Desert truffles in the Maamora Forest, Morocco: local nomenclature, harvesting practices, ethnoecology, ethnophenology, and resource availability

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Research

Abstract

Background: Desert truffles are regarded as noble delicacies with multiple medicinal properties, attracting strong scientific interest worldwide. Maamora Forest, where some of them have been harvested for centuries, provides a privileged setting for studying traditional practices. Thus, this study explores these practices, along with ethnoecological and ethnophenological knowledge they encompass, as well as the threats and behaviors that may compromise sustainability.

Methods: This ethnomycological survey, conducted among 149 truffle hunters across the five Maamora Forest cantons, was based on a semi-structured questionnaire complemented by personal field observations. The specimens collected from the pickers were identified using molecular analyses. Collected data were analyzed using descriptive statistics, Pearson's Chi-square test, Multiple Correspondence Analysis, non-metric Multidimensional Scaling, and Variance Permutational Multivariate Analysis.

Results: Results show that desert truffle harvesting is mainly practiced by elderly, unemployed individuals, particularly married women. They are often experienced and regular gatherers. Significant differences were noted across cantons regarding local nomenclature and harvesting practices. Study also highlights a deep empirical understanding of phenology. Main factors threatening sustainability of this resource are overgrazing, urbanization, drought, reforestation with exotic species, and use of pickaxes. Premature harvesting, overexploitation and poor post-harvest practices also contribute to truffle habitats degradation and substantial losses of a large part of the harvest.

Conclusions: This work constitutes the first ethnomycological assessment of desert truffles in the Maamora Forest. It enriches local ecological knowledge and supports future research in ecology and biodiversity conservation, while advocating for integrated sustainable management strategies including awareness-raising, cooperative structuring, and domestication trials.

Keywords: Ethnomycology, Knowledge transmission, Truffle hunter, Truffle sustainability, *Delastria rosea*, *Tuber oligospermum, Terfezia arenaria*.

Background

The term "desert truffles" is commonly used to refer to truffles generally found in arid and semi-arid ecosystems. They are hypogeous fungi, corresponding to the fructification of underground mycelium, and take the form of edible tubers. Desert truffles occur in several European Mediterranean countries, notably France, Greece, Italy, Portugal, and Spain (Díez *et al.* 2002, Tejedor-Calvo *et al.* 2021, Therville *et al.* 2013). They are also present in the Middle East, especially in Iran, Iraq, Kuwait, Lebanon and Saudi Arabia (Owaid 2018, Zambonelli *et al.* 2014). In Africa, they are found particularly in North countries, including Algeria, Egypt, Libya, Morocco, and Tunisia (Kaddouri *et al.* 2024), as well as in Kalahari region of Southern Africa (Trappe *et al.* 2014). Desert truffles have also been documented in Australia (Trappe *et al.* 2008) and in the arid regions of Central China (Lu *et al.* 2022). Most hypogeous fungi are mycorrhizal, forming symbiotic associations with plants, particularly those of the genus *Helianthemum*, or with trees belonging to various phyla (Andrino *et al.* 2025, Díez *et al.* 2002).

Harvested for over 3,000 years (Shavit & Shavit 2014), desert truffles are valued for their organoleptic qualities, nutritional value, and multiple traditional uses. They are largely consumed in North Africa, the Middle East, especially Gulf countries, and Europe, where they play a central role in many festive and local dishes and are often regarded as a delicacy comparable to meat (Ferreira *et al.* 2023). Desert truffles are also valued for their medicinal benefits. They are used to treat various ailments, including eye diseases, particularly trachoma, and are also well known for their stimulating effect on sexual function, as well as for strengthening the immune system and exhibiting anticancer, antibacterial, antioxidant, and antiviral properties (Barkat 2025, Lee *et al.* 2020, Tejedor-Calvo *et al.* 2021).

In addition, desert truffles are used as a food source in arid regions where resources are limited, and their commercialization contributes to the income of local populations (Fellaki *et al.* 2025, Pieroni 2016). Morocco holds a relatively rich potential for hypogeous fungal taxa, with around ten species belonging to genera *Delastria*, *Picoa*, *Terfezia*, *Tirmania*, and *Tuber*. The main areas of occurrence include Maamora Forest, Doukkala Sahel, Eastern Highlands, and, to a lesser extent, South Sahara (Kaddouri *et al.* 2024). In Maamora, species found are *Delastria rosea*, *Terfezia arenaria*, *T. leptoderma*, *Tuber oligospermum*, *T. asa*, *T. gennadii*, *T. lacunosum*, and *T. sphaerospermum*; most of them are endemic to the forest (Abourouh 2020, Khabar 2002).

Despite the growing interest in desert truffles within Maamora forest, several gaps remain. Available studies have mainly addressed taxonomic, ecological, and distributional aspects of hypogeous fungi (e.g., Abourouh 2020, Kaddouri *et al.* 2024, Khabar 2002), whereas detailed ethnomycological documentation of harvesting practices, the influence of gatherers' socio-demographic characteristics on these practices and on knowledge transmission, as well as perspectives from local communities on anthropogenic pressures and climate constraints that may affect desert truffle sustainability, remains to be established to our knowledge. In this context, local knowledge, its modes of transmission, and the ethnoecological and ethnophenological dimensions provide a relevant framework for investigation.

It is within this context that present study is situated. It aims to document knowledge of desert truffle gatherers in Maamora Forest, focusing on harvesting practices, techniques used, modes of transmission, search indicators, perceived fruiting periods, associated ecological knowledge, and locally identified natural and human threats. The study also discusses effects of harvesting practices on desert truffle sustainability.

