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BRIEF REPORT

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The importance of botanic gardens for global change research—New insights into Cambridge's hidden truffle kingdom

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Social Impact Statement

Botanic gardens offer unique opportunities for unravelling responses of plant life to climate change. Despite investigations into their aboveground sphere, the belowground realm is usually neglected. Cambridge University Botanic Garden now illuminates the hidden world of one of the most sought-after culinary delicacies—the Burgundy truffle. The garden's plant diversity, the serendipity of a truffle dog, and our curiosity-driven research agenda reveal insights into 278 truffle fruitbodies that grew symbiotically with an unusually high number of host species. Our study reinforces the power of botanic gardens to disentangle ecosystem processes and emphasizes the proximity of scientific and public interests in truffles.

KEYWORDS

Cambridge University Botanic Garden, climate change, ectomycorrhizal fungi, fungi-host interaction, John S. Henslow, mushrooms, symbiotic plant species, truffle dogs

1 | INTRODUCTION

As ambassadors for our ecosystems, botanic gardens not only offer plant conservation, knowledge exchange, and public engagement but also provide unique living laboratories for understanding biological and ecological responses to global climate change. The belowground cosmos of plant life, soil organisms, and fungi-host interactions is, however, rarely considered in the thriving research portfolios of botanic gardens around the world.

Like many botanic gardens, Cambridge University Botanic Garden (CUBG) has fostered a unique research and teaching platform for plant science and horticulture since its foundation in 1846

(Glover, 2022). With a total of 8061 vascular plant species across 40 acres, CUBG is ideally situated for addressing biological and ecological questions within the emerging arenas of global climate change and biodiversity research. The long-term dedication of CUBG to facilitate plant science follows the main motivation of its founder J.S. Henslow (Kohn et al., 2005), who was a physical scientist before becoming a pioneering botanist and Charles Darwin's mentor. Yet, the garden's belowground sphere has been broadly neglected. Only a few recordings of soil microorganisms as well as mycological investigations into the phenology, productivity, and diversity of fungi species and their symbiotic host interactions exist.

Amongst the most exclusive gourmet foods worldwide (Hall et al., 2003), fruitbodies of the Burgundy truffle (*Tuber aestivum* Vittad.) exceeded 1500 Euro per kilogram in winter 2022/23 (https://www.tartufo.com/en/truffle-prices/). Burgundy truffles can be harvested throughout most of the year and across much of Europe where pH levels of alkaline topsoil range from around 6.5–8.5 (Stobbe, Egli, et al., 2013). Notwithstanding a long history of human consumption and scientific investigation, the belowground lifecycle and complex host association of this ectomycorrhizal ascomycete remain largely uncertain (Büntgen et al., 2017; Büntgen & Egli, 2014; Moser et al., 2017; Stobbe, Stobbe, et al., 2013). A better understanding of the extent of possible symbiotic plant species is, however, needed to allow farmers to prepare their plantations for a projected warmer and drier climate (IPCC, 2021), in which the intensity and frequency of weather extremes is expected to increase (Olonscheck et al., 2021), species move northward (Čejka et al., 2020), habitats become vulnerable (Büntgen et al., 2022), and certain tree species are likely to suffer more than others (Vitali et al., 2017).

Here, we capitalize on the huge diversity of plant species in CUBG and present insights from the Garden's first truffle project. Based on a semisystematic survey, we assess the fruiting behaviour and host range of a highly prized hypogeous ectomycorrhizal fungus. We then discuss limitations of our approach and outline how botanic gardens may contribute to answer pending questions in truffle research, and more generally help to understand how biological and ecological systems are affected by climate change, an important task that has been proposed for the fungal kingdom recently (Andrew et al., 2017).

2 | DATA AND METHODS

Located in the east of England, about 100 km north of London around 52°11′ N, 00°07′ E, and 6 m asl (Figure 1a), CUBG comprises 8061 tree, shrub, and herbaceous species within a well-managed parkland area of 16 ha (Figure 1b). The circa 2000 tree species, for which ages often exceed 150 years and provenance is usually known (Glover, 2022), are growing in taxonomically defined sections. Hence, the garden is structured into spatial units of Aceraceae, Betulaceae, Fagaceae, Fabaceae, Magnoliaceae, Moraceae, Oleaceae, Sapindaceae, Tiliaceae, and Ulmaceae. The garden's fertile soil with pH > 7 is influenced by alkaline gravel, and Cambridge's oceanic climate exhibits annual precipitation totals of ∼560 mm (with declining tendency over the past decade). The coldest months are December and January with average minimum and maximum temperatures around 2.0°C and 7.8°C (https://www.metoffice.gov.uk/). The warmest months are July and August with average minimum and maximum temperatures around 12.6°C and 22.9°C (with increasing tendency over the past decade).

