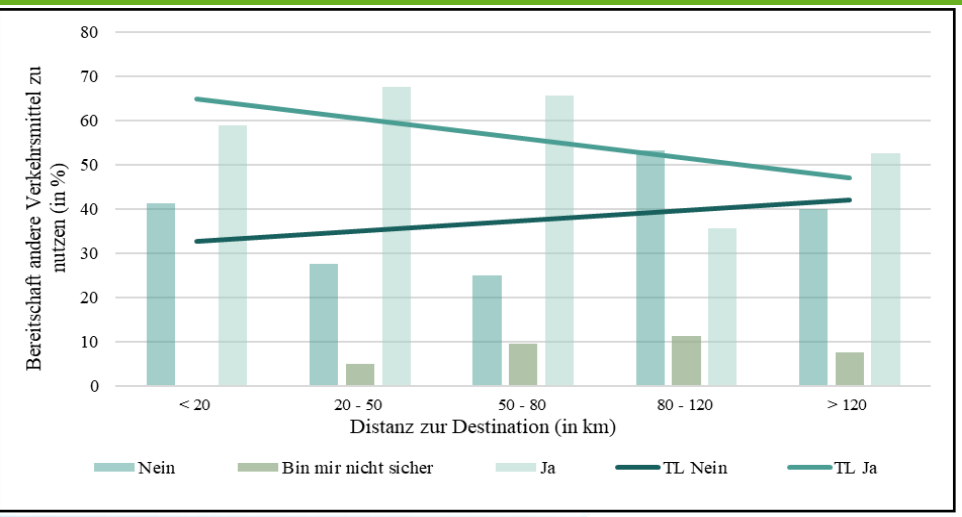

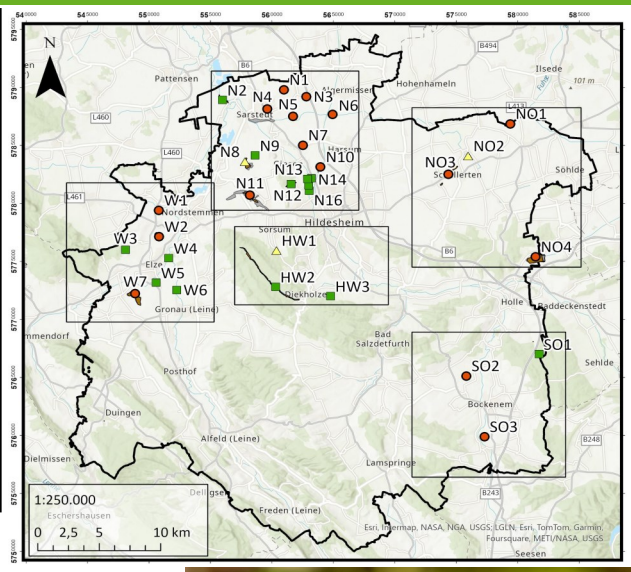

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Influence of Geoecological Factors on Burgundy Truffle (*Tuber aestivum var. uncinatum*) Habitat in the Transition between the German Central Low Lands and Mid-Mountain Range.

Einfluss geoökologischer Faktoren auf den Lebensraum der Burgundertrüffel (Tuber aestivum var. uncinatum) am Übergang von der Norddeutschen Tiefebene zum deutschen Mittelgebirgsraum.

Andres Stucke

Abstract

This study investigates the geoecological factors affecting the habitat, distribution, and productivity of Burgundy Truffles (*Tuber aestivum var. uncinatum*) in the German Mid-Mountain Range, particularly near Hildesheim, using a systematic literature review based on the PRISMA protocol to gather data on soil properties, host trees, and favourable climatic conditions. Findings indicate that calcareous soils with high pH and calcium carbonate content are optimal for truffle growth. The presence of specific host trees, such as oaks and hazels, combined with adequate soil moisture and temperature, is crucial for truffle development. Considering potential climate change impacts, the study underscores the importance of adapted soil management and environmental strategies to enhance sustainable truffle production in Central Europe.

Keywords: Burgundy truffle, *Tuber aestivum var. uncinatum*, truffle habitats, truffle distribution and dispersal, Central Europe

Zusammenfassung

Diese Studie untersucht die geoökologischen Faktoren, die den Lebensraum, die Verbreitung und die Produktivität von Burgundertrüffeln (*Tuber aestivum var. uncinatum*) im deutschen Mittelgebirge, insbesondere nahe Hildesheim, beeinflussen. Dabei wird eine systematische Literaturrecherche nach dem PRISMA-Protokoll verwendet, um Daten zu Bodenbeschaffenheit, Wirtspflanzen und günstigen klimatischen Bedingungen zu sammeln. Die Ergebnisse zeigen, dass kalkhaltige Böden mit hohem pH-Wert und Kalziumkarbonatgehalt optimal für das Trüffelwachstum sind. Das Vorhandensein spezifischer Wirtspflanzen wie Eichen und Haselnüsse, kombiniert mit ausreichender Bodenfeuchtigkeit und Temperatur, ist entscheidend für die Trüffelentwicklung. Angesichts potenzieller Klimawandelauswirkungen betont die Studie die Bedeutung angepasster Bodenbewirtschaftung und Umweltstrategien zur Förderung einer nachhaltigen Trüffelproduktion in Mitteleuropa.

Schlüsselwörter: Burgunder Trüffel, *Tuber aestivum var. uncinatum*, Trüffelhabitate, Trüffelverbreitung, Mitteleuropa

1. Introduction

Truffles, highly valued fungi that belong to the genus *Tuber* and the phylum Ascomycota, are not just gastronomically important but also ecologically significant. These fungi, known for their distinctive aroma, form symbiotic relationships with the roots of certain trees and shrubs, a type of relationship known as ectomycorrhizal symbiosis (Thomas et al. 2019). This mutualistic interaction plays a crucial role in the health and diversity of forest ecosystems. There are various species of truffles, with some of the most notable being the black truffle (*Tuber melanosporum*), the white truffle (*Tuber magnatum*), and the Burgundy truffle (*Tuber aestivum syn. uncinatum*). These species are primarily found in Europe, with different species thriving in different ecological niches (Bertault et al. 1998). The natural production of truffles has decreased over time, leading to increased interest in truffle cultivation as an agricultural alternative (Şen 2022).

The Burgundy truffle, a widely distributed truffle species in Europe (see Fig. 1), is not just a culinary delight but also a key player in the ecosystem. Renowned for its mild aroma and subtle flavour, it's a truffle that fascinates people. Burgundy truffles thrive in calcareous soils and are typically found from May to December, sometimes until March. They form symbiotic relationships with various tree species, including oaks (*Quercus spp.*), hazels (*Corylus spp.*), and European beeches (*Fagus sylvatica*) (Stobbe et al. 2013; Steidinger et al. 2022; Hilszczańska et al. 2018). For a long time, *T. aestivum* and *T. uncinatum* were considered separate species. However, genetic studies have shown that they are identical. The differences in colour and aroma (with *T. uncinatum* being darker and more intense in aroma) are likely influenced by environmental factors and climatic conditions (Molinier et al. 2013; Paolocci et al. 2004). This highlights the intricate balance of nature and the importance of preserving these unique ecosystems. Beyond truffles, Europe harbors *Elaphomyces spp.* (deer truffles) and other truffle-like fungi. The one thing they all have in common is that they grow hypogeous, that is, underground.

1.1 Truffle Cultivation in Europe's History and Present

It is expected that the truffle culture originated in France and Italy. However, historical records show that it developed in many European countries at the same time.

Nevertheless, the first known successful attempt to cultivate truffles is generally attributed to the French agronomist Joseph Talon from the Vaucluse department in south-eastern France in the 19th century (Le Tacon et al. 2015). He is credited with the innovation of planting acorns collected under truffle-producing oaks, which led to the establishment of truffle plantations (Novak 2015). Therville et al. (2013) report that truffle plantations have been established in southwestern France (Périgord) and south-eastern France (mainly Vaucluse and Drôme) since the mid-19th century.

Truffles have been known in Poland since at least the 17th century. Stanislaw Czerniecki published the first Polish cookbook with truffle recipes in 1682. Truffles were popular among the Polish nobility and used in various dishes. The Polish scientist Count Michał Jan Borch contributed to the understanding of truffles, and the whitish truffle (*Tuber borchii*) is named after him (Rosa-Gruszecka et al. 2017).

The use of truffles in Poland declined after World War II due to social and economic changes, including the impact of Soviet communist control. However, the 21st century has seen a renaissance in truffle cultivation and interest in Poland, with the establishment of truffle orchards and renewed research efforts (Rosa-Gruszecka et al. 2017). The situation is similar in Germany. Studies about the establishment of truffle orchards in Germany and Poland have been known since the 19th century (Stobbe et al. 2012). Hesse (1891) writes about the location of *T.r aestivum* in Germany (translation in English):

> *"Within the curved humus, interspersed with thin tree roots and mixed with many limestone fragments, or even in the massive depths of calcareous soil covered with little humus but a lot of leaf litter, or also in boggy, sandy loam, deep alluvial loam, and silt soil under the shade of oaks (including cork oaks), beech trees (including hornbeam), ash trees, hazel trees, less often aspen, elder, maple, and even more rarely pines, the summer truffle finds its resting place. Although it generally avoids daylight, it is also occasionally found epigeous[1], i.e., with its apex protruding above the soil surface, especially when it occurs on steep slopes in scree or within so-called silt soil. Very often, Tuber excavatum Vitt., "the wood truffle," appears in its company, sometimes residing in the same nest; much less frequently, one observes in its vicinity the fruiting bodies of Tuber mesentericum Vitt., Tuber rufum Pico, Tuber macrosporum Vitt., Hydnobolites cerebriformis Tul., Balsamia fragiformis Tul., Pachyphloeus melanoxanthus Tul., and Tuber rutilum Hesse.*
>
> *[1] I have so far found 3 fruiting bodies of Tuber aestivum Vitt. epigeously (see Vol. I, p. 36, note)."*

Also, in a negotiation of the Hils-Solling-Forst-Verein (1892) is reported on the occurrence and artificial spread of the truffle. The report states: "Truffles were already sought in ancient times. In Germany, it is especially the administrative district of Hildesheim and a part of the neighbouring Duchy of Brunswick that supply truffles; in any case, they are probably almost the only areas in which truffles are regularly sought." (Hils-Solling-Forst-Verein, 1892, p. 29). It should be noted that the "Duchy of Brunswick" surrounded the administrative district of Hildesheim from northeast to southwest and thus bordered it to the south at this time. The European truffle culture, which thrived until the mid-20th century, was significantly disrupted by the First and Second World Wars. These conflicts caused widespread devastation and economic challenges, leading to a marked decline in truffle cultivation and hunting across Europe (Stobbe et al. 2013; Allen & Bennett 2021; Rosa-Gruszecka et al. 2017).

In the 1970th, a new cultivation approach leads to a new truffle culture in France, Italy, and Spain (Samil et al. 2008). There are also reports of truffle hunts or cultivation trials in many other European countries (Păcurar et al. 2019; Shamekh et al. 2013; Weden et al. 2009). Most cultivated truffles are *T. melanosporum* and *T. aestivum var. uncinatum*.

1.2 Legal Situation

The increasing media attention and culinary events of the last few years have led to a growing interest in autochthonous truffle species in Germany. The developing truffle culture has the potential to enrich Germany's gastronomic landscape. On the other hand, the legal protection of truffles must be considered in the context of nature conservation and the preservation of biodiversity.

As a component of the mycological flora, truffles are an integral part of forest ecosystems. Their mycorrhizal symbioses with trees contribute to forests' vitality and nutrient cycle. This ecological value justifies their inclusion in protective measures regulated in Germany by the Federal Nature Conservation Act (BNatSchG) and state-specific ordinances. The BNatSchG prohibits the wanton damage or destruction of wild plants (§ 39 BNatSchG). In addition, federal states can enact special species protection regulations that also regulate the removal and use of truffles (§ 54 BNatSchG). In principle, *Tuber spp.* are considered a protected species (Annex 1 (to § 1) BArtSchV). This legal framework aims to protect natural truffle populations from exploitation and potential endangerment.

These restrictions do not apply to truffle cultivation on agricultural land. Rather, depending on land use and intensity, the plantations are considered either permanent crops or agroforestry systems.