We formulate the following hypotheses: (i) ethnomycological knowledge and harvesting practices vary significantly across the five cantons of the Maamora Forest; (ii) socio-demographic characteristics shape harvesting behaviors as well as knowledge transmission; and (iii) perceived resource decline and its underlying drivers are spatially structured across cantons.

Materials and Methods

Study area

Maamora Forest lies within a rectangle measuring 69 km in length (West to East) and 38 km in width (North to South). It is situated at coordinates ranging from 6° to 6° 45′ West longitude and from 34° to 34° 20′ North latitude, Northeast Moroccan capital Rabat, and between this city and Kenitra in North (Fig. 1). Cork oak woodland (*Quercus suber* L.) covers a total area of over 60,000 ha, accounting for nearly 11 % of global surface area (Benabid 2000). Rest of area is occupied by exotic species such as *Acacia* spp., *Pinus* spp., or *Eucalyptus* spp. (Benabou *et al.* 2022), or corresponds to bare spaces.

Maamora Forest is divided into five cantons (A, B, C, D, and E) (Fig. 1), and exhibits variable climatic conditions. Annual rainfall gradually decreases from West (650 mm) to East (350 mm), rain falls from October to May, mainly in November, December, and January, and average monthly temperatures range between 12 °C (January) and 25 °C (August) (Cherki & Gmira 2013). In general, Maamora bioclimate is sub-humid with mild winters in the West (Canton A and Canton B Western part), and semi-arid with temperate winters in the East (Benabou *et al.* 2022). Soils, slightly acidic, are characterized by presence of sandy horizon, with depth ranging from 30 cm to 7 m. Sandy layers rest either on Miocene marls or Pliocene sandstones, and entire sequence is underlain by red sandy clay formed during the Villafranchian (Aroui-Boukbida *et al.* 2016). Forest reaches a maximum elevation of approximately 280 m at its Southeastern part.

In the Maamora Forest, local population is estimated at about 300,000 inhabitants (Laaribya *et al.* 2014), corresponding to an average density of approximately 4.5 inhabitants per hectare. The main socio-economic activities carried out by men include extensive livestock grazing, various forestry activities (e.g., wood and cork harvesting and reforestation), and other jobs such as guarding. Women are more involved in collecting forest products, notably deadwood, aromatic and medicinal plants, acorns, and desert truffles. The marketing of certain woody and non-woody products (e.g., charcoal) is more often carried out by men, especially young people (Qarro 2016).

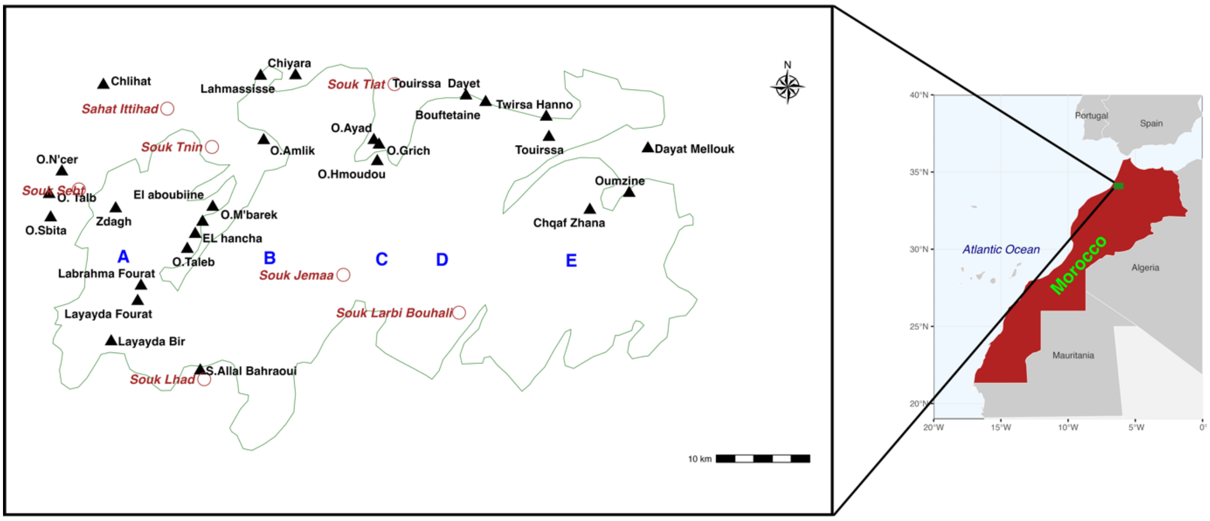

Figure 1. Maamora Forest location [right], forest five cantons (A, B, C, D and E), and survey sites (▲villages and ○ markets) [left] (Map generated using R v 4.5.1 with packages sf, ggplot2, r natural earth data, cowplot, and ggspatial).

Ethnomycological survey

This research was carried out from February 2023 to May 2025 through an ethnomycological survey conducted among desert truffle hunters in the five cantons of the Maamora Forest. Semi-structured questionnaire (Alexiades 1996) was established in local dialect (*darija*) and structured into two main parts. The first one is about hunter profile, including gender, age, family situation, education level, employment and monthly income. The second concerns various aspects of traditional desert truffle gathering practices, encompassing vernacular names, pickers categories, gatherers number by household, experience years, harvesting frequency, whether desert truffles are gathered individually or with other people, daily search time and distance covered, picking techniques, collected desert truffles types, transport containers, knowledge transfer, current availability perception compared to the last 10 years, regression factors, ethnophenology (the annual harvesting period of desert truffles) and ethnoecological aspects (associated host plants, main search locations and perceived signs of desert truffle presence).