Truffles were harvested by an experienced scent-detection dog, a Beagle, from September 2017 to March 2018 (Figure 1c,d), and again from August 2019 to January 2020. Hunting during the first period was performed one to three times per month, whereas hunts of the second phase took place on two consecutive days every 2 weeks (Čejka, Thomas, et al., 2022). Each hunt lasted around 2–3 h along the same pathway across the entire garden. Once the Beagle indicated presence of a truffle, the fruitbody was excavated, placed in a paper bag, and subsequently analysed in the laboratory (Figure 1e). Date, location, weight, ripeness, and potential host tree were recorded for each fruitbody (following protocols introduced by Büntgen et al., 2017). Importantly, most trees in the garden grow more than 10 m apart from each other, and solitary specimens without a crown overlap facilitate the assignment of their symbiotic truffle fruitbodies. Soil depth and distance from potential host tree were added for each truffle during the second hunting period. Fruitbody production was expressed as day of the year, where 1 DOY corresponds to 1 January and truffle finds after December were simply added. Bivariate scatter plots, Pearson's correlation coefficients, and linear mixed-effects models were used to assess possible relationships between all parameters. Statistical analyses were performed in R 4.0.5, using GGPLOT for visualization and NLME for linear mixed-effects models.

3 | RESULTS AND DISCUSSION

Biweekly truffle hunts with a scent-detection dog between September 2017 and January 2020 revealed a total of 278 Burgundy truffles in CUBG (Figure 2a). Harvests of the first and second hunting periods resulted in 177 and 101 fruitbodies, respectively. Mean (median) fruitbody weight was 13.9 (8.9) g, with individual truffles ranging from 0.5–98.8 g (standard deviation of 14.9). The individual truffle fruitbodies most likely formed symbiotic relationships with at least 19 different tree species, including hosts from six genera (*Betula*, *Carpinus*, *Corylus*, *Fagus*, *Ostrya*, and *Quercus*) and two families (Fagaceae and Betulaceae). The most productive genus was *Corylus* with 96 fruitbodies, followed by *Quercus* and *Fagus* with 84 and 57 fruitbodies, respectively. *Betula*, *Carpinus*, and *Ostrya* were only associated with five, 17, and 19 truffles. The most productive symbiotic partner was an evergreen *Quercus ilex* that produced 23 and 32 truffles in the first and second hunting period. A *Corylus colurna* and a large *Fagus sylvatica* 'Miltonensis' were associated with 47 and 39 fruitbodies (Figures 1b–d and 2). These trees also hosted the largest truffle specimens of 100 g (*C. colurna*), 90 g (*Q. ilex*), and 60 g (*F. sylvatica*). Most truffles were ripe with ochre to dark brown gleba