1.3 The Burgundy Truffle Habitat and Cultivation

The Burgundy truffle shows remarkable ecological adaptability, which explains its wide distribution in Europe (Molinier et al. 2016). This includes geological properties such as the geological substrate, soil and chemical parameters (pH value, Ca^{2+}, $CaCO_3$ content, C/N ratio), soil structure, altitude, forest type and condition, and the presence of specific host trees. These can be used as indicators for truffle grounds, especially when combined with species such as orchids and insects. (Rosa-Gruszecka et al. 2021).

It thrives in soils with varying textures, from sandy to clayey, and a pH value from slightly acidic to strongly alkaline, but prefers calcareous soils (Chevalier & Sourzat 2012; Robin et al. 2016). The content of organic material can vary greatly, but sufficient nutrient availability should be ensured in conjunction with a balanced C/N ratio. A good soil structure with crumb formation is important for optimal aeration and drainage to avoid waterlogging. Climatically, the Burgundy truffle needs sufficient moisture in spring, warm summers with occasional rainfall, and mild, frost-free autumn temperatures for the ripening of the fruiting bodies (Chevalier & Sourzat 2012). The genetic diversity of the *T. aestivum* suggests the presence of ecological types adapted to specific environmental conditions (Molinier et al. 2016), which underlines this truffle species' ecological and genetic variability.

The cultivation of *T. aestivum* involves a combination of advanced techniques and careful environmental management, but it faces several challenges. Successful cultivation can be achieved through artificial mycorrhization and planting oak and hazel trees on suitable soil. This method relies on the symbiotic relationship between the tree roots and the truffle mycelium, which enhances nutrient uptake and growth (Stobbe et al. 2013). Establishing effective tree plantations requires careful monitoring of soil conditions and mycorrhization processes. The long-term sustainability and productivity of such plantations depend on successfully addressing these challenges (Guerin-Laguette 2021). Modern techniques, such as mycelial inoculation, allow for the production of plants adapted to specific climatic and soil conditions, significantly improving the success rate of truffle plantations by ensuring optimal interactions between the fungus and its host plant (Zambonelli et al. 2015).

Soil moisture and temperature are critical factors influencing the monthly variations of *T. aestivum* DNA in the soil. A study conducted in a highly productive truffle orchard highlighted the importance of these parameters for maximizing truffle production. This underscores the need for precise control of soil conditions to ensure sustainable truffle cultivation (Todesco et al. 2019). The soil's pH also plays a crucial role in mycorrhization and truffle growth. An optimal pH of around 7.51 was identified, with suboptimal pH levels leading to reduced mycorrhization. Adjusting the pH within a year can improve mycorrhization rates and support truffle production (Thomas 2013).

Microbial communities in the soil, particularly ectomycorrhizal fungi, significantly impact the productivity of truffle plantations. A study on *Tuber borchii* found that other ectomycorrhizal species like *Tuber maculatum* and *Tomentella coerulea* can influence the plantation's productivity. This competition for soil resources highlights the complex ecological interactions that must be managed for successful truffle cultivation (Ori et al. 2023). Furthermore, the genetic diversity and colonization dynamics of *Tuber melanosporum* in artificial truffle fields revealed that the genetic variation of harvested truffles was not affected by the inoculation source or tree species. This suggests that inoculation has a limited impact on genetic diversity, with other factors, such as climatic conditions and soil parameters, playing more significant roles (Bertault et al. 2001).

1.4 Research Questions

The precise geological, climatic, and biotic factors that determine the habitat of the Burgundy truffle are largely explored in South Europe, e.g., France, Italy, and Spain. Despite its wide distribution in Europe, the Burgundy truffle (*Tuber aestivum syn. uncinatum*) remains understudied in Central and East Europe. Especially in the lower mountain range in Germany, where historical records indicate its presence in the Innerste and Leine low mountain range (Hesse 1891; Hils-Solling-Forst-Verein 1892), there is a lack of current, systematic surveys on its distribution and detailed investigations into the specific site factors that influence its occurrence and productivity. Furthermore, climate change's effects on this truffle species' distribution and productivity are poorly understood. However, this knowledge is crucial for sustainable management and the protection of natural populations.

The aim of this study is to systematically record and critically evaluate the existing scientific knowledge on the habitat preferences of the Burgundy truffle in complete Europe by means of a systematic literature review according to the PRISMA protocol (Page et al. 2020) and find implications for the German low mountain range, with a focus on the Innerste and Leine Uplands. Therefore, the following research questions were developed:

- Which geological, climatic, and biotic factors influence the occurrence and productivity of the Burgundy truffle across different regions of Europe, and how has this knowledge been applied in truffle cultivation?
- What do these findings imply for potential truffle habitats in the German low mountain range and sustainable management strategies in this region?

2. Methods

To answer the research questions, a literature review based on the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) was chosen to create an overview of the existing research results. The PRISMA is the method of a standard approach for conducting systematic reviews and meta-analyses (Page et al. 2021). It offers the opportunity to carry out a detailed and structured procedure for the identification, selection, evaluation, and synthesis of research results in a specific research area and, through a transparent literature selection process, ensures high reproducibility of the results (Rethlefsen et al. 2021). The procedure was adapted for this study and follows the steps a) literature search and selection, b) data extraction, and c) synthesis. Additionally, the literature was analyzed for data frames with quantitative information about soil parameters and biota.

2.1 Literature Search and Selection

The systematic literature search was conducted in the dimensions literature database (Digital Science 2024) to investigate *T. aestivum*. Dimensions Analytics was utilized for its robust search capabilities and comprehensive visual tools, which facilitate the extensive exploration of research papers, grants, patents, and other relevant documents. The platform aids in identifying pertinent literature, provides AI-generated insights, and tracks ongoing research activities through recently awarded grants. Additionally, its advanced search options, natural language processing, and efficient export features contribute to the depth and efficiency of this literature review. The initial search query included the terms "burgundy truffle," "tuber aestivum," "tuber uncinatum," and "tuber aestivum var uncinatum" in titles and abstracts to generate a broad database of relevant publications. A total of 251 entries were found,

and the search results were exported on March 11, 2024. The research queue and the results are shown in the appendix (App. 1).

The study selection followed a two-stage screening process. In the first screening, 117 publications were excluded due to mention of genetics, aroma, methodology, health aspects, irrelevant spatial areas, or lack of connection to the search terms in the title.

In the second screening, 50 of the remaining 134 articles were excluded due to mention of genetics, aroma, methodology, health aspects, irrelevant spatial areas, or lack of connection to the search terms in the abstract. Additionally, six were classified as "not available," and two duplicates were removed. Ultimately, 76 publications remained for full-text analysis and further evaluation of *T. aestivum* habitats (Tab. 1). The regional reference is unclear in a significant number of studies; therefore, it has been excluded from further consideration in this analysis.

2.2 Data Extraction and Synthesis

The extraction path is shown in the Appendix (App. 2). The studies were examined using ChatGPT-4 (OpenAI 2024a, 2024b), and content regarding the habitat was extracted from the results and discussion sections. Data extraction from scientific literature poses several significant challenges, including the vast volume of available publications, the diversity of data formats, and the variability in language (English, French, Italian, and other) and terminology used across different studies. Manual extraction is time-consuming but also prone to human error and inconsistency, which can compromise the reliability of the extracted data. Additionally, the need to accurately interpret complex scientific jargon and synthesize information from various sources further complicates the process. Moreover, automated extraction with GPT guarantees consistent data handling and interpretation, reducing the variability introduced by human extractors. This consistency is crucial for maintaining the integrity and reliability of scientific analyses. To extract data, a so-called "prompt" was used to analyse the results and discussion sections. The goal was to ensure a clear understanding of the findings, particularly about the truffle habitat. The prompt request for a truffle habitat. The output of ChatGPT-4 shows summaries of the papers highlighting the key points of the results and discussions (OpenAI, personal communication 2024a). To shorten the information a get the most important information, ChatGPT-4 was asked to summarize the results of the first prompt answers in three sentences (OpenAI, personal communication 2024b).

Afterward, the condensed summaries were manually supplemented and classified into three categories, with the distinguishing criteria: "Wild truffle," "Truffle cultivation," and "Miscellaneous.” These categories were chosen to provide a clear and structured organization of the information, facilitating easier analysis and reference. "Wild Truffle" focuses on naturally occurring truffles, their habitats, ecological interactions, and foraging methods; "Truffle Cultivation" addresses agricultural practices, cultivation techniques, soil management, and economic aspects of truffle farming; "Miscellaneous" captures additional relevant information that doesn't fit into the other two categories, ensuring comprehensive coverage of the topic. Within the criteria “Wild truffles”, the subcategories “Distribution and Habitat Preferences” and “Truffle Dispersal by Fauna and Biota” were established. Within the criteria “Truffle cultivation”, the subcategories “Inoculation and Mycorrhiza”, “Influence of Soil Properties and Soil Management”, and “Management Strategies and Ecological Interaction” were introduced (see Tab. 1). Within the criteria “Miscellaneous”, the subchapters “Climate Change and Geographic Interaction” and “Miscellaneous” were built. For every subcategory a comprehensive overview of related

literature summaries was created (see in Chapter 3. Results). The sub-chapters are intended to equalize the flood of information and provide a better overview.

These results serve as a basis for the discussion of implications, limitations, and perspectives for future research in the concluding remarks. By illuminating the diverse facets of the examined subject areas in detail, this analysis contributes to the expansion of the knowledge horizon. It emphasizes the importance of interdisciplinary approaches to address the complex challenges in the research and management of the habitat conditions of *T. aestivum*.

2.3 Statistics

To find the optimal habitat parameter, the 76 remained publications were examined for usable data tables and converted into a uniform data structure. This included integrating datasets from 14 studies, which encompassed 111 datasets (App. 3). The other studies presented their results in graphs and plots, so direct data export was not possible.

Statistical analysis of the data was conducted using the R programming language (R Core Team 2024) in RStudio (RStudio Team 2024) with the libraries tidyverse, readr, corrplot, and ggplot2. Initially, the data was imported, and descriptive statistics for numerical columns of the first 20 columns were calculated, including mean, standard deviation, minimum, maximum, and median. Subsequently, the numerical data was converted into a long format to create box plots with ggplot2. For the analysis of vegetation data, the absolute and relative frequencies of species were calculated, and the results were visualized in a bar chart with ggplot2. The data was transformed into an appropriate format and visualized using ggplot2 to display the distribution of absolute and relative frequencies of the different species. The charts were provided with appropriate axis labels and a minimalist design to ensure readability.

2.4 Quality Assessment

To ensure the quality of the studies included in the systematic review, specific criteria were applied during the literature search. The search was limited to publications with a Digital Object Identifier (DOI), which ensures unambiguous identification and citability. Additionally, only studies from scientific publishers were considered to ensure a minimum standard of quality and peer review. Although grey literature was not included in the formal PRISMA analysis due to its potential methodological limitations, it was considered in the introduction and discussion to provide a more comprehensive overview of the state of research. However, it should be noted that some of the studies cited in the discussion were published in-house at faculties or universities and, therefore, did not undergo a peer-review process, which may limit their validity.

Tab. 1: Concise overview of the various studies conducted on Burgundy truffles' ecological and management aspects, highlighting their key findings and focus. Some studies can be found in more than one category (underlined), as they address a range of topics. Studies in bold are used for the statistical analyses.