This questionnaire was the basis for interviews with 149 gatherers. Recruitment relied on a purposive sampling strategy targeting active gatherers, complemented by opportunistic recruitment at the main contact locations. An exploratory phase in several *douars* helped us to identify localities involved in harvesting (Fig. 1). Identification of additional douars and harvesting sites was facilitated by information provided by intermediaries (an informal snowball approach), although these intermediaries were not included among the respondents. Interviews were conducted in the forest at harvesting sites, as well as in certain *douars* (sales points) and in weekly markets (*souks*) where desert truffles are traded (Fig. 1). Eligible participants were individuals who self-identified as gatherers and had harvested in the Maamora Forest during the current season. They were enriched by personal observations (Musante & DeWalt 2010) carried out during several field trips alongside desert truffle hunters.

Desert truffles identification

Desert truffle samples were collected from hunters and identified at genus level in the Research Unit AgroPhysiology, AgroBiotechnologies & Environment (APABE), Natural Resources and Sustainable Development Laboratory, Sciences Faculty, Ibn Tofail University, Kenitra, Morocco, using ecological and macroscopic characteristics. Each specimen was dried, packaged, labeled and deposited in our mycological herbarium under the local voucher codes APABE-UIT F1, APABE-UIT F2, APABE-UIT F3, and APABE-UIT F4, corresponding respectively to samples of: *Terfezia* sp.1, *Terfezia* sp.2, *Tuber* sp., and *Delastria* sp. (Table 1). Identifications were subsequently completed at UATRS Division Laboratory, National Center for Scientific and Technical Research (CNRST), Rabat, Morocco, using molecular biology tool.

DNA extraction, amplification and sequencing of the ITS Region

DNA extraction, amplification, and sequencing of the ITS region techniques were described by laboratory Report No. 61BIO02, File No. D311/24. According to this genomic DNA was extracted from cultured fungal mycelium using the automated *MagPurix Plant DNA Extraction Kit* (Zinexts Life Science Corp., Taiwan). DNA concentration and purity were assessed spectrophotometrically with a *Nanodrop 8000* (Thermo Fisher Scientific, USA). ITS region of rDNA was amplified with universal primers ITS-1F and ITS4-R and confirmed with primers NS7/NS8. PCR reactions were performed with MyTaq DNA Polymerase Kit (Bioline) on a Verity thermal cycler (Applied Biosystems), and sequencing was carried out using the Sanger method.

Phylogenetic analysis

ITS1 and ITS4 primers (White *et al.* 1990) were used for species-level identification. From resulting reads, consensus sequences were generated in R (v4.5.1) with Biostrings and DECIPHER packages (Bioconductor) (Wright 2016) and then manually edited to correct ambiguous nucleotides. Validated sequences were submitted to GenBank; corresponding accession numbers are listed in Table 1. To identify closest relatives, consensus sequences generated in this study were queried against GenBank (NCBI; https://blast.ncbi.nlm.nih.gov/Blast.cgi) using BLAST and then aligned with matching entries (Altschul *et al.* 1990). Alignments were performed using MAFFT v7.526, with L-INS-i algorithm and a maximum of 1000 iterative refinements (Katoh & Standley 2013). Phylogenetic analysis was performed using IQ-TREE v3.0.1 (Nguyen *et al.* 2015). Best-fit evolutionary model (HKY+R2) was automatically selected by ModelFinder (Kalyaanamoorthy *et al.* 2017) among 968 models tested. Phylogenetic tree was reconstructed using maximum likelihood method, with topological optimization by Nearest Neighbor Interchange (NNI). Clade support was assessed with 1000 ultrafast bootstrap replicates (UFBoot2) and SH-aLRT test (1000 replicates) (Nguyen *et al.* 2015). Visualization of phylogenetic tree was carried out with online tool iTOL version 7 (Letunic *et al.* 2021).

Statistical analysis

Statistical analyses were performed using R software version 4.5.1. Descriptive statistics were employed to calculate percentages related to various sociodemographic characteristics of desert truffle hunters, as well as ethnomycological variables concerning knowledge and harvesting practices in Maamora Forest. A bivariate analysis based on Pearson's Chi-squared test was conducted to examine correlations between the five cantons of the forest and each of the variables studied in the survey.

A Multiple Correspondence Analysis (MCA) was then carried out to explore the desert truffle species harvested across the different cantons, using *FactoMineR* package (Le *et al.* 2008) and figures were produced with *ggplot2* package (Wickham 2016). MCA was performed on a categorical dataset in which rows correspond to individual informants (n = 149). The active variables were three binary (Yes/No) variables derived from the multiple-choice question on harvested species (*Delastria rosea*, *Tuber oligospermum* or *Terfezia arenaria*), with Yes = species reported/collected and No = not reported. Canton (A-E) was included as a supplementary (illustrative) qualitative variable and therefore did not contribute to the computation of the dimensions. To improve the readability, only the "Yes" modalities of the species variables are displayed, although the MCA was computed using all modalities (Yes/No).

To analyze factors associated with perceived regression of desert truffles, as mentioned by some respondents, a nMDS (non-metric multidimensional scaling) method was applied using the *metaMDS* function from the *vegan* package (Oksanen *et al.* 2025), based on Bray-Curtis dissimilarity distances. The reported factors were projected onto the factorial space using the *envfit* function (*vegan*). The significance of the fitted vectors was tested with 999 permutations, and significant vectors ($p \leq 0.05$) were subsequently scaled according to their correlation coefficients (R^2) before being projected onto the ordination. Finally, a Permutational Multivariate Analysis of Variance (PERMANOVA) was employed to examine the significant influence of canton on the reported factors affecting desert truffle abundance, using the adonis2 function from the *vegan* package.

