presented a bold package of measures within the Biodiversity Strategy 2030, the Farm to Fork and the European Climate Law (European Commission, 2019), which include actions that directly affect edible ECMF cultivation and conservation. Several aspects of ECMF cultivation and their ecological and socioeconomic importance are mentioned in these documents, showing how ECMF can contribute to the EGD goals. The Farm to Fork and Biodiversity strategies mutually reinforce and bring together nature, farmers, businesses and consumers to work towards a sustainable future (European Commission, 2020a). With the new Biodiversity Strategy, the European Commission aims to bring nature back into our lives (European Commission, 2020b). ECMF can play an important role in this awareness. As already stated, several species can adapt to a range of edaphoclimatic environments or locations. Many have high economic value and represent important seasonal goods and services for many rural communities (see Table 1 and Figure 2), for example, mycotourism represents an average income of 32 million euros per year in the Spanish region of in Castilla y Léon (Bonet et al., 2014; Buntgen et al., 2017; Martínez-Ibarra et al., 2019; Oliach et al., 2020; Tahvanainen et al., 2016). Their diversity brings various opportunities in terms of different food, pharmaceutical and health applications, and production flexibility and is critical to developing cultural, recreational and mycotourism activities.

Implementing support from European funds to develop *Terfezia* and other ECMF production will improve the quality of life of rural populations in Europe and contribute to their sustainable exploitation.

On the other hand, ECMF contributes to halting biodiversity loss. Moreover, their role in improving plant health and soil quality, leading to decreased nutrient losses and increased CO2 sequestration, directly affects the production of healthy and environmentally friendly food, the Farm to Fork strategy (European Commission, 2020c).

Their recognised nutritional value and importance as a source of biocompounds with industrial applications make them a strategic product directly impacting rural development by creating new revenue sources. All these contributions meet objectives of the Farm to Fork strategy, such as (i) ensure food security, nutrition and public health; (ii) mitigate climate change and adapt to its impacts; (iii) preserve the affordability of food while generating fairer economic returns and (iv) ensure food security, nutrition and public health (European Commission, 2020c). ECMF cultivation and exploitation will therefore play an important role in future food production (Farm to Fork strategy), environmental protection (EU Biodiversity strategy for 2030) and climate change (Climate Law).

5 | CONCLUSIONS

ECMF cultivation evolved in recent decades due to technological development and increased research. Cultivation of species of high economic value, such as truffles, has contributed to this evolution. Understanding the factors that affect their production, such as forest management, is crucial to efficient and sustainable production. The development of research and discovery of new species with productive potential also bring new business opportunities.

ECMF are inextricably linked to forestry and agricultural activities, which are associated with rural areas. Developing new production techniques and business models and creating support to promote ECMF production is increasingly more important for the development of rural communities. Notably, the activities associated with ECM sporocarp production are in line with the guidelines of the EGD and related European policies, which aim at a more sustainable Europe, value its endogenous natural resources and empower rural communities.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

IF wrote the manuscript with AC. CC supervised the project. All authors contributed to editing the final paper.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the supporting information.

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