Mean focus	Focus areas	Authorship	No. of Studies	Chapter
Wild truffle	Distribution and Habitat Preferences	Azar 2023; Barry et al. 1994, 1995; Benucci et al. 2011; Büntgen et al. 2016; Chatin 1887; Deveau et al. 2019; Gogan Csorbaine et al. 2013; Gryndler et al. 2014, 2015, 2017b; **Hilszczańska et al. 2008, 2018, 2019**; Ławrynowicz et al. 2008; Leonardi et al. 2021; Ljubojević et al. 2022; Molinier et al. 2016; **Moser et al. 2017**, Păcurar et al. 2018; Robin et al. 2016; Rosa-Gruszecka et al. 2016, 2017; Splivallo et al.2019; Stäubli et al., 2022; Stobbe et al. 2012, 2013b; Streiblová et al. 2010	28	3.1.1
Wild truffle	Truffle Dispersal by Fauna and Biota	Hilszczańska et al. 2016; **Innangi et al. 2020**; **Menta et al. 2014**; Ori et al. 2021; Piattoni et al. 2013, 2014; Pinto et al. 2017; Salerni et al. 2013	8	3.1.2
Truffle cultivation	Inoculation and mycorrhiza	**Álvarez-Lafuente et al. 2018**; **Benucci et al. 2012**; Bruhn et al. 2012; Huang et al. 2021; Iotti et al. 2012; Miko et al. 2014; Nahm et al. 2019; Ori et al. 2020; Shamekh et al. 2014; Stobbe et al. 2013a; Thomas 2012	11	3.2.1
Truffle cultivation	Influence of Soil Properties and Soil Management	**Bragato et al. 2021**; Büntgen et al. 2016; Chevalier 2012a, b; Chevalier and Sourzat 2012; **García-Montero et al.** 2009**, 2014**; Gryndler et al. 2017a; Nahm et al. 2019; Rossbach et al. 2019; Salerni et al. 2014; Thomas 2021; Todesco et al. 2019	13	3.2.2
Truffle cultivation	Management Strategies and Ecological Interaction	Belfiori et al. 2012; Büntgen et al. 2017, Miko et al. 2014; Molinier et al., 2013; **Nahberger et al., 2021**; Piñuela et al., 2021; Pargney and Brimont 1993; Rosa-Gruszecka et al. 2017; Salerni et al. 2013; Stobbe et al. 2012; Todesco et al. 2019; Zambonelli et al. 2015	12	3.2.4
Miscellaneous	Climate Change and Geographic Interaction	Čejka et al. 2020, Chevalier and Frochot 1989, Gogan Csorbaine et al. 2007, Păcurar et al. 2019, Steidinger et al. 2022, **Wedén et al. 2004**, **Wedén 2009**	7	3.3.1
Miscellaneous	Miscellaneous	Bratek et al. 2013; Calvo et al. 2020; Rosa-Gruszecka et al. 2021; Thomas 2014	4	3.3.2

3. Results

This chapter presents a comprehensive synthesis of the results from the literature extraction and investigation into the habitat conditions of the Burgundy truffle. The aim is to provide a detailed overview of the current research landscape regarding the habitat characteristics of *T. aestivum* in Europe. The primary focus is to address the consistency and potential divergence of habitat descriptions for this species across different geographical regions of Europe. Specifically, it explores the extent to which habitats in the sparsely recorded Central and Northern European countries align with those in the extensively studied Southern European and global areas. This includes an analysis of the physical, biological, and climatic conditions of the sites, with a particular focus on whether and to what extent the habitats of *T. aestivum* have expanded and adapted from an originally subtropical and Mediterranean climate zone to the more temperate latitudes and specific environmental conditions of Central Europe.

This analysis aims to understand the geological, climatic, and biotic factors influencing the occurrence and productivity of the Burgundy truffle in different regions by critically evaluating research results from various studies in Europe. Additionally, it seeks to deduce the implications of these findings for potential truffle habitats in the German low mountain range, sustainable management strategies, and the protection of natural truffle populations. The synthesis of research results is structured into sections that highlight key findings, significant trends, patterns, and deviations within the specific research area. This structured presentation allows for quick comprehension of the progress in research on the habitat conditions of T. aestivum and how these findings contribute to forming a coherent overall picture. The integrated consideration of physical, biological, and climatic aspects provides valuable insights into the current conditions and challenges faced in the habitats of the Burgundy truffle and sheds light on the evolutionary nature of the species and its adaptability to changing environmental conditions.

By critically evaluating research results from a variety of studies in Europe, this analysis enables a deeper understanding of the complex interactions within and between the habitats of the Burgundy truffle. The synthesis of research results is structured into sections that highlight key findings and significant trends, patterns, and deviations within the specific research area. This structured presentation allows for quick comprehension of the progress in research on the habitat conditions of T. aestivum and how these findings contribute to forming a coherent overall picture. The integrated consideration of physical, biological, and climatic aspects provides valuable insights into the current conditions and challenges faced in the habitats of the Burgundy truffle and sheds light on the evolutionary nature of the species and its adaptability to changing environmental conditions.

3.1 Wild Truffle

3.1.1 Distribution and Habitat Preferences

This subchapter seeks to identify the geological, climatic, and biotic factors that influence the occurrence and productivity of *T. aestivum* in various European regions, summarizing 28 studies. This knowledge will help to answer the research question to identify potential truffle habitats in the German low mountain range and develop sustainable cultivation and habitat management practices, ensuring the conservation of natural truffle populations.

The soil properties are one of the most important parameters. Hilszczańska et al. (2008) highlight that *T. aestivum* prefers calcareous Rendzina soils with a higher pH. This preference is supported by Păcurar et al. (2018), who indicate that Rendzina and brown luvic soils provide optimal growth conditions, while alluvial soils are less suitable. Hilszczańska et al. (2019) confirm that high soil calcium carbonate content significantly promotes the fruiting of *T. aestivum*. Robin et al. (2016) emphasize that *T. aestivum* can adapt to a variety of geological substrates, thriving in a range of soil textures and adapting to soils with varying pH and nutrient content. Streiblová et al. (2010) also note the species' preference for calcareous, lime-rich soils. Azar (2023) underscores the importance of soil types like Lithosol and Rendzina for the ectomycorrhizal symbiosis with *Zelkova carpinifolia*. Gryndler et al. (2017) show that calcium carbonate and specific organic compounds significantly stimulate the growth of *T. aestivum hyphae*. Gryndler et al. (2015) emphasize the importance of soil temperature and moisture for the growth and spatial spread of *T. aestivum*. Gryndler et al. (2014) reveal that *T. aestivum* can also occur in non-host plants, suggesting a broader ecological presence.

Gryndler et al. (2015) indicate that sufficient soil moisture and optimal temperature are critical for truffle development. Moser et al. (2017) highlight the role of climatic factors in determining suitable habitats, with specific thermophilic shrub and herb species indicating warm, dry, and calcareous conditions favourable for *T. aestivum*. Stobbe et al. (2012) document the adaptability of truffles to various climatic and geological conditions, suggesting potential for expanding truffle cultivation north of the Alps.

Hilszczańska et al. (2008) and Gryndler et al. (2014) note that *T. aestivum* is associated with various deciduous trees and can also occur in non-host plants, suggesting a broader ecological presence. Stobbe et al. (2013) demonstrate the potential for symbiosis with conifers such as *Picea abies*, highlighting the adaptability of *T. aestivum* to various host trees. Benucci et al. (2011) and Hilszczańska et al. (2016) document high ectomycorrhizal diversity in hazel and hornbeam truffle orchards, emphasizing the importance of host tree selection. Hilszczańska et al. (2018) show that plant diversity correlates with higher truffle fruiting body production, emphasizing the role of vegetation in truffle habitats. Leonardi et al. (2021) uncover remarkable diversity of other T. species coexisting in *T. magnatum* rich areas in Italy, indicating complex ecological interactions.

Molinier et al. (2016) provide insights into the genetic complexity of *T. aestivum*, indicating high genetic variability and adaptability to diverse environmental conditions. Stäubli et al. (2022) reveal high genetic diversity and an adaptive reproductive strategy, suggesting significant ecological flexibility. Gryndler et al. (2017) and Deveau et al. (2019) emphasize the complex interactions between truffles and their soil microbiome, highlighting the need for further research on these symbiotic relationships. Splivallo et al. (2019) investigate the microbiome of *T. aestivum*, showing that microbial communities are predominantly influenced by location-specific factors.

Büntgen et al. (2016) report no significant radioactive contamination in *T. aestivum* post-Chernobyl, ensuring safety for consumers. Barry et al. (1994, 1995) demonstrate the ability of truffle ascocarps to autonomously uptake nutrients, underscoring the importance of soil quality and structure. Rosa-Gruszecka et al. (2017) highlight the historical appreciation and resurgence of truffle cultivation in Poland. Chatin (1887) introduces *T. uncinatum* as a distinct species, emphasizing its ecological preferences and economic potential. Rosa-Gruszecka et al. (2016) identify insects involved in truffle spore dispersal, emphasizing the ecological importance of these interactions and the need for further research, particularly in emerging truffle industries.

Gogan Csorbaine et al. (2013) identify specific ecological characteristics of truffle habitats in Hungary, including dominant soil types like Gleysols and Chernozems influenced by water and a forest-steppe climate favourable for *T. aestivum* production. Stobbe et al. (2013) support the potential for *T. aestivum* to form a symbiosis with *Picea abies*, expanding its ecological range. Hilszczańska et al. (2016) document high mycorrhization in a *T. aestivum* garden with oaks and hazelnuts, highlighting the importance of host tree selection and soil management for truffle cultivation. Ljubojević et al. (2022) document the morphological variability of *T. aestivum* in Bosnia and Herzegovina, contributing to the understanding of this truffle species' physical characteristics.

3.1.2 Truffle Dispersal by Fauna and Biota

This subchapter summarizes eight studies and analyses the findings on the dispersal of Burgundy truffles and the influence of soil biota on the habitat. Dispersal ways are one way to understand the distribution and niche ecology of T*. aestivum*.

The study by Ori et al. (2021) demonstrates that slug mycophagy causes morphological changes in *T. aestivum* spores, enhancing their mycorrhizal capability with oak seedlings, and highlights the role of slugs as effective short-distance dispersers of Tuber spores. Piattoni et al. (2014) and Piattoni et al. (2013) similarly show that wild boars play a crucial ecological role in truffle spore dispersal, with digestion altering spore morphology, improving mycorrhizal capacity, and maintaining spore viability. This activity is crucial for the genetic diversity and spatial structuring of truffle populations. However, Salerni et al. (2013) indicate that wild boar activity, particularly soil disturbance during foraging, negatively impacts summer truffle harvests, suggesting that protective measures like fencing can significantly enhance truffle production. Furthermore, Innangi et al. (2020) reveal that *T. aestivum* presence significantly alters soil chemistry and biological activity, increasing pH, reducing organic carbon and nitrogen contents, and impacting microbial activity and soil fertility. Menta et al. (2014) and Pinto et al. (2017) further investigate the impact of *T. aestivum* on soil biogeochemistry and microarthropod communities, showing significant changes in soil properties such as increased pH and reduced organic carbon content. Specific soil microarthropods varied within and outside brûlé zones, indicating the direct influence of truffle mycelium on its surroundings. These studies underscore the need for further research to fully understand these ecological interactions and their implications for soil health and truffle production.

Hilszczańska et al. (2016) document high mycorrhization in a *Tuber aestivum* garden with oaks and hazelnuts, identifying a diversity of ectomycorrhizal fungal taxa that vary between host species. This study emphasizes the importance of host tree selection and soil management practices for the composition of mycorrhizal communities and the effective management of truffle habitats. Collectively, these findings highlight the complex ecological interactions between truffles, soil biota, and fauna, providing crucial insights for the sustainable management and cultivation of *T. aestivum*.

3.2 Truffle Cultivation

3.2.1 Inoculation and Mycorrhization

This subchapter summarizes eleven studies and presents insights on the effectiveness of different inoculation methods, their impacts on host plants and the surrounding soil ecosystem, and the long-term implications for truffle cultivation and habitat management.

Álvarez-Lafuente et al. (2018) illustrate the successful inoculation of *Castanea sativa* seedlings with *T. aestivum*, *T. uncinatum*, and *T. brumale*, demonstrating the potential for dual-use of chestnut forests for truffle production. These promising results highlight the potential for yield increase and improved plant performance in nurseries, particularly through the use of *T. brumale*. Shamekh et al. (2014) explored the potential for cultivating summer truffles (*T. aestivum*/*uncinatum*) in Finland, a region not traditionally associated with truffle production. Despite the challenges posed by Finland's boreal climate, including very low winter temperatures occasionally dropping below −30°C, the inoculated oak seedlings (*Quercus robur* and *Q. pubescens*) survived, particularly with additional winter protection using fabric, plastic, and branches. Additionally, Benucci et al. (2012) and Bruhn et al. (2012) demonstrate successful mycorrhisation of *Carya illinoinensis* with *T. borchii* and *T. aestivum*. These studies open new avenues for truffle production in pecan plantations and confirm the importance of selecting the seedling production method for a high colonisation rate, which is crucial for truffle production. They also underscore the relevance of adjusting soil pH to create optimal conditions for truffle production. Huang et al. (2021) and Iotti et al. (2012) show that truffle inoculation not only promotes the growth of host plants and enhances their stress resistance but also influences the physicochemical

properties of the soil and potentially exerts selective effects on specific microbial communities. These findings highlight the positive impacts of truffle symbiosis on the host plant and soil ecosystem and emphasise the importance of careful selection of inoculation methods and strict quality control. Miko et al. (2014) and Ori et al. (2020) reveal the seasonal sensitivity of *T. aestivum* spore quality and the successful mycorrhisation with *Arbutus unedo*. These studies indicate the need for timely optimised harvesting and inoculation for effective truffle cultures and underscore the economic significance of combining truffle production with the cultivation of edible fruits and honey. Stobbe et al. (2013), Thomas (2012), and Nahm et al. (2019) highlight specific ecological conditions and the importance of soil characteristics, particularly pH, for the successful cultivation of *T. aestivum*. They show that natural colonisation by *T. aestivum* in certain habitats is unlikely, underscoring the need for active inoculation measures and long-term monitoring to promote the establishment and production of *T. aestivum*.