Results

Molecular identification and phylogenetic analysis

Three ascocarps of four analyzed in this study (*Terfezia* sp.1, *Terfezia* sp.2, and *Tuber* sp.) yielded ITS1-5.8S-ITS2 sequences of 656, 592, and 654 base pairs (bp), respectively (Fig. 2). Concerning *Delastria* sp., no results were obtained.

Figure 2. Desert truffle species picked in Maamora forest: a) *Terfezia arenaria* b) *Tuber oligospermum*, and c) *Delastria rosea*.

In the genus *Terfezia* ITS phylogeny (Fig. 3), the two species clustered within *T. arenaria* clade, which was strongly supported (ML-BS = 100 %), together with reference sequences (MW508702 and MW508706) from Portugal.

Figure 3. Maximum likelihood (ML) tree based on ITS sequences, depicting *Terfezia arenaria* APABE UIT F1 ‘PX129066’ and *Terfezia* arenaria APABE UIT F2 ‘PX129067’ phylogenies. *Delastria rosea* was used as the outgroup. ML support values (≥ 75 %) are shown at nodes. Sequences obtained in the present study are shown in green. Scale bar indicates expected number of changes per site.

In the genus *Tuber* (Fig. 4), analyzed species clustered within *T. oligospermum* clade, with strong support (ML-BS = 98,2 %), together with *T. oligospermum* reference sequence CMI_UNIBO4231 (KF021623), originating from the same forest as our study. These groupings show that our specimens correspond to species *Terfezia arenaria and Tuber oligospermum*, without notable divergence from available reference material.

Consensus sequences have been deposited in GenBank (NCBI) with the following accession numbers: *Terfezia arenaria* APABE-UIT F1, **‘**PX129066**’**; *Terfezia arenaria* APABE-UIT F2, **‘**PX129067’ and *Tuber oligospermum* APABE-UIT F3, **‘**PX129068**’** (Table 1).

Local naming of desert truffles harvested in the Maamora Forest

Local population assigns indigenous names to the wild desert truffle species they collect (Table 1). Twelve vernacular names have been recorded for three species of desert truffles picked: five for *Terfezia arenaria*, six for *Tuber oligospermum*, and one for *Delastria rosea.* This nomenclature is based on ecological characteristics such as habitat, growth mode, fruiting body appearance, and host plant, morphological traits as color and texture, as well as organoleptic characteristics above all taste.

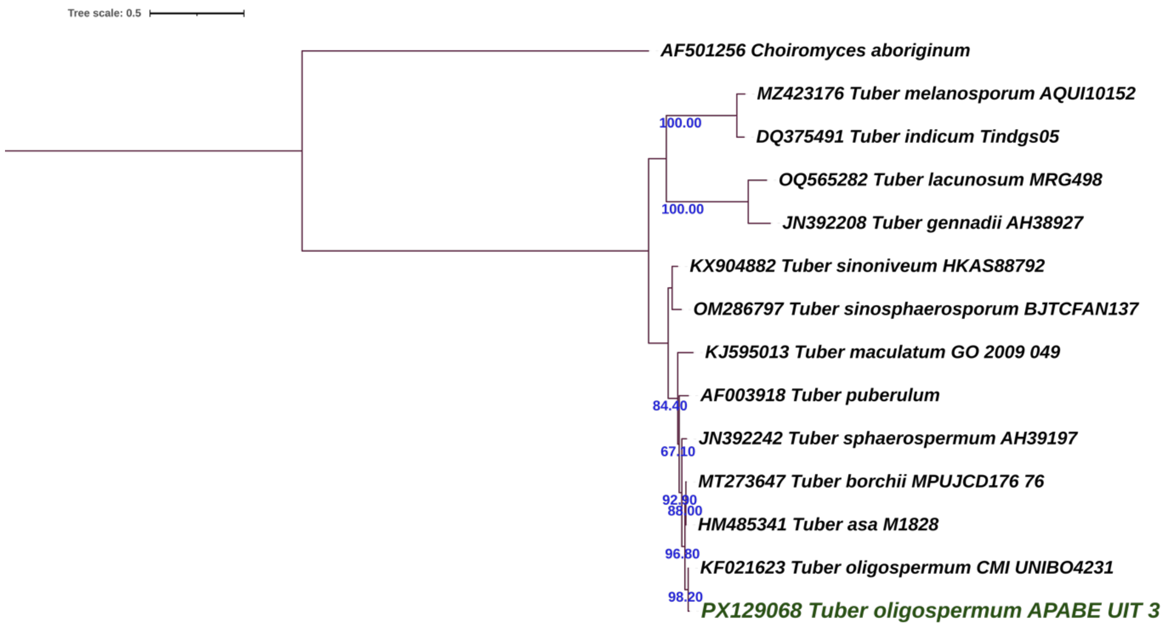

Figure 4. Maximum likelihood (ML) tree based on ITS sequences, depicting *Tuber oligospermum* APABE UIT F3 'PX129068' phylogeny. *Choiromyces aboriginum* was used as the outgroup. ML support values (≥ 67 %) are shown at nodes. Sequences obtained in the present study are shown in green. Scale bar indicates expected number of changes per site.

Table 1 Scientific names, accession numbers, and vernacular names of desert truffles according to canton.