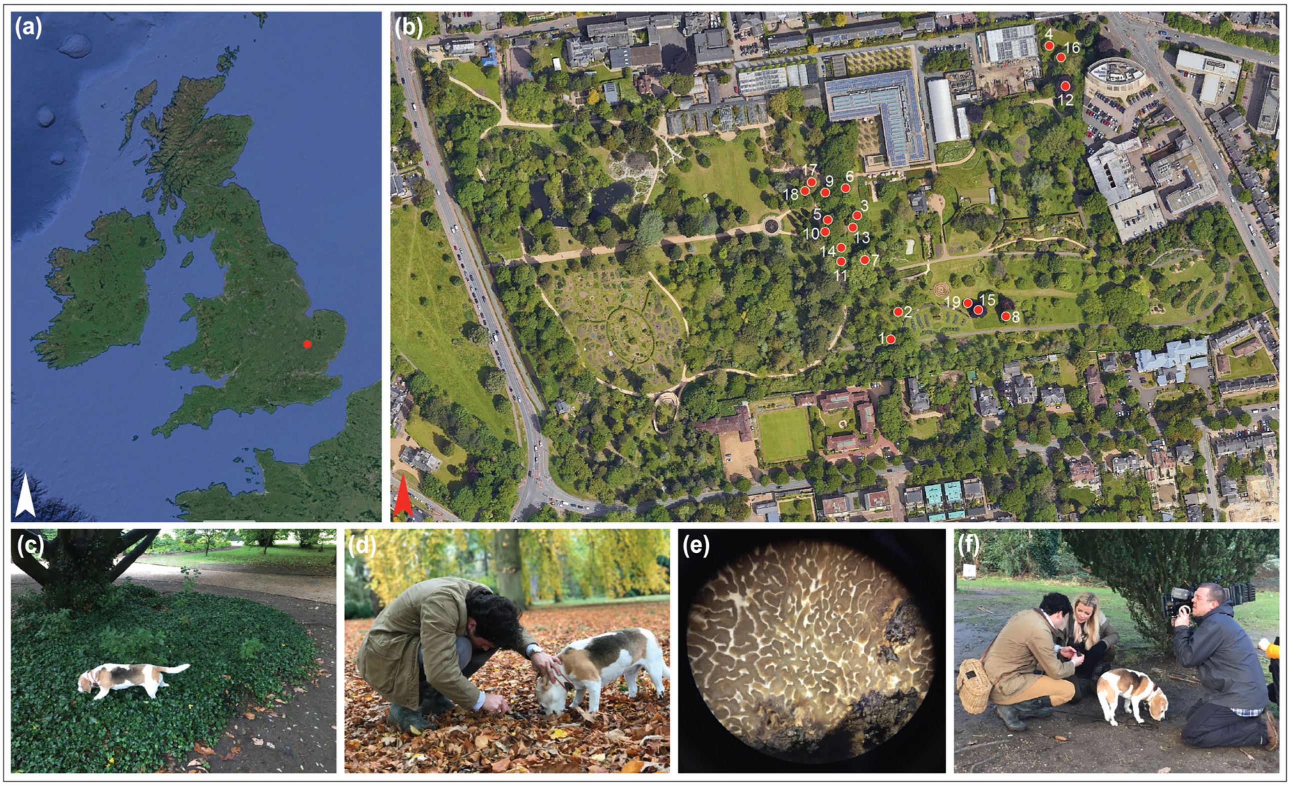

FIGURE 1 (a) Location of Cambridge in the south-east of England, circa 100 km north of London (52°11′ N, 00°07′ E, and 6 m asl). (b) Cambridge University Botanic Garden (CUBG) comprising 8061 vascular plant species across 40 acres, with red dots indicating the location of 19 potential truffle host trees (1 = *Betula pubescens*, 2 = *Betula papyrifera*, 3 = *Carpinus betulus*, 4 = *Carpinus caroliana*, 5 = *Corylus avel. Heterophilla*, 6 = *Corylus avellana* T1, 7 = *Corylus avellana* T2, 8 = *Corylus colurna* T1, 9 = *Corylus colurna* T2, 10 = *Corylus maxima* (*var. purpurea*), 11 = *Ostrya carpinifolia*, 12 = *Fagus sylvatica f. purpurea* T1, 13 = *Fagus sylvatica*, 14 = *Fagus sylvatica Miltonensis*, 15 = *Fagus sylvatica f. purpurea* T2, 16 = *Fagus sylvatica f. laciniata*, 17 = *Quercus ilex*, 18 = *Quercus rosacea*, and 19 = *Quercus trojana*). (c,d) Truffle hunt in CUBG under a very productive evergreen *Quercus ilex* (17) and near a large *Fagus sylvatica* 'Miltonensis' (14). (e) Microscopic magnification of the ripe gleba of an aromatic Burgundy truffle (*Tuber aestivum*) excavated in CUBG in January 2018. (f) Truffle hunt and film production for a BBC Countryfile documentary on CUBG's first truffle project in January 2018, which describes a prominent example of public engagement that can be achieved at the crossroads of innovative research, botanic gardens, and environmental challenges

and well-structured spores (Figures 1e and 2). Only a few fruitbodies were classified as overripe with soft and partly rotten gleba. All truffles were located within the upper 10 cm of organic and mineral soil and at an average distance of 4 m from their host trees (Figure 2a). Weight and ripeness ($df = 150$, $F = 5.86$, p value $= 0.0167$), as well as soil depth and weight ($df = 54$, $F = 5.77$, p value $= 0.0198$), were significantly correlated; that is, larger truffles were riper and grew deeper in the soil. Fruitbodies were found from mid-August to late-March.

Although we are confident in attributing the individual truffle fruitbodies to solitary trees, molecular evidence would be needed to confirm the ectomycorrhizal status of host plants. The observed range of potential host partners includes Mediterranean evergreen or semi-evergreen species like *Q. ilex* and *Quercus trojana*, as well as many broadleaf trees abundant in the temperate zones of Eurasia, such as *Betula pubescens*. Native to Europe and Asia are *F. sylvatica*, *Carpinus betulus*, *C. colurna*, and *Ostrya carpinifolia*, whereas *Betula papyrifera* is native to North America. All species are known to form ectomycorrhiza and some of them have been described as symbiotic partners for different truffle species (Chevalier et al., 2002; Craddock, 1992; Csorbainé, 2011; Gryndler, 2016). However, to our knowledge, *Carpinus caroliana*, *Corylus maxima*, and *Quercus rosacea* have never been directly associated with Burgundy truffles.