3.2.2 Influence of Soil Properties and Soil Management

This subchapter summarises the findings of 13 studies on the influence of soil properties and soil management on the production of *T. aestivum*. Various research groups that have shown that both the physicochemical properties of the soil and targeted management practices are crucial factors for the successful cultivation and natural dissemination of these valuable mycorrhizal fungi. The study by Bragato et al. (2021) highlights the importance of specific soil properties, particularly the Chernozem soil type, for truffle production. The high content of organic matter and soluble nitrogen in these soils correlates positively with the distribution and abundance of *T. aestivum*, emphasising the need for effective management and maintenance of soil quality. Similarly, Büntgen et al. (2016) and Chevalier (2012) show that truffles can thrive in various European regions, provided that the soil conditions, especially calcium content, are suitable for their growth. These findings underline the ecological flexibility of Burgundy truffles and the importance of tailored soil cultivation and irrigation methods to enhance truffle production. Furthermore, Chevalier and Sourzat (2012), as well as García-Montero et al. (2014 and 2009), highlight the crucial role of specific soil characteristics and climatic conditions in the successful cultivation of truffles. The selection of host trees and measures for soil improvement and irrigation are critical for mycorrhisation and fruit body formation. The studies by Gryndler et al. (2017) and Rossbach et al. (2019) provide important insights into soil receptivity for truffle cultivation, particularly the role of inorganic and organic soil components. These findings call for further research to develop sustainable truffle cultivation and habitat management practices that consider soil chemistry and specific climatic requirements. Salerni et al. (2014) and Thomas (2021) emphasise the importance of ectomycorrhizal communities for the habitat and productivity of truffles, as well as the resilience of ectomycorrhizae to extreme environmental conditions. The careful selection of host trees and the complex dynamics of competition and synergy between fungal species are significant for the management of truffle plantations.

Finally, Todesco (2019) and Nahm et al. (2019) demonstrate that the effectiveness of management techniques and understanding of soil parameters are crucial for truffle production, while natural colonisation by *T. aestivum* in certain habitats without targeted inoculation measures is unlikely.

3.2.3 Management Strategies and Ecological Interaction

This subchapter discusses twelve studies about the management strategies and ecological interactions of the *T. aestivu*m and related species within their habitats and truffle plantations based on insights from various studies. The synthesis illustrates how the management of truffle habitats and understanding their ecological interactions are essential for optimizing truffle production and preserving

their ecosystems. Belfiori et al. (2012) and Büntgen et al. (2017) highlight the reduction of mycorrhizal biodiversity in cultivated truffle plantations compared to natural habitats and the complex ecological factors influencing truffle maturation. These findings indicate the need to develop management practices that promote ecological diversity and consider the specific requirements of truffle development. Miko et al. (2014) and Molinier et al. (2013) emphasise the seasonal sensitivity of truffle spore quality and the dynamic, competitive relationships within truffle ecosystems. These results underscore the importance of timely optimized harvesting and adapting truffle cultivation to local climatic conditions to maximize productivity.

Nahberger et al. (2021) and Pargney and Brimont (1993) discuss the significant impacts of mycorrhization on the biomass and morphology of host plant roots, as well as ultrastructural changes during mycorrhization. These studies highlight the complex interactions between plants, fungi, and soil organisms, emphasizing the need for a deep understanding of these dynamics for successful truffle cultivation. Piñuela et al. (2021) and Rosa-Gruszecka et al. (2017) highlight the role of management practices such as mulching and irrigation, as well as the historical and revived appreciation for truffles in Poland. These insights provide an understanding of the importance of tailored cultivation techniques and the need to combine modern practices with traditional knowledge. Salerni et al. (2013) and Stobbe et al. (2012) highlight the negative effects of wild boar activity on truffle production and the diversity of truffle species in certain regions, emphasizing the importance of protective measures and effective habitat management. These studies demonstrate how crucial it is to understand the interactions between soil fauna and mycorrhizal plants and to develop appropriate strategies for their control. Todesco (2019) and Zambonelli et al. (2015) discuss the impacts of climatic and soil conditions on truffle production and the advancements in truffle cultivation, including genetic research. These findings underscore the importance of adapting management strategies to ecological requirements and the potential improvements through advanced cultivation techniques.

3.3 Miscellaneous

3.3.1 Climate Change and Geographic Interaction

This synthesis examines the impact of climate change on the geographic distribution and interaction of *T. aestivum* based on seven current research findings. This comprehensive analysis highlights that the geographical areas suitable for truffle cultivation will adapt in response to climate change. It bothers both, wild truffle and truffle cultivation. Čejka et al. (2020) predict a potential decrease in suitable sites for the Burgundy truffle in the Czech Republic, while the cultivation potential for the Périgord truffle might increase. This underscores the necessity of making ecological adjustments in truffle cultivation practices to align with new climatic conditions, ensuring economic and ecological sustainability. Chevalier and Frochot (1989) and Gogan Csorbaine et al. (2007) highlight the ecological adaptability of the Burgundy truffle, emphasizing the importance of adjusted soil cultivation and cultural methods. The ecological and economic benefits of truffle cultivation, such as soil quality improvement and biodiversity promotion, contribute to strengthening rural economies. Păcurar et al. (2019) show that specific climatic and soil conditions in Transylvania provide optimal sites for *T. aestivum* growth. The application of GIS-based spatial analysis delivers crucial data for truffle cultivation and sustainable management of truffle habitats. Steidinger et al. (2022) document a high climate sensitivity of summer truffles, with truffle productivity correlating with the phenology of host trees. This underscores the need for adaptation measures in truffle management and further research on the effects of climate change on key ectomycorrhizal species. Weden et al. (2004) and Wedén (2009) illustrate the ecological

adaptability of the Burgundy truffle to soil structures and chemistry in Sweden, highlighting the potential for expanding truffle production to new geographic areas.

3.3.2 Miscellaneous

Finally, the last four studies have shed light on particular topics. Bratek et al. (2013) emphasize how using dogs for truffle hunting has improved the discovery of truffle species in the Carpathian-Pannonian region and how commercial harvesting practices influence our perception of their abundance. In the context of climate change, the distribution areas of truffle species may shift, while the decline of traditional habitats could limit their expansion. The researchers underscore the need for taxonomic revisions and molecular studies to understand truffle biodiversity and their ecological interactions better. Calvo et al. (2020) highlight the significant economic role of truffle harvesting and trade, particularly of *T. aestivum* and *T. borchii*, in the Monti Sicani Regional Park in Sicily. The study points out that although currently unregulated, truffle harvesting and trade represent significant income sources and have the potential to boost the local economy and employment in economically weaker areas. The researchers emphasize the need for regulation and education to promote sustainable practices and ensure the long-term protection of truffle habitats. Rosa-Gruszecka et al. (2021) present an innovative "Virtual Truffle Hunt" method based on 12 parameters to identify potential sites for Burgundy truffles in Poland. This method successfully identified new truffle sites, highlighting the importance of specific environmental conditions for truffle growth and offers advantages over GIS-based methods. The potential application in other European regions could facilitate the systematic assessment of truffle potential in forests. Thomas (2014) demonstrates that *T. melanosporum* mycorrhizae can survive under suboptimal climatic conditions, such as those in the United Kingdom, underscoring the importance of adapting cultivation strategies to specific climatic conditions. Climatic factors such as sunlight hours, summer rainfall, and temperatures are crucial for fruit body formation without showing a significant correlation to the degree of mycorrhization.

3.4 Data Analysis

This chapter presents data of 14 appropriate studies (Tab.2), encompassing 111 datasets. The geographical distribution shows a wide range of European countries. Nevertheless, it cannot be assumed that these studies are representative for Europe, as the data collection and processing as well as the presentation of the data deviate too much from each other. Accordingly, no in-depth data analysis was carried out and only a descriptive statistical evaluation was used. The numerical results of the statistics can be found in the appendix (App. 3).

Outliers are excluded from boxplots to maintain clarity in the visualizations. Boxplots summarize data distributions through medians and quartiles, and outliers, as deviations, distract from these overall patterns. Outliers are critical in statistical analysis as they indicate observations that deviate significantly from the central tendency, defined as being more than 1.5 times the interquartile range (IQR) beyond the quartiles. The exclusion of outliers leads to a robust dataset by reducing the influence of extreme deviations that can skew the results.

Tab. 2: Studies involved in the statistical analysis and the regions where the data was recorded

Authors	Region
Alvarez-Lafuente et al. 2018	Lab, South Germany, Swiss, Italy
Benucci et al. 2012	Lab
Bragato et al. 2021	Hungary
Garcia-Montero et al. 2014	Spain
Hilszczańska et al. (2008, 2018, 2019)	Poland
Innangi et al. 2020	Northern Italy

Authors	Region
Menta et al. 2014	Spain, Italy
Moser et al. 2017	South Germany
Nahberger et al. 2021	Lab
Stobbe et al. 2013b	South Germany
Weden et al. (2004, 2009)	Sweden, France

3.4.1 Soil Nutrients

The parameters measured include the C/N ratio, $CaCO_3$ content, total carbon (Ctot), moisture, organic nitrogen (Norg), total nitrogen (Ntot), pH in water (pH(H2O)), pH in KCl (pH(KCl)), soil organic matter (SOM), and total organic carbon (TOC). The y-axis represents the percentage of these components in the soil, ranging from 0% to 50% (Fig. 1).

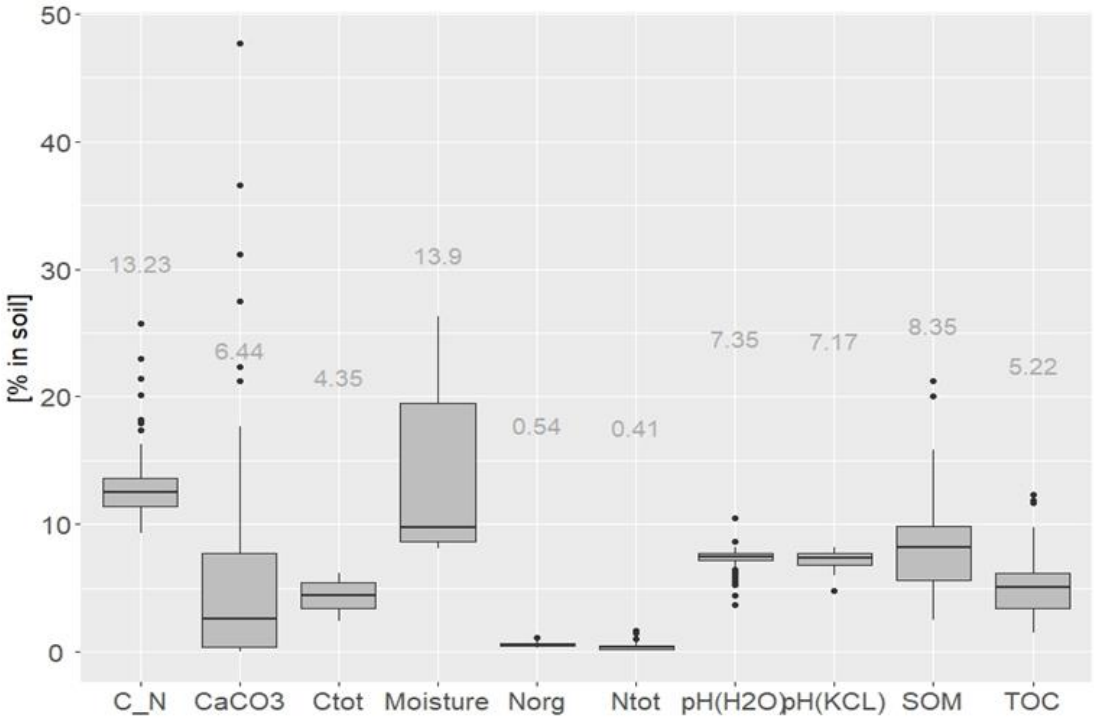

Fig. 1: Soil parameters at locations where *T. aestivum* was found. Numbers over the boxplots show the mean value of the parameter.