Scientific name /		**Vernacular name**				
local voucher	**Accession**	**Canton A**	**Canton B**	**Canton C**	**Canton D**	**Canton E**
Delastria rosea Tul. & C.Tul APABE-UIT F4	-	**terfess l'har**	**terfess l'har**	-	-	-
Terfezia arenaria (Moris) Trappe APABE-UIT F1 APABE-UIT F2	PX129066 PX129067	**terfess** **terfess l'rose** **alkam'a**	**terfess terfess l'rose** **alkam'a** **terfess l'hmar**	**terfess** **terfess d'erbiae**	**terfess**	**terfess**
Tuber oligospermum Tul. & C. Tul.Trappe APABE-UIT F3	PX129068	**terfess taïda** **terfess l'byad** **l'khraj** **l'hadri**	**terfess taïda** **terfess l'byad**	**terfess taïda** **dkar** **l'majjit**	**terfess** **taïda** **dkar**	**terfess taïda** **terfess l'byad**

Due to pinkish hue of their ascocarps, *Terfezia arenaria* is named "**terfess l'rose**" (pink truffles) and "**terfess l'hmar**" (red truffles), whereas "**terfess l'byed**" designates *Tuber oligospermum*. Local population also uses name "**terfess dkar**" (male truffles) for *Tuber oligospermum*, due to its firmer texture compared to *Terfezia arenaria*.

Additionally, based on its habitat, *Tuber oligospermum* are also known as "**terfess taïda**" (pine truffles), as it is commonly harvested beneath pine trees. Conversely, *Terfezia arenaria is* sometimes referred to as "**terfess d'erbiae**" (vegetable truffles), in reference to its host-plant, *Tuberaria guttata*. The term "**terfess**" is based on fruit bodies observation mode and generally refers to all desert truffles species because of their hypogeous nature. Word "**al-kamah**", meaning "hidden" is also sometimes used. In contrast, "**l'khraj**" refers to desert truffles ascocarps emergence at soil surface.

Delastria rosea is named "**terfess l'har**", which means "bitter truffle" because of its taste.

Nevertheless, some ethnic terms, such as "**l'majjite**" and "**l'hadri**", have no specific meaning but are used to refer to *Tuber oligospermum.*

Our survey revealed desert truffle names not previously documented, such as "**l'majjite**", "**terfess d'erbiae**", "**terfess l'byed**", "**l'hadri**" and "**l'khraj**".

Comparison between cantons reveals both common and localized vernacular names. Name "**terfess**" is mentioned for all cantons. "**terfess l'rose**" is used only in cantons A and B, whereas "**terfess l'hmar**" is recorded only in canton B. Term "**alkam'a**" is employed exclusively in cantons A and B, while "**terfess d'erbiae**" is specific to canton C.

For *Tuber oligospermum*, "**terfess taïda**" is reported across all surveyed areas. "**terfess l'byad**" is used in cantons A, B and E, while "**dkar**" is mentioned only in cantons C and D. More specific names, such as "**l'khraj**" and "**l'hadri**" are limited to canton A, whereas "**l'majjit**" is used solely in canton C. In addition, "**terfess l'har**" referring to *Delastria rosea*, is mentioned in cantons A and B.

Hunters socio-demographic characteristics

Among 149 hunters (Table2), 73.2 % are female and 26.8 % male (2.73/1 women per men). This predominance of women can be observed in all cantons, with rates ranging from 81.48 % to 70.59 %. Even in canton C, where gender distribution is slightly more balanced, women remain majority (58.06 %).

Sixty-four percent of 149 respondents are aged 45 and over. This age group dominates across all cantons. It is followed by 31-44 group with 26.2 %, notably in cantons E (35.29 %) and A (31.48 %). In contrast, young people aged from 16 to 30 are very underrepresented (9.4 % only) and are mainly found in canton C (29.03 %). They are scarcely represented in cantons A and B, and completely absent from cantons D and E.

A large proportion of desert truffle hunters are illiterate, representing majority in each canton (76.47 %, 74.19 %, 71.43 %, 68.52 % and 68.42% in cantons E, C, B, A and D, respectively). Individuals with primary education are less represented, with percentages ranging from 26.32 % in canton D to 17.65 % in canton E. Those with secondary education constitute a small minority across all cantons, varying from 10.71 % in canton B to 5.26 % in canton D.

Table 2. Socio-demographic characteristics of truffle hunters.

Informant variable	**Canton N (%)**				
	A	**B**	**C**	**D**	**E**
Gender					
Female	44 (81.48)	20 (71.43)	18 (58.06)	15 (78.95)	12 (70.59)
Male	10 (18.52)	8 (28.57)	13 (41.94)	4 (21.05)	5 (29.41)
Group age					
≥ 45	35 (64.81)	21 (75.00)	15 (48.39)	14 (73.68)	11 (64.71)
16-30	2 (3.70)	3 (10.71)	9 (29.03)	0 (0.00)	0 (0.00)
31-44	17 (31.49)	4 (14.29)	7 (22.58)	5 (26.32)	6 (35.29)
Education level					
Illiterate	37 (68.52)	20 (71.43)	23 (74.19)	13 (68.42)	13 (76.47)
Primary	14 (25.93)	5 (17.86)	6 (19.35)	5 (26.32)	3 (17.65)
Secondary	3 (5.56)	3 (10.71)	2 (6.45)	1 (5.26)	1 (5.88)
Occupation					
Farmer	4 (7.41)	6 (21.43)	8 (25.81)	1 (5.26)	0 (0.00)
Forest guardian	1 (1.85)	1 (3.57)	0 (0.00)	1 (5.26)	0 (0.00)
Retired	3 (5.56)	2 (7.14)	0 (0.00)	1 (5.26)	0 (0.00)
Shepherd	1 (1.85)	1 (3.57)	0 (0.00)	1 (5.26)	3 (17.65)
Unemployed	45 (83.33)	18 (64.29)	23 (74.19)	15 (78.96)	14 (82.35)
Monthly income					
0 DH	45 (83.33)	18 (64.29)	23 (74.19)	15 (78.95)	14 (70.59)
1 000-2 000 DH	5 (9.26)	5 (17.86)	1 (3.23)	1 (5.26)	0 (0.00)
500-1 000 DH	4 (7.41)	5 (17.86)	7 (22.58)	3 (15.79)	3 (29.41)
Family situation					
Married	49 (90.74)	25 (89.29)	20 (64.52)	18 (94.74)	16 (94.12)
Single	2 (3.70)	2 (7.14)	9 (29.03)	1 (5.26)	1 (5.88)
Widower	3 (5.56)	1 (3.57)	2 (6.45)	0 (0.00)	0 (0.00)