Although truffle cultivation has become a global endeavour, it still centres on a small number of host species amongst *Quercus* and *Corylus*. Expanding the range of symbiotic partners used in both truffle cultivation and experimentation may not only lead to better modes of fruitbody production but also affords a degree of resilience in a world where a rapidly changing climate along with increasing pests and diseases present multiple and accelerating challenges (Čejka, Isaac, et al., 2022; Thomas & Büntgen, 2019). Botanic gardens, therefore, provide an ideal environment in which to explore such interactions further.

In addition to the ecological and mycological insights this study provides, innovative research in CUBG offers new opportunities to attract a wide public fascinated by and concerned about the environment we live in. Disseminated through talks and broadcasted prominently (Figure 1f), our truffle project is an exemplar for science communication combining innovative research, botanic garden collections, and environmental challenges. Moreover, we are confident that our findings are relevant for a new generation of

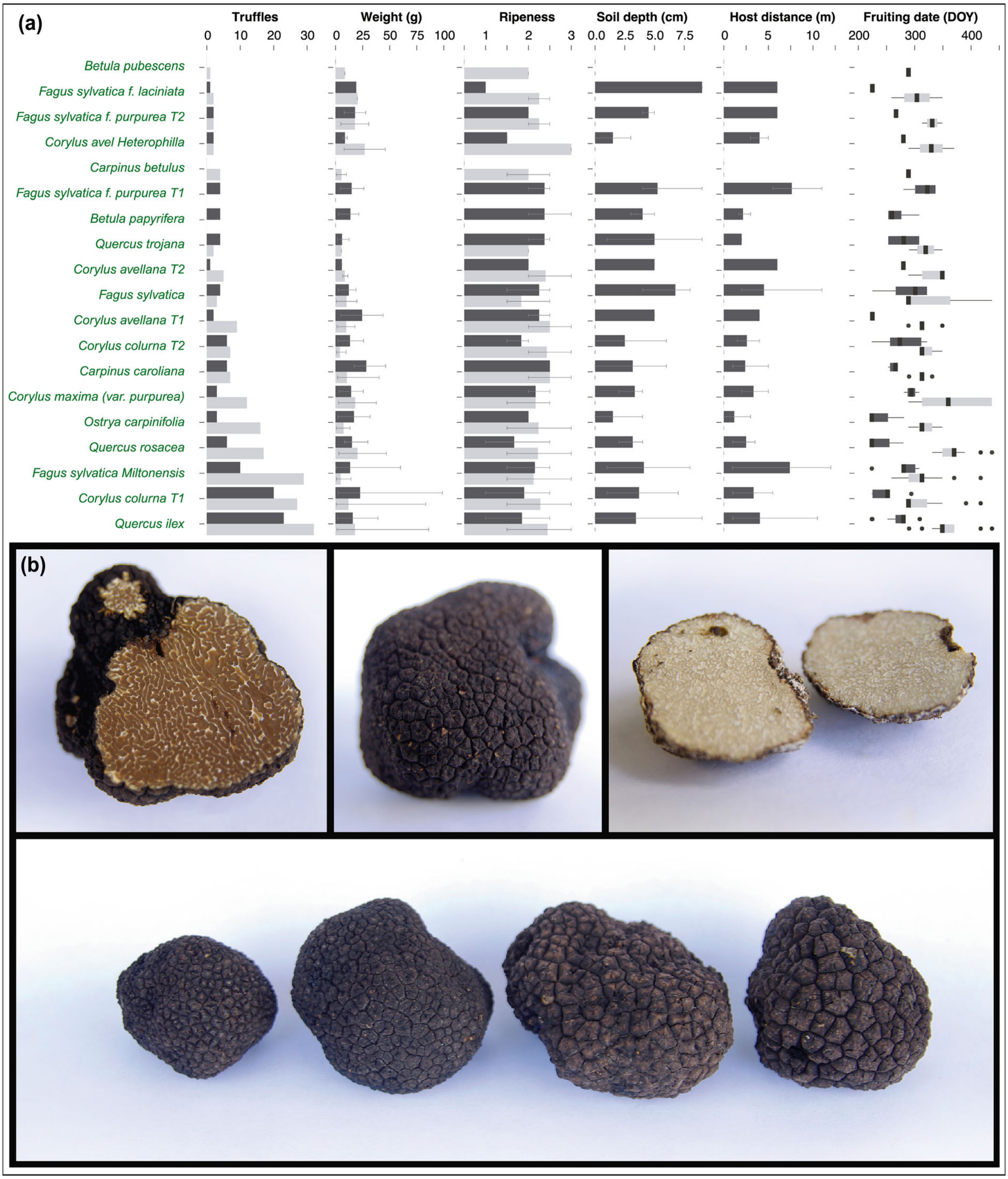

FIGURE 2 (a) Characteristics of 278 Burgundy truffles (*Tuber aestivum*) harvested in Cambridge University Botanic Garden (CUBG). Light (dark) grey bars refer to the first (second) hunting period from Sep 2017 to Mar 2018 (Aug 2019 to Jan 2020). First column shows the total number of truffles found under each tree, followed by the weight, ripeness, soil depth, host distance, and fruiting date. Bars and whiskers show mean values and minimum–maximum ranges, respectively. Boxplots show interquartile ranges, with bars and points referring to minimum–maximum ranges and outliers, respectively. (b) Examples of truffle fruitbodies, including ripe and unripe specimens (upper left and right images), and different seizes, weights, and surface structures (bottom images)

truffle farmers in the United Kingdom and elsewhere, who may need to plant a variety of hosts for their plantations to adapt to a warmer and drier climate. Given the wide range of tree species that potentially form symbiotic relationships with Burgundy truffles (Figure 2) and reported evidence that mixed forest stands are more resilient to climate change (Vitali et al., 2017), there is little argument for monocultural truffle plantations. In fact, mixed species plantations are likely to produce a higher quality and quantity of truffles under the predicted increase in the intensity and frequency of both spring frosts and summer heatwaves (Olonscheck et al., 2021). In this regard, and in line with much of central Europe (Büntgen, Urban, et al., 2021), we cannot ignore that southeast England experienced a cluster of severe summer droughts since 2016 (Turner et al., 2021). The world's longest meteorological record, the Central England Temperature series, shows that recent anthropogenic warming is unprecedented in the past three and a half centuries, and that this trend not only affects the UK's plant phenology (Büntgen et al., 2022), but likely also impacts fungi-host interactions (Büntgen & Egli, 2014).