Each box plot displays the median, interquartile range (IQR), and potential outliers for the soil parameters. The C/N ratio shows a median value around 13% with a wide range of data. The upper whisker extends to about 25%, indicating variability in the C/N ratio across samples, with some outliers exceeding 40%. The $CaCO_3$ content has a median of approximately 6.44%, with a lower range of variability compared to the C/N ratio. However, notable outliers extend above 30%, reflecting some inconsistencies in soil calcium carbonate levels.

Total carbon (Ctot) presents a more compact distribution with a median around 4.35% and a smaller IQR, though a few outliers extend beyond 4%. Moisture content indicates a high median value around 13.9% with a broad range extending up to 30%, showcasing significant variability and several outliers above this range. Organic nitrogen (Norg) has a very low median value close to 0.54%, with minimal variability and outliers that are not highly significant.

Total nitrogen (Ntot) similarly has a low median value of about 0.41% with very little variability and a few minor outliers. The pH measured in water (pH(H2O)) shows a median value around 7.35, with a narrow distribution and minimal outliers, indicating consistency in pH levels across samples. The pH in KCl (pH(KCl)) exhibits a similar trend with a median close to 7.17 and low variability, though there are a few outliers.

Soil organic matter (SOM) has a median value around 8.35%, with a wider IQR compared to total carbon, indicating more variability in SOM content. Outliers extend beyond 10%, reflecting differences in organic matter levels across samples. Total organic carbon (TOC) displays a similar pattern to SOM, with a median value around 5.22%, a moderate IQR, and some outliers.

The data suggests that while most soil parameters have consistent median values, parameters like the C/N ratio, CaCO3 content, moisture, and SOM exhibit significant variability. This variability indicates differences in soil composition and quality across different samples, which is crucial for soil management, fertility, and agricultural productivity. The presence of outliers in almost all parameters suggests localized areas with significantly different soil characteristics, requiring tailored soil management practices to optimize agricultural outputs or maintain ecological balance. The consistency in pH levels suggests a stable soil pH environment across the samples, beneficial for most crops. Overall, this analysis provides a comprehensive overview of soil health and quality, informing better soil management decisions.

3.4.2 Minerals

The analysis of mineral data included box plots (Fig. 2) to visualize the distribution of values for each mineral fraction: clay, sand, and silt. The y-axis represents the percentage of each mineral fraction, ranging from 0% to 100%. Each box plot provides a visual summary of the data distribution, highlighting the median, interquartile range (IQR), and potential outliers.

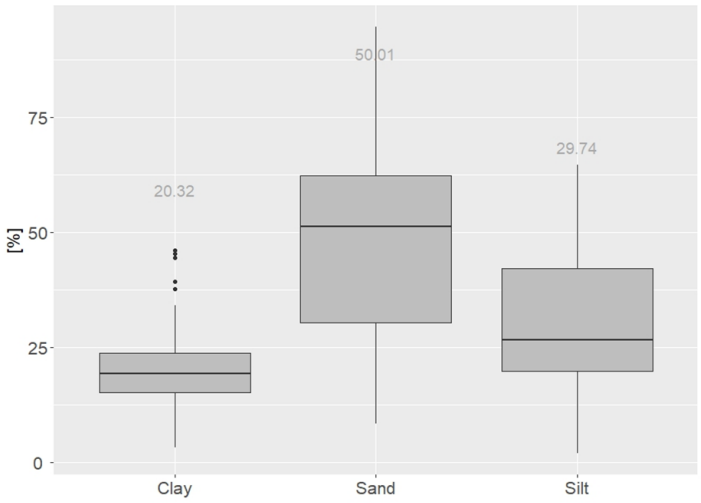

Fig. 2: Distribution of the mineral fractions. Numbers over the boxplots show the mean value of the parameter.

The box plot for clay shows a median value around 20%, with a relatively narrow interquartile range. The lower whisker extends to about 10%, while the upper whisker reaches 30%. There are a few outliers below 10%, indicating some variability but generally consistent clay content across samples. Sand has a higher median value around 50%, with a broad interquartile range extending from approximately 35% to 70%. The lower whisker is near 20%, and the upper whisker approaches 80%, indicating substantial variability in sand content. The wide range and lack of significant outliers suggest diverse sand fractions across different samples. The silt fraction shows a median value around 30%, with an interquartile range spanning from 20% to 40%. The lower whisker extends to about 10%, while the upper whisker reaches 55%, indicating moderate variability. There are no significant outliers, suggesting a relatively consistent distribution of silt content.

The box plots illustrate the different distribution patterns for clay, sand, and silt in the soil samples. Sand shows the most considerable variability, reflecting a diverse range of sand content in the samples. Clay, on the other hand, has a more consistent distribution with fewer outliers. Silt falls in between, with moderate variability and no extreme values.

These differences in distribution highlight the heterogeneity of soil mineral composition, which can significantly impact soil properties and behaviour. Understanding the proportions and variability of these fractions is crucial for soil management, agricultural practices, and environmental studies. The data suggests that soil samples in this analysis have a wide range of sand content, while clay and silt are more uniformly distributed, providing valuable insights into the soil texture and potential implications for soil fertility and structure.

3.4.3 Precipitation and Temperature

Figure 3 shows in the left box the precipitation, and in the right box, temperature values of Tuber habitats. The box plot representing precipitation data shows the spread and distribution of annual precipitation measurements in millimetres. The central box captures the interquartile range, indicating the middle 50% of the data. The median, represented by the line within the box, provides a measure of central tendency. The whiskers extend to the most extreme data points within 1.5 times the interquartile range from the 25th and 75th percentiles, encapsulating the bulk of the data while excluding outliers. Outliers, plotted as individual points beyond the whiskers, represent values that deviate significantly from the rest of the dataset, highlighting years with unusually high or low precipitation.

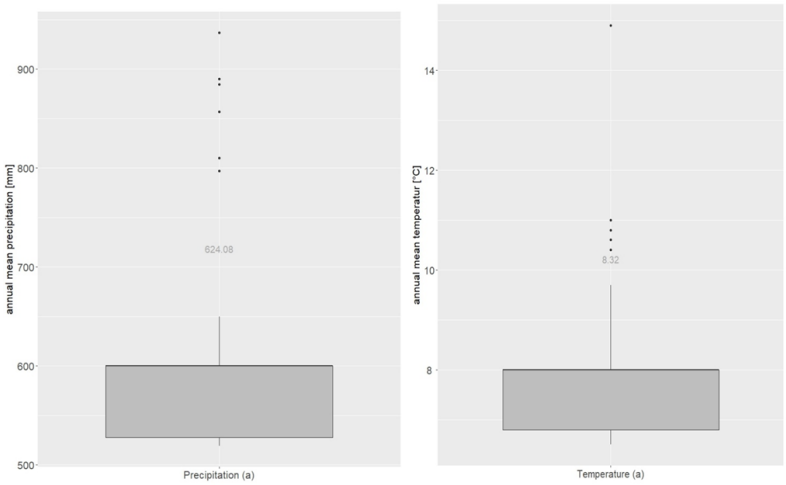

Fig. 3: Left: Annual mean precipitation [mm/a]. Right: Annual mean temperature [°C/a]). Numbers over the boxplots show the mean value of the parameter.

The temperature box plot similarly illustrates the distribution of mean annual temperatures in degrees Celsius. The box delineates the interquartile range, which houses the central 50% of temperature observations. The median temperature is marked by a line within the box, offering a sense of the typical temperature value. Whiskers extend to the most extreme values that fall within 1.5 times the interquartile range from the lower and upper quartiles, thereby covering the majority of the data while excluding extreme values. Outliers, indicated as points beyond the whiskers, signify temperature measurements that are exceptionally higher or lower than the typical range, underscoring anomalous temperature years.

3.4.4 Vegetation

The studies provide an overview of possible symbiosis partners of *T. aestivum*. Some have been recorded and verified in the laboratory, others in the field. The data collected enables the question of better management options to be examined. The results shown in Figure 4 show that the trees observed in the 14 studies correspond to the frequently described tree species *Quercus spp.*, *Corylus avellana*, and *Fagus sylvatica*. However, rarer symbiotic partners such as *Abies alba* and *Prunus spp.* are also mentioned.

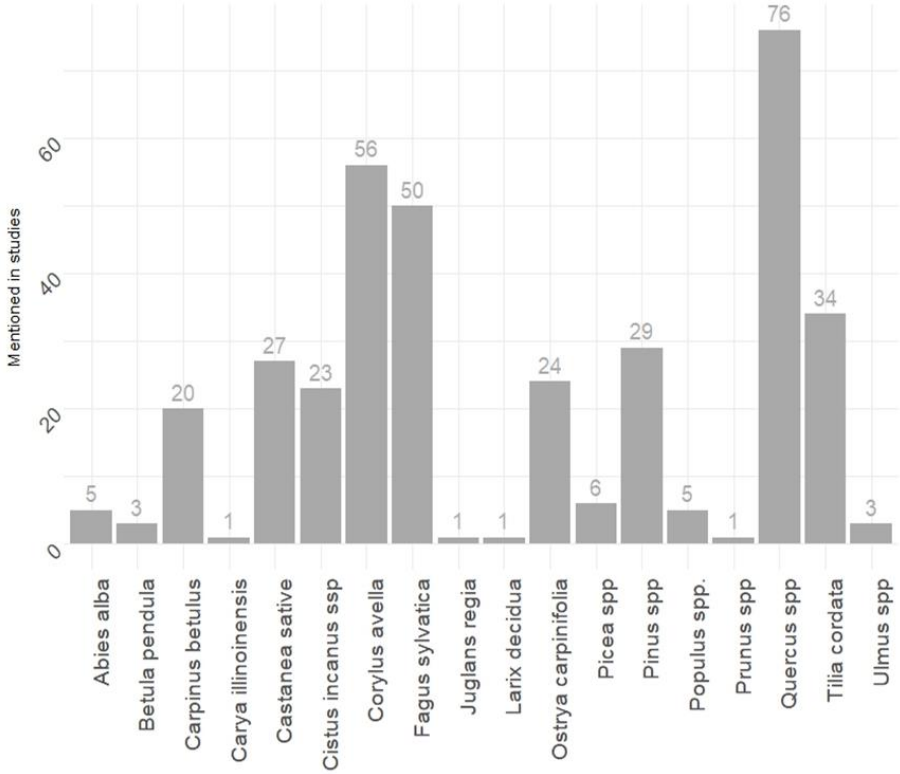

Fig. 4: Frequency of various tree species mentioned in scientific studies. Numbers over the bar plots show the count of the species.

Several factors might contribute to the prominence of certain species in scientific studies. Species like *Quercus spp.* and *Corylus avella* may be of particular ecological, economic, or cultural significance, prompting more extensive research. Their roles in forest ecosystems, commercial uses, or importance in biodiversity conservation could drive the high number of mentions. Conversely, the lower frequency of mentions for species like *Abies alba* and *Ulmus spp.* could indicate less research focus, possibly due to their narrower geographic range, lesser economic importance, or other factors limiting their study.

4. Discussion

This study is poised to delve into the geological, climatic, and biotic factors that influence the occurrence and productivity of the Burgundy truffle across Europe. While the truffle has been extensively studied in southern Europe, particularly in France, Italy, and Spain, it remains a novel area of study in Central and Eastern Europe. Historical records hint at its presence in Germany's lower mountain range, notably in the Hildesheim and former Braunschweig areas. However, current systematic surveys and detailed site investigations are yet to be conducted.

This study critically evaluates existing literature to identify potential habitats, predict climate change impacts, and inform sustainable management and protection strategies for natural truffle populations. The research focuses on (4.1) identifying factors influencing Burgundy truffle occurrence and productivity in Europe and (4.2) implications for potential habitats in Germany's low mountain range and ideas for sustainable management in this region, underlining the crucial role of our work in the conservation of this valuable species.