Most desert truffle hunters across five cantons are unemployed, with rates ranging from 64.29 % to 83.33 %. Farmers appear more frequently in cantons B (21.43 %) and C (25.81 %) but are nearly absent in canton D (5.26 % only) and completely absent in canton E. Forest guardians, retired, and shepherds are only marginally represented across all cantons, with each group rarely exceeding 7 %. However, we noticed that third category is slightly more represented in canton E with 17.65 %.

Majority of desert truffle gatherers report having no monthly income, with proportions ranging from 83.33 % in canton A to 64.29 % in canton B. Those earning between 500 and 1 000 DH per month are less represented, with proportions ranging from 29.41 % in canton E to 7.41 % in canton A. Informants with a monthly income between 1 000 and 2 000 DH constitute a small minority and are entirely absent in canton E.

Gathered data indicates that married individuals (85.91 %), who are more frequently engaged in desert truffle gathering, are represented across all cantons (94.74 % to 64.52 %), while single individuals (10.07 %) are more common in canton C (29.03 %). Widowers account for only a small minority (4,03 %).

Ethnomycological knowledge and practices

Variables studied in ethnomycological survey concerning desert truffle hunter profiles, their harvesting practices, availability and phenology perceptions, as well as species gathered and knowledge transmission modes across the five cantons of the Maamora Forest are presented in table 3. Chi-square test analysis results showed that 10 out of the 13 variables investigated exhibited a statistically significant correlation ($p < 0.05$), indicating clear differences in knowledge between the five cantons of the Maamora Forest.

Desert truffle hunter profiles (Q_1 to Q_3; Table 3)

Chi-square test highlighted apparent differences between Maamora Forest five cantons studied concerning several aspects of desert truffle gathering such as gatherers categories ($\chi^2 = 20.34$, $p = 0.0004$), their number per household ($\chi^2 = 14.12$, $p = 0.0069$), and hunting experience ($\chi^2 = 21.11$, $p = 0.0068$).Regular gatherers are predominant in cantons B (82.14 %), A (81.48 %), E (76.47 %), and D (68.42 %), while canton C shows opposite trend, with 61.29 % occasional gatherers. In cantons B and A, desert truffle hunting often involves three to four household members (71.43 % and 60.38 %, respectively). Conversely, in cantons D, C and E, it is mainly practiced by one to two people (60.38 %, 67.74 % and 64.71%, respectively). Furthermore, respondents expressed a strong attachment to desert truffle collection activity, locally known as ''*N'terfsso*'' or ''*N'saydo terfess*'', which is perceived as a key moment in their annual calendar.

A notable proportion of gatherers in cantons A, B and E reported having long-term experience in truffle gathering of more than 16 years (43.14 %, 43.14 % and 43.14%, respectively). In contrast, respondent majority in canton C (58.06 %) have practiced this activity for less than 7 years. Data also reveal a significant number of gatherers with intermediate experience of 8 to 15 years in canton D (41.18 %).

Harvest practices and field techniques (Q4 to Q10; Table 3)

No significant differences were observed between responses to questions concerning "weekly harvesting frequency" ($\chi^2 = 7.15$, $p = 0.1282$), "Who do you hunt truffles with?" ($\chi^2 = 4.19$, $p = 0.3932$), or "daily search time" ($\chi^2 = 1.05$, $p = 0.9026$). Nevertheless, majority of gatherers reported harvesting truffles 4 to 5 days per week in cantons A, B, C and E (59.62 %) (51.85%, 71.43 % and 70.59 %, respectively). Only canton D stands out, with greater part of respondents reporting harvesting 6 to 7 days per week (63.16 %).

Furthermore, group harvesting is predominant across all cantons, with rates exceeding 81.82 % and even reaching 100 % in canton E. In contrast, individual gathering remains marginal or even non-existent; 0 % in the same canton. Several respondents indicated that whole family goes out together to gather truffles, leaving only few members at home to supervise or carry out household tasks. These findings indicate that desert truffle hunting in Maamora Forest is primarily a collective activity, often carried out by families or small friends or neighbors organized groups, usually consisting of at least three people.

Long search periods of 7 to 8 hours per day are common across all cantons, ranging from 70.59 % in canton E to 58.62 % in canton C. A significant correlation ($\chi^2 = 18.51$, $p = 0.0010$) was found between cantons and daily distance covered by gatherers. Majority of respondents in cantons C, B and A (70.00 %, 67.86 % and 61.23 %, respectively) reported covering distance of 6 to 10 km per day. In contrast, canton D stands out with 84.21 % of gatherers covering longer distance of 11 to

19 km. Canton E presents an intermediate profile, with relative majority (58.82 %) reporting long distances, compared to 41.18 % reporting shorter ones.

Table 3. Studied variables in ethnomycological survey on desert truffle hunter knowledge.