4 | CONCLUSION AND OUTLOOK

The plant diversity and biogeographic setting of CUBG, the serendipity of an experienced truffle dog, and a curiosity-driven research agenda revealed the location, maturation, and host association of 278 truffles. The ectomycorrhiza fruitbodies of one of the most highly prized and sought-after culinary delicacies had a mean weight of 14 g, grew exclusively in the upper soil layer, and likely formed symbiotic relationships with at least 19 different host species from six genera: *Betula*, *Carpinus*, *Corylus*, *Fagus*, *Ostrya*, and *Quercus*. An evergreen *Q. ilex*, a *C. colurna*, and a large weeping *F. sylvatica* 'Miltonensis' produced most truffles: 55, 47, and 39, respectively. Our eco-physiological findings not only engaged a wide public through seminars, lectures, talks, and documentary filming but also offer guidance for truffle farmers to adapt their plantations for projected climate change. Further data collection and processing should consider fine-scale eco-archaeological excavation and genetic exploration to address how populations of the Burgundy truffle are moving across CUBG and from where they originate (Büntgen, Peter, et al., 2021; Molinier et al., 2016; Staubli et al., 2022). An additional focus should be on the detection and description of morphological differences between forms and varieties of fruitbodies that possibly present physiologically based intraspecific variation and responses to abiotic factors.

Continuing the intellectual voyage of J.S. Henslow that started almost 200 years ago in Cambridge, our study provides new eco-mycological insights, offers opportunities to attract a wide public fascinated by and concerned about our environment, and suggests that truffle farmers may have to plant a variety of host plants to adapt their plantations for a warmer and drier climate. Along these lines, we are convinced that the network of botanic gardens around the world should play a more prominent role in protecting biodiversity and understanding biological and ecological responses to climate change—past, present, and future. Innovative research may range from a local to global scale, in which either individual gardens, or network initiatives, facilitate the assessment of the impact of anthropogenic climate change. In their function as living scientific laboratories, botanic gardens provide controlled environmental settings for experimental approaches that cannot be found elsewhere.

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CONFLICT OF INTEREST

The authors declare no competing interests.

AUTHOR CONTRIBUTIONS

Ulf Büntgen conceived the study and wrote the paper together with Giada Centenaro and valuable input from Beverley J. Glover, Alma Piermattei, Paul W. Thomas, and Tomáš Čejka. Giada Centenaro performed the analyses under the supervision of Ulf Büntgen. All authors contributed to discussion and interpretation, and Ulf Büntgen revised the manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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