4.1 Geological, Climatic, and Biotic Factors for Truffle Habitats and Cultivation in Europe

The preferred soils for *T. aestivum* are calcareous Rendzina and brown luvic soils (Molinier et al., 2016), characterized by high pH and significant calcium carbonate content. The statistical results for $CaCO_3$ show values between 0 and up to 48 % soil content. The average percentage is around 6.44 %, supported by Molinier et al. (2016), who expect potential truffle occurrences from 5% $CaCO_3$ (Fig. 5).

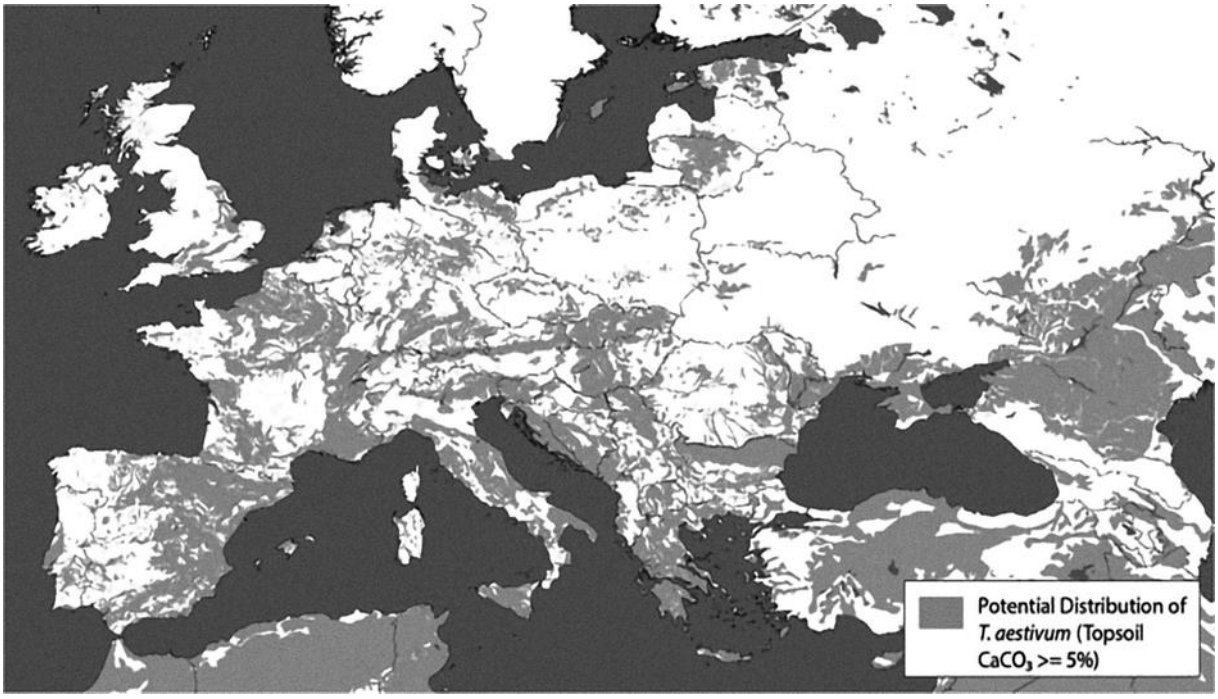

Fig. 5: Potential distribution of *T. aestivum* in Europe (according to Molinier et al. 2016).

Research by Hilszczańska et al. (2008) and Păcurar et al. (2018) indicates that these Rendzina soil types provide optimal conditions for truffle growth due to their texture and nutrient levels. High calcium carbonate and specific organic compounds significantly promote the fruiting of *T. aestivum* (Gryndler et al. 2017). Furthermore, Robin et al. (2016) emphasizes that *T. aestivum* shows adaptability to various soil textures and nutrient contents, thriving in soils with varying pH and nutrient levels. The statis-

tical results show C/N ratios between 9 and 17, with a mean ratio of 13.23, enhancing nutrient availability and soil fertility and fostering better plant growth and crop yield. This range supports effective nutrient cycling and balanced soil nutrient status.

Biotic factors are equally significant in influencing truffle ecology and productivity. The Burgundy truffle forms ectomycorrhizal relationships with a variety of deciduous and coniferous trees, with high diversity observed in hazel and hornbeam orchards (Benucci et al., 2011; Hilszczańska et al., 2016). However, the statistical results show *Quercus spp.* with 71 counts, *Corylus avellana* with 56, and *Fagus sylvatica* with 50 counts as primary host trees. This is supported by Stobbe et al. (2013), who present that around 40% of all host trees are *Quercus spp.*, 11.4 *C. avellana*, and 12,4 % are *F. sylvatica* (Fig. 6).

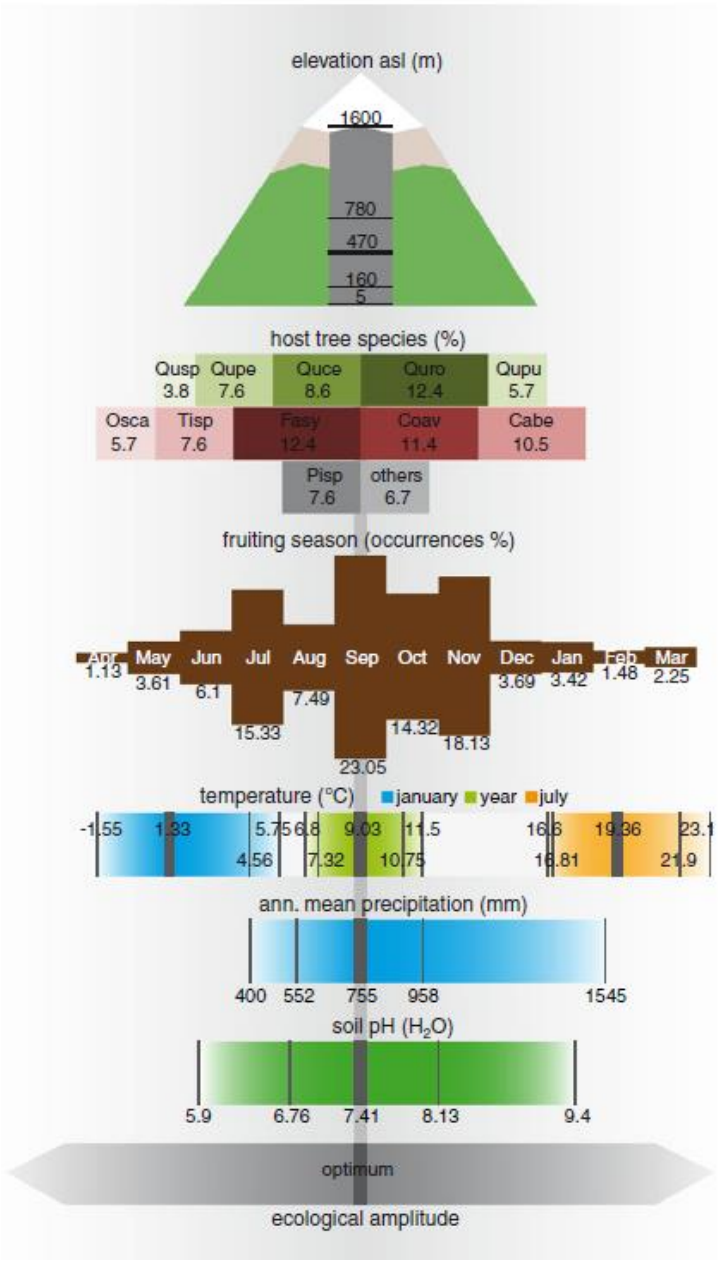

Fig. 6: The ecological amplitude of *T. aestivum*, encompassing all relevant biotic and abiotic factors (after Stobbe et al. 2013). The thick central line in each partial graphic represents the optimal conditions, followed outward by the standard deviation and the minimum and maximum values. Host plants are shown in relative proportions.

The selection of host trees is critical, as higher plant diversity correlates with increased truffle production (Hilszczańska et al., 2018). However, Gryndler et al. (2014) show non-host plants' relations with plants in the shrub and herb layer. Moving to the soil community, soil conditions, particularly the presence of calcareous elements and organic matter, impact the composition of ectomycorrhizal communities, which in turn affects truffle productivity.

Research emphasizes the importance of specific host trees, such as hazel and oak, in sustaining diverse ectomycorrhizal fungi, which is critical for the successful cultivation and management of *T. aestivum* (Benucci et al. 2011; Hilszczańska et al. 2016; Stobbe et al. 2013). In terms of dispersal, fauna such as slugs and wild boars play vital roles in truffle spore dispersal, influencing the genetic diversity and spatial distribution of truffle populations. Ori et al. (2021) and Piattoni et al. (2014) demonstrate that these animals enhance the mycorrhizal capability of truffle spores through digestion, which is crucial for maintaining genetic diversity and promoting truffle population growth. On the other hand, the disruptive foraging behaviour of wild boars can negatively impact truffle harvests, suggesting that protective measures, such as fencing, are necessary to enhance truffle production (Salerni et al. 2013). Insects like beetles and flies also contribute to spore dispersal, influencing truffle production both positively and negatively (Rosa-Gruszecka et al. 2016).

Climatic conditions play a crucial role in the development of the Burgundy truffle. Gryndler et al. (2015) highlight that the truffle thrives in warm, dry environments with sufficient soil moisture. These conditions are typically found in Mediterranean and subtropical climates but also in temperate zones, suggesting the potential for expanded cultivation beyond traditional habitats. Stobbe et al. (2012) document the truffle's adaptability to different climatic conditions, including areas north of the Alps, indicating cultivation opportunities in more temperate regions like Germany's low mountain range. Further research supports the significant influence of temperature, precipitation, and sunlight hours on truffle distribution and habitat suitability. Studies show that *T. aestivum* can adapt to various climatic conditions, ranging from Mediterranean to temperate zones (Büntgen et al. 2016; Gryndler et al. 2015). Statistical results indicate a mean temperature of 8.32°C and mean precipitation of 624 mm in the observed study areas, aligning with findings by Stobbe et al. (2013). This adaptability allows *T. aestivum* to thrive in diverse environmental conditions, underscoring the importance of understanding climatic factors in truffle cultivation and conservation.

Additionally, research by Čejka et al. (2020) suggests that climate change could enhance truffle cultivation potential in Central Europe despite uncertainties. Conversely, Steidinger et al. (2022) highlight that recurring hot, dry summers could decline summer truffle yields, indicating the dual impact of climate change. Thomas (2014) further emphasizes that climatically-derived fruiting triggers, such as sunshine hours, summer rainfall, and summer temperatures, are crucial for successful truffle production. These insights illustrate the complex relationship between climate and truffle ecology, necessitating integrated management strategies to ensure sustainable truffle production in varying climatic conditions.

The cultivation of *T. aestivum* in Europe has evolved through various innovative approaches, emphasizing the importance of soil management and its environmental impacts. Truffle cultivation primarily focuses on optimizing soil conditions, selecting suitable host trees, and employing effective inoculation techniques to enhance truffle production. The ecological flexibility of *T. aestivum* allows it to thrive in diverse environments, making it possible to cultivate these truffles beyond their known traditional Mediterranean habitats into more temperate regions, including Central Europe.

Inoculation methods play a significant role in establishing truffle mycorrhizae on host plants. Successful inoculation techniques involve introducing truffle spores or mycelium to the roots of young trees, facilitating the formation of ectomycorrhizal associations. Álvarez-Lafuente et al. (2018) illustrate the successful inoculation of *Castanea sativa* seedlings with *T. aestivum*, demonstrating the potential for dual-use of chestnut forests for truffle production. Effective inoculation not only promotes the growth of host plants but also enhances their stress resistance and influences the physicochemical properties of the soil. Studies by Huang et al. (2021) and Iotti et al. (2012) show that truffle inoculation can exert selective effects on specific microbial communities, highlighting the positive impacts of truffle symbiosis on both the host plant and the soil ecosystem.

Inoculation typically involves selecting high-quality truffle spores or mycelium and ensuring their viability before application. The spores are often mixed with a carrier medium, such as water or gel, to facilitate their application to the tree roots. After inoculation, the seedlings are monitored to ensure successful mycorrhization, which can be confirmed through microscopic examination of root samples. Proper inoculation techniques and strict quality control are essential to achieving high rates of mycorrhization and successful truffle cultivation.