Variable	Canton A	Canton B	Canton C	Canton D	Canton E	X^2	P value
Q_1: Picker categories	N = 54	N = 28	N = 31	N = 19	N = 17	20.34	0.0004*
Occasional	10 (18.52 %)	5 (17.86 %)	19 (61.29 %)	6 (31.58 %)	4 (23.53 %)		
Regular	44 (81.48 %)	23 (82.14 %)	12 (38.71 %)	13 (68.42 %)	13 (76.47 %)		
Q_2: Picker number by household	N = 53	N = 28	N = 31	N = 19	N = 17	14.12	0.0069*
1-2	21 (39.62 %)	8 (28.57 %)	21 (67.74 %)	14 (73.68 %)	11 (64.71 %)		
3-4	32 (60.38 %)	20 (71.43 %)	10 (32.26 %)	5 (26.32 %)	6 (35.29 %)		
Q_3: Truffle hunting experience	N = 51	N = 27	N = 31	N = 17	N = 17	21.11	0.0068*
≤ 7 Years	11 (21.57 %)	4 (14.81 %)	18 (58.06 %)	6 (35.29 %)	5 (29.41 %)		
8 to 15 Years	18 (35.29 %)	7 (25.93 %)	8 (25.81 %)	7 (41.18 %)	5 (29.41 %)		
≥ 16 Years	22 (43.14 %)	16 (59.26 %)	5 (16.13 %)	4 (23.53 %)	7 (41.18 %)		
Q_4: Harvesting frequency	N = 52	N = 27	N = 28	N = 19	N =17	7.15	0.1282
4-5 Days per week	31 (59.62 %)	14 (51.85 %)	20 (71.43 %)	7 (36.84 %)	12 (70.59 %)		
6-7 Days per week	21 (40.38 %)	13 (48.15 %)	8 (28.57 %)	12 (63.16 %)	5 (29.41 %)		
Q_5: Who do you hunt truffles with?	N = 46	N = 22	N = 23	N = 16	N = 17	4.19**	0.3932
With a group	43 (93.48 %)	18 (81.82 %)	21 (91.30 %)	15 (93.75 %)	17 (100 %)		
Alone	3 (6.52 %)	4 (18.18 %)	2 (8.70 %)	1 (6.25 %)	0 (0.00 %)		
Q_6: Daily distance covered	N = 49	N = 28	N = 30	N = 19	N = 17	18.51	0.0010*
11-19 Km	19 (38.77 %)	9 (32.14 %)	9 (30.00 %)	16 (84.21 %)	10 (58.82 %)		
6-10 Km	30 (61.23 %)	19 (67.86 %)	21 (70.00 %)	3 (15.79 %)	7 (41.18 %)		
Q_7: Daily search time	N = 46	N = 26	N = 29	N = 18	N = 17	1.05	0.9026
5-6 hours	17 (36.96 %)	8 (30.77 %)	12 (41.38 %)	6 (33.33 %)	5 (29.41 %)		
7-8 hours	29 (63.04 %)	18 (69.23 %)	17 (58.62 %)	12 (66.67 %)	12 (70.59 %)		
Q_8: a/ *Terfezia arenaria* presence signs	N = 35	N = 16	N = 12	N = 15	N = 15	11.02	0.0264*
Cracks close to host-plant	13 (37.14 %)	13 (81.25 %)	4 (33.33 %)	6 (40.00 %)	5 (33.33 %)		
Sound emitted after tapping ground with stick	22 (62.86 %)	3 (18.75 %)	8 (66.67 %)	9 (60.00 %)	10 (66.67 %)		
b/ Pine truffle signs	N = 16	N = 11	N = 19	N = 3	N = 8		
Cracks	5 (31.25 %)	4 (36.36 %)	0 (0.00 %)	0 (0.00 %)	2 (25.00 %)	8.95**	0.0623
Random probing around host-tree	11 (68.75 %)	7 (63.64 %)	19 (100.00 %)	3 (100.00 %)	6 (75.00 %)		
Q_9: a/ *Terfezia arenaria* extraction techniques	N = 51	N = 21	N = 14	N = 16	N = 17	29.25**	0.0002*
Stick	27 (65.85 %)	8 (38.10 %)	3 (21.43 %)	5 (31.25 %)	7 (41.18 %)		
Hand	5 (12.20 %)	13 (61.90 %)	5 (35.71 %)	5 (31.25 %)	3 (17.65 %)		
Others (knife/Spoon stick/Pickaxe)	9 (21.95 %)	0 (0.00 %)	6 (42.86 %)	6 (37.50 %)	7 (41.18 %)		
b/ Pine truffle extraction	N = 18	N = 13	N = 21	N = 3	N = 9	-	-
Pickaxe	18 (100.00 %)	13 (100.00 %)	21 (100.00 %)	3 (100.00 %)	9 (100.00 %)		

Q_{10}: Transport containers	N = 54	N = 28	N = 31	N = 19	N = 17	31.39	0.0001*
Plastic or mesh bags	13 (24.07 %)	6 (21.43 %)	19 (61.29 %)	2 (10.53 %)	5 (29.41 %)		
Plastic bucket	27 (50.00 %)	13 (46.43 %)	7 (22.58 %)	4 (21.05 %)	5 (29.41 %)		
Backpack or waist pouch	14 (25.93 %)	9 (32.14 %)	5 (16.13 %)	13 (68.42 %)	7 (41.18 %)		
Q_{11}: a/Availability	N = 54	N = 28	N = 31	N = 19	N = 17	17.72	0.0014*
Sparsely available	30 (55.56 %)	7 (25.00 %)	21 (67.74 %)	5 (26.32 %)	5 (29.41 %)		
Rare	24 (44.44 %)	21 (75.00 %)	10 (32.26 %)	14 (73.68 %)	12 (70.59 %)		
b/ Availability compared to the last 10 years:			N = 127				
Less abundant			100.00 %			-	-
Q_{12}: a/ *Terfezia* and *Tuber* ethnophenology	N = 44	N = 24	N = 27	N = 17	N = 16	39.68**	0,0001*
March-April	17 (38.64 %)	13 (54.17 %)	10 (37.04 %)	6 (35.29 %)	5 (31.25 %)		
Early March-Early May	8 (18.18 %)	8 (33.33 %)	16 (59.26 %)	11 (64.71 %)	11 (68.75 %)		
Late February-Late April	19 (43.18 %)	3 (12.50%)	1 (3.70%)	0 (0.00 %)	0 (0.00 %)		
b/ *Delastria* ethnophenology	N = 5	N = 3	-	-	-	-	-
December-January	5 (100.00 %)	3 (100.00 %)	-	-	-		
Q_{13}: Knowledge transfer	N = 51	N = 27	N = 29	N = 18	N = 17	19.55	0.0122*
Friend	7 (13.73 %)	7 (25.93 %)	14 (48.28 %)	6 (33.33 %)	7 (41.18 %)		
Grand Parent	21 (41.18 %)	12 (44.44 %)	5 (17.24 %)	2 (11.11 %)	6 (35.29 %)		
Parent	23 (45.10 %)	8 (29.63 %)	10 (34.48 %)	10 (55.56 %)	4 (23.53 %)		

*Significant difference at p = 0.05 level.

** Chi-squared test with simulated p-value (based on 10,000 replicates) using Monte Carlo.

Results show significant variability in techniques used to locate *Terfezia arenaria* across studied cantons (χ^2 = 11.02, p = 0.0264). Visible fissures near *Helianthemum guttatum* (Fig. 5a), host plant locally known as "**teqssiss**" or "**e'rbiae**", are mainly used in canton B (81.25 %), while cantons A, C, D and E rely more on probing soil with a short stick (62.86 %, 66.67 %, 60.00 % and 66.67 %). In contrast, for pine truffles, no significant differences were observed between cantons (χ^2 = 8.95, p = 0.0623), indicating homogeneity in practices. Vast majority of gatherers, 100 % in cantons C and D, identify possible locations through random recognition around pine tree known across all cantons as "*Taïda*". Ground fissures, although classical indicators for other species, are less frequently mentioned for these desert truffles (Fig. 5b), particularly in cantons A and B (31.25 % and 36.36 %, respectively).

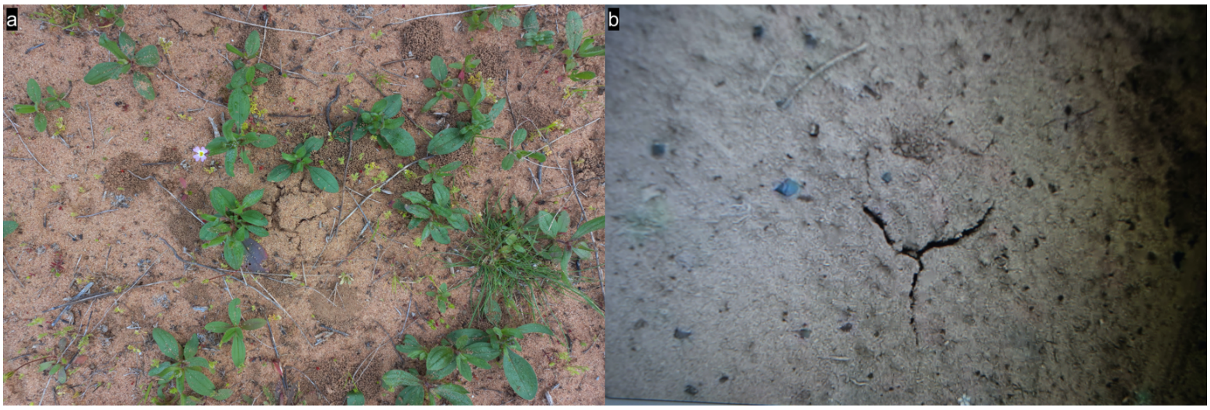

Figure 5. Soil cracks indicating: a) *Terfezia arenaria* presence near *Helianthemum guttatum*, b) Pine truffles

Regarding truffle extraction techniques (Fig. 6), our results reveal significant variability across studied cantons (χ^2 = 29.25, p = 0.0002). In cantons A and E, use of a stick is predominant (65.85 % and 41.18 %, respectively), whereas in canton B, manual extraction is most common method (61.90 %). In many cases, especially among female gatherers, manual extraction is carried out with gloves. In contrast, mixed tools (knife, spoon, pickaxe) are primarily used in cantons C, D and also E (42.86 %, 37.50 % and 41.18 %, respectively). It is important to note that 100 % of pine truffle gatherers reported using only pickaxe for extraction.

Figure 6. *Terfezia arenaria* extraction techniques: a) stick use; b-c) Hand extraction; d) knife use.

Containers used during desert truffle gathering varied significantly between cantons (χ^2 = 31.39, p = 0.0001). Plastic or mesh bags were predominantly used in canton C (61.29 %), while plastic buckets were the most common in cantons A and B (50.00 % and 46.43 %, respectively). In contrast, cantons D and E stood out for their high use of backpacks or waist pouch (68.42 % and 41.18 %, respectively) (Fig. 7).

Accompanying desert truffle gatherers in field allowed us to directly observe some of practices mentioned