Selecting the right host trees is fundamental to successful truffle cultivation. Many tree species have been associated with truffles, but whether they actually produce truffles can be a gamble until the trees mature and bear fruit. Specific trees, like hazelnuts (*C. avellana*) and oaks (*Quercus spp*.), are crucial because they foster diverse communities of ectomycorrhizal fungi. These fungal partners are essential for successful truffle cultivation and management. Research by Benucci et al. (2011) and Hilszczańska et al. (2016) has shown that orchards with a wider variety of ectomycorrhizal fungi, thanks to the chosen host trees, tend to be more productive. Generally, hazel and oak trees are particularly favoured for truffle cultivation. These trees provide the necessary nutrients and support for the growth of truffle mycorrhizae. Hazel trees are often chosen for their fast growth and ability to form dense root systems, which enhance mycorrhization. Oak trees, on the other hand, are long-lived and create stable environments for truffle production over many years.

Soil management is a critical component of successful truffle cultivation. The preferred soils for *T. aestivum* do not differ from natural habitats. In contrast, Bragato et al. (2021) emphasize the importance of Chernozem soils, which are rich in organic matter and soluble nitrogen, for truffle cultivation. Chernozem soils are known for their high fertility, dark colour, and excellent structure, making them ideal for truffle production. The high content of organic matter in these soils supports the growth of mycorrhizal fungi, while the soluble nitrogen provides essential nutrients for both the truffle and its host trees. However, soil management practices must maintain the high pH and calcium carbonate levels necessary for truffle development. Techniques such as liming and the addition of organic matter are commonly used to improve soil quality. Liming involves the application of lime (calcium carbonate) to the soil to increase its pH and enhance calcium levels, creating a favourable environment for truffle mycorrhizae. This practice is essential in regions where soil pH is naturally lower, as truffles thrive in alkaline conditions. The addition of organic matter, such as compost or manure, improves soil structure, increases nutrient availability, and enhances microbial activity, all of which are beneficial for truffle cultivation. Gryndler et al. (2015) and Moser et al. (2017) highlight the role of soil temperature and moisture in determining suitable habitats for *T. aestivum*, with specific thermophilic shrub and herb species indicating favourable conditions. Irrigation systems can be implemented to ensure consistent soil moisture levels, especially in regions with irregular rainfall patterns. Drip irrigation is commonly

used in truffle orchards as it delivers water directly to the root zone, reducing water wastage and promoting efficient water use. This method also helps to maintain the microclimate around the truffle mycorrhizae, preventing the soil from drying out and ensuring optimal conditions for truffle growth.

Soil chemistry also plays a significant role in truffle cultivation. Research by Gryndler et al. (2017) and Rossbach et al. (2019) provides important insights into soil receptivity for truffle cultivation, particularly the role of inorganic and organic soil components. These findings call for further research to develop sustainable truffle cultivation and habitat management practices that consider soil chemistry and specific climatic requirements. Understanding the chemical composition of the soil, including nutrient levels and pH, is essential for creating optimal conditions for truffle mycorrhizae. Soil tests and regular monitoring help identify nutrient deficiencies or imbalances, allowing for targeted amendments to improve soil fertility.

Additionally, targeted soil management practices, such as mulching and soil aeration, are employed to enhance soil conditions for truffle cultivation. Mulching involves covering the soil surface with organic or inorganic materials to conserve moisture, regulate soil temperature, and reduce weed competition. Mulching also improves soil structure and increases organic matter content, creating a more favourable environment for truffle mycorrhizae. Soil aeration techniques, such as tilling or using aeration equipment, improve soil porosity and root penetration, promoting healthy root systems and mycorrhizal development.

4.2 Implications for the Innerste and Leine Uplands

The mid-mountain range in the Hildesheim and former Braunschweig area features a complex geological framework marked by diverse rock formations, particularly on the hill sites. The foundation is primarily composed of Variscan orogeny rocks, including metamorphic schists and gneisses formed during the Paleozoic era. These ancient rocks are heavily folded and faulted. Overlying this Variscan basement are extensive Mesozoic sedimentary rocks, predominantly Triassic sandstones, limestones, and marls, followed by Jurassic and Cretaceous deposits. The Cretaceous formations on the hill sites, consisting of chalk and marl, are particularly noteworthy. The hill sites experience a temperate maritime climate, classified as Cfb according to the Köppen climate classification, characterized by mild temperatures with average annual temperatures ranging from 8°C to 10°C. Annual precipitation averages between 600 to 800 mm, with a relatively even distribution throughout the year. This climate supports a diverse vegetation cover on the hills, predominantly composed of deciduous forests with species such as *F. sylvatica* (beech), *Q. robur* (oak), and *C. betulus* (hornbeam), alongside coniferous stands of *P. abies* (spruce) and *P. sylvestris* (pine). The soils on the hill sites are primarily derived from weathered rock and loess deposits, classified as Luvisols and Cambisols. These soils are rich in nutrients.

The study's literature results for the Burgundy truffle's habitat preferences and distribution are multifaceted and crucial for both scientific understanding and practical applications. The findings from the systematic review provide essential insights that can inform sustainable management strategies, conservation efforts, and future research directions. What are the implications for the Hildesheim area?

The synthesis of existing literature reveals that *T. aestivum* thrives in calcareous soils with high pH and calcium carbonate content, as found in the German low mountain range (Hilszczańska et al., 2008; Păcurar et al., 2018; Robin et al., 2016). The Variscan orogeny rocks, coupled with Mesozoic sedimentary layers of limestone and marl, create an optimal geological framework for truffle habitats. The temperate maritime climate of the Hildesheim area, with moderate temperatures and well-distributed

annual precipitation, mirrors the climatic conditions favourable for truffle productivity noted in Southern Europe (Moser et al. 2017; Stobbe et al. 2012). This suggests that the geological and climatic conditions in this region are conducive to establishing and maintaining Burgundy truffle populations.

Climate change poses a significant threat to the distribution and productivity of Burgundy truffles. The findings indicate that truffle habitats are highly sensitive to changes in temperature and precipitation patterns (Čejka et al. 2020; Steidinger et al. 2022). The Hildesheim area, characterized by its temperate climate, may experience shifts in suitability due to increased temperatures and altered precipitation regimes. Understanding these dynamics is critical for developing adaptive management strategies that can mitigate the adverse effects of climate change on truffle habitats.

The insights into soil and vegetation characteristics highlight the importance of specific soil management practices to sustain truffle populations. The presence of nutrient-rich Luvisols and Cambisols, along with the diverse vegetation cover, supports the ecological requirements of *T. aestivum* (Hilszczańska et al. 2018; Gryndler et al. 2017). Effective soil management, including maintaining soil pH and calcium levels, and selecting appropriate host trees such as *F. Sylvatica*, *Q. robur*, and *C. avellana*, are crucial for promoting truffle mycorrhization and fruiting (Hilszczańska et al. 2016; Benucci et al. 2011).

The high ectomycorrhizal diversity observed in natural and cultivated truffle habitats underscores the ecological complexity and the need for conservation efforts (Leonardi et al. 2021). Protecting the biodiversity of truffle-associated species and their habitats is vital for the long-term sustainability of truffle populations. The study emphasizes the importance of conserving natural forests and implementing habitat restoration projects that mimic the ecological conditions of truffle-rich environments (Hilszczańska et al. 2016).

The lack of systematic surveys and detailed investigations in Central Europe, particularly in the German low mountain range, points to the need for continued research and monitoring (Stobbe et al. 2012; Rosa-Gruszecka et al. 2017). Establishing long-term research programs that track Burgundy truffles' distribution, productivity, and ecological interactions can provide valuable data to inform management practices. Additionally, leveraging modern technologies such as GIS-based spatial analysis can enhance our understanding of suitable habitats and assist in identifying new potential sites for truffle cultivation (Păcurar et al. 2019).

4.3 Limitations

4.3.1 Method Criticism

This study employed an experimental literature analysis using an AI-supported database. The database may have gaps, potentially distorting the evidence base. For instance, AI-supported databases can have incomplete coverage, which might lead to biased conclusions (Bedué & Fritzsche 2021). The chosen search terms (‘burgundy truffle,’ ‘tuber aestivum,’ ‘tuber uncinatum,’ and ‘tuber aestivum var uncinatum’) might have omitted important literature, leading to incomplete data. Additionally, the study could be affected by publication bias, where studies with significant findings are more likely to be published and thus included in the database (Song et al. 2010). The chosen studies may also introduce selection bias, possibly favouring those with more significant or positive results (Ioannidis 2005).

The quality of the included literature varies, with differences in peer-review status, journal impact factors, and methodological rigor potentially affecting the reliability of the analysis. This variability can

lead to heterogeneous outcomes, impacting the validity of the meta-analysis (Higgins et al. 2011). There may be geographical bias in the studies, limiting the generalizability of the findings to other regions or contexts. For instance, research shows that regional biases can significantly affect the outcomes and interpretations of meta-analyses (Munafò et al. 2017). The literature search might be biased toward studies published in certain languages, excluding relevant research published in other languages (Egger et al. 1997).

The data extraction process from the studies needs evaluation for standardization and accuracy, ensuring consistency across the analysis. The limitations of the AI tool, including its inability to interpret context or nuance as a human researcher might, could have impacted the findings. AI tools often struggle with context and nuance, which are critical for accurate data interpretation (Ferrucci et al. 2010). The use of ChatGPT (generative pre-trained transformer) poses another issue, as AI-generated errors are difficult to identify and necessitate human review. The ethical and moral implications of relying on AI for such tasks in the future require discussion. This study adopts a progressive stance on AI integration.

Furthermore, the statistical analysis lacked the depth for comprehensive evaluation and verification due to the incomparability of the methods and starting situations. Future studies would benefit from standardization. Additionally, the sample size of 14 studies is insufficient for drawing representative conclusions (Borenstein et al. 2009). The study's reproducibility is crucial, with the availability of the dataset and analysis tools to other researchers being necessary for validation purposes. By addressing these additional points, this chapter provides a more comprehensive critique and suggests pathways for improving future research methodologies.

4.3.2 Study Limitations

The study identifies several key research gaps and limitations that must be addressed to comprehensively understand the factors influencing Burgundy truffle cultivation and conservation. A primary limitation is the variability in data quality across sources, as data were collected from studies with different methodologies, sample sizes, and analytical techniques, leading to inconsistencies in results and interpretations. Standardizing data collection methods in future studies would enhance the reliability and comparability of findings.

Another significant gap is the lack of long-term empirical data on the impact of climate change on truffle distribution. Current insights are based on short-term observations and modelling studies, which may not fully capture the complex and dynamic nature of climate change effects on truffle ecology. Long-term monitoring programs are essential to track changes in truffle habitats, productivity, and ecological interactions over extended periods, providing clearer insights and refining predictive models (Čejka et al. 2020; Steidinger et al. 2022).

Additionally, while the role of fauna, such as slugs and wild boars, in truffle spore dispersal is acknowledged, there is limited understanding of the broader impacts of these interactions on truffle populations. Research should focus on quantifying these effects, understanding the behaviour of key faunal species, and developing mitigation strategies to manage their impact on truffle habitats (Piattoni et al. 2014; Salerni et al. 2013).

The study also does not extensively cover the economic and social aspects of truffle cultivation, which are crucial for understanding the sustainability and viability of truffle farming. Future research should

investigate market dynamics, economic benefits, cultural significance, community engagement, and the potential for truffle farming to support rural development (Calvo et al. 2020).

Furthermore, some regions with potential for truffle cultivation remain underexplored. Expanding research to these areas through field surveys and ecological studies would provide valuable information on truffle presence, soil and climatic conditions, and potential host plants, enhancing the overall understanding of truffle ecology and supporting the identification of new cultivation sites (Rosa-Gruszecka et al. 2021).

Addressing these research gaps and limitations through coordinated efforts and multidisciplinary approaches will provide a more comprehensive understanding of truffle ecology and support the development of effective strategies for truffle cultivation, conservation, and sustainable use. Future research should focus on optimizing inoculation techniques, exploring the long-term effects of climate change, and developing adaptive management practices to ensure the conservation and sustainable production of this valuable fungal resource. Integrating innovative methods and accounting for climatic changes are key components for the sustainable use and protection of Burgundy truffles.

4.4 Conclusion

In conclusion, this chapter underscores the intricate interplay of geological, climatic, and biotic factors that are crucial to the successful cultivation and conservation of Burgundy truffles (*Tuber aestivum var. uncinatum*) across Europe. The synthesis of current literature highlights the importance of specific soil characteristics, climatic conditions, and biotic interactions in fostering truffle productivity. This study has identified a confluence of factors that make Germany's low mountain range, particularly the Hildesheim and former Braunschweig areas, a promising location for establishing and maintaining Burgundy truffle populations.

The optimal soils for *T. aestivum* are calcareous Rendzina and brown luvic soils with high pH and significant calcium carbonate content. In the German low mountain range, particularly in the Hildesheim and former Braunschweig areas, the presence of Variscan orogeny rocks coupled with Mesozoic sedimentary layers of limestone and marl creates a favourable geological framework for truffle habitats. These characteristics mirror regions known for successful truffle production in Southern Europe. Climatic conditions play a paramount role in truffle development. *T. aestivum* thrives in warm, dry environments with sufficient soil moisture, typically found in Mediterranean and temperate zones. The region's temperate maritime climate, characterized by moderate temperatures and well-distributed precipitation, further reinforces its suitability for truffle cultivation. While the study suggests some adaptability to different climates, potential impacts of climate change on temperature and precipitation patterns highlight the need for adaptive management strategies to ensure long-term sustainability. Biotic factors, including the selection of host trees and interactions with fauna, are equally significant. The Burgundy truffle forms ectomycorrhizal relationships with a variety of deciduous and coniferous trees, with high diversity observed in hazel and hornbeam orchards. Selecting appropriate host trees like *F. sylvatica* (European beech), *Q. robur* (English oak), and *C. avellana* (hazel) fosters the necessary ectomycorrhizal fungi communities for truffle development. Additionally, maintaining healthy populations of fauna like slugs and wild boars, which contribute to spore dispersal, is vital for truffle population health. These interactions are critical for maintaining genetic diversity and spatial distribution of truffle populations.

The geological and climatic conditions in the German low mountain range are conducive to establishing and maintaining Burgundy truffle populations. The presence of nutrient-rich Luvisols and Cambisols, coupled with diverse vegetation cover, supports the ecological requirements of *T. aestivum*. Effective soil management, including maintaining soil pH and calcium levels and selecting appropriate host trees, is crucial for promoting truffle mycorrhization and fruiting. The synthesis of existing literature provides essential insights that can inform sustainable management strategies, conservation efforts, and future research directions.

Finally, the study can answer the research questions:

1. **What geological, climatic, and biotic factors influence the occurrence and productivity of the Burgundy truffle in Europe?**

A combination of geological, climatic, and biotic factors influences the occurrence and productivity of the Burgundy truffle in Europe.

Burgundy truffles thrive in calcareous soils, such as Rendzina and brown luvic soils, which are rich in calcium carbonate. The high pH and significant calcium carbonate content in these soils are essential for truffle development. Regions with Variscan orogeny rocks and Mesozoic sedimentary layers of limestone and marl provide the optimal geological framework for truffle habitats. These substrates are conducive to creating the necessary soil conditions for truffle growth.

Climatic conditions play a paramount role in truffle development. *T. aestivum* prefers warm environments, and optimal conditions are typically found in Mediterranean and temperate zones, where temperatures are conducive to truffle development. Adequate soil moisture is crucial, but the truffle also thrives in relatively dry environments. Well-distributed annual precipitation supports soil moisture levels necessary for truffle growth. While traditionally associated with Mediterranean climates, Burgundy truffles have shown adaptability to various climatic conditions, including temperate zones north of the Alps. However, climate change poses risks, with potential impacts from increased temperatures and altered precipitation patterns, highlighting the need for adaptive management strategies.

Biotic factors, including the selection of host trees and interactions with fauna, are equally significant. The truffle forms ectomycorrhizal relationships with specific host trees, such as *Fagus sylvatica* (European beech), *Quercus robur (English* oak), and *Corylus avellana* (hazel). These trees support diverse ectomycorrhizal fungi communities essential for truffle mycorrhization and fruiting. The presence of specific organic compounds and a diverse microbial community in the soil promotes truffle fruiting. High calcium carbonate levels and balanced C/N ratios (carbon to nitrogen) enhance soil fertility and truffle productivity. Fauna such as slugs and wild boars play vital roles in spore dispersal, contributing to the genetic diversity and spatial distribution of truffle populations. These animals help maintain healthy truffle populations through their natural behaviours, although their foraging can also pose challenges that need to be managed.

Understanding and optimizing these geological, climatic, and biotic factors are crucial for the effective cultivation and conservation of Burgundy truffles in Europe.

2. **What are the implications for potential habitats in Germany's low mountain range?**

The implications for potential habitats in Germany's low mountain range, particularly in the Hildesheim and former Braunschweig areas, are significant for establishing and maintaining Burgundy truffle populations. The geological conditions in these regions align favourably with the presence of calcareous

soils rich in calcium carbonate, often associated with Variscan orogeny rocks and Mesozoic sedimentary layers. These characteristics are similar to regions in Southern Europe known for successful truffle production, suggesting a strong potential for truffle cultivation in the German low mountain range.

The temperate maritime climate of this area, characterized by moderate temperatures and well-distributed precipitation, further supports its suitability for truffle habitats. These climatic conditions align with the ecological requirements of *T. aestivum*, which thrives in warm, dry environments with sufficient soil moisture. The adaptability of the truffle to various climatic conditions, including temperate zones north of the Alps, reinforces the potential for successful cultivation in this region. However, the potential impacts of climate change on temperature and precipitation patterns must be considered, emphasizing the need for adaptive management strategies to ensure long-term sustainability.

Biotic interactions play a crucial role in the potential for truffle cultivation in the German low mountain range. The selection of appropriate host trees, such as *Fagus sylvatica* (European beech), *Quercus robur* (English oak), and *Corylus avellana* (hazel), is essential for fostering the necessary ectomycorrhizal fungi communities that support truffle development. These trees are well-suited to the region's soils and climate, further enhancing the potential for truffle cultivation. Maintaining healthy populations of fauna, such as slugs and wild boars, which contribute to spore dispersal, is also vital for the health and genetic diversity of truffle populations. Effective soil management practices, including maintaining high pH and calcium levels, and ensuring the presence of specific organic compounds and a diverse microbial community, are crucial for promoting truffle mycorrhization and fruiting.

Overall, the geological, climatic, and biotic conditions of Germany's low mountain range provide a promising foundation for the cultivation and conservation of Burgundy truffles. By addressing the potential impacts of climate change and optimizing soil and vegetation management practices, the region can become a significant area for truffle production, contributing to the conservation and sustainable use of this valuable fungal resource.

Future research should focus on long-term empirical studies to monitor the impacts of climate change on truffle habitats, productivity, and ecological interactions. Standardizing data collection methods will enhance the reliability and comparability of findings. Expanding research to underexplored regions through field surveys and ecological studies will provide valuable information on truffle presence, soil and climatic conditions, and potential host plants. Additionally, integrating socio-economic dimensions, such as market dynamics and cultural significance, will support the sustainability and viability of truffle farming. Innovative soil management practices, optimized inoculation techniques, and adaptive management strategies are essential for enhancing truffle productivity and ensuring the conservation and sustainable use of this valuable fungal resource.

In summary, this chapter underscores the importance of an integrated approach to Burgundy truffle cultivation and conservation, encompassing geological, climatic, and biotic factors. By addressing identified research gaps and leveraging modern technologies, we can contribute to the conservation of this valuable fungal resource and expand its cultivation potential beyond traditional habitats.

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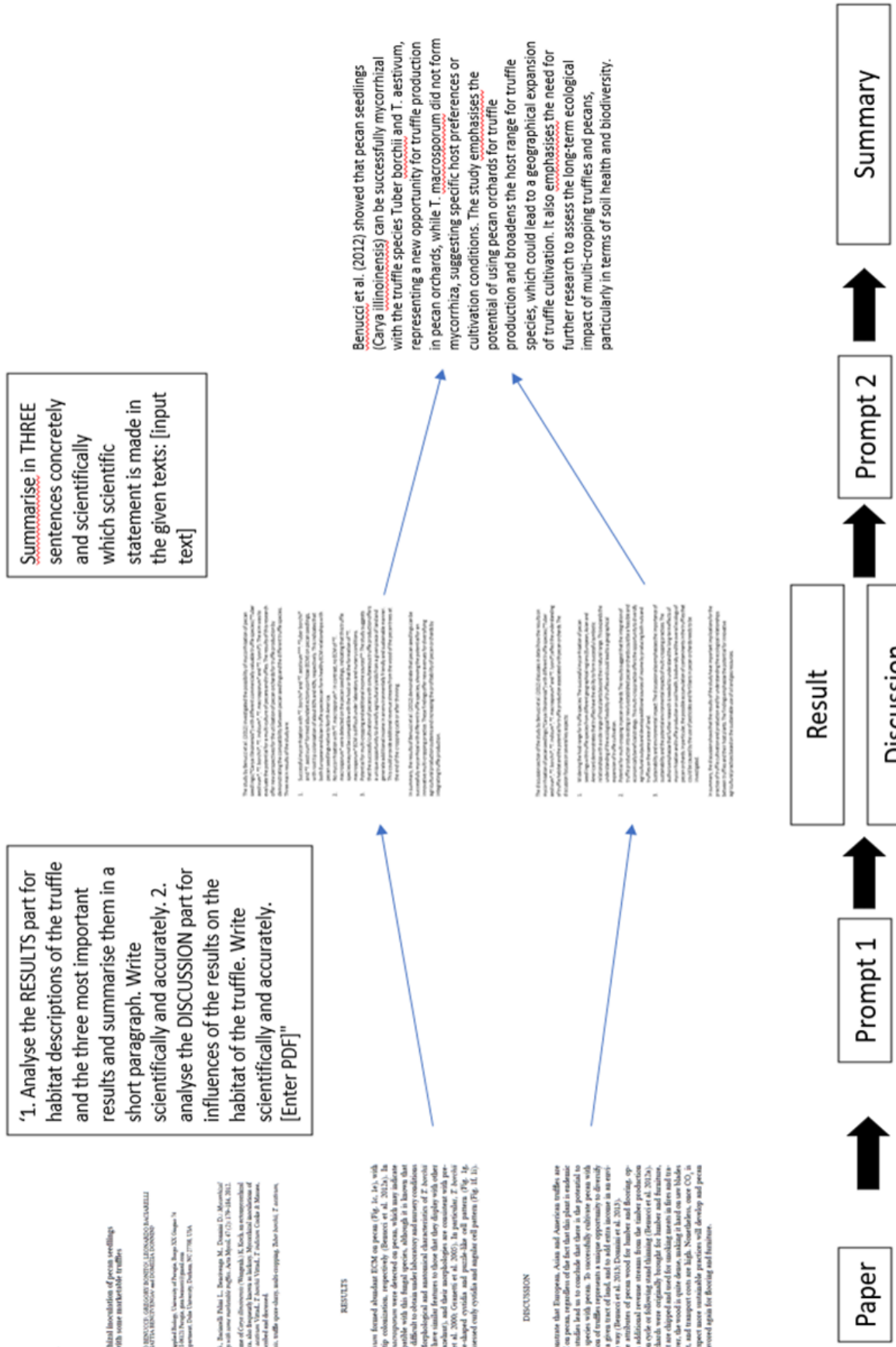
6. Appendix

6.1 Appendix 1: Literature Data

Literature data can be found under the following link:

https://www.researchgate.net/publication/381297883_Dimensions-Publication-2024-03-11_15-12-23

6.2 Appendix 2: Literature Extraction Process



6.3 Appendix 3: Data Table

	min	max	median	mean	sd
Moisture [%]	8.10	26.30	9.78	13.90	6.80
Clay [%]	3.30	46.00	19.40	20.32	9.43
Silt [%]	2.00	64.70	26.60	29.74	15.80
Sand [%]	8.40	94.60	51.22	50.01	21.82
pH_h2o	3.70	10.50	7.49	7.35	0.79
pH_kcl	4.80	8.20	7.40	7.17	0.72
CaCO3 [%]	0.00	47.70	2.53	9.58	6.44
TOC [%]	1.45	12.34	5.07	2.50	2.50
SOM [%]	2.49	21.22	8.19	4.07	4.07
Ctot [%]	2.38	6.20	4.40	1.28	1.28
Norg [%]	0.26	1.06	0.49	0.20	0.20
Ntot [%]	0.14	1.66	0.35	0.30	0.30
C_N [%]	9.28	25.72	12.51	3.14	3.14
Prec [mm]	519	937	600	624.08	116.64
Temp [°C]	7	15	8	8.321	1.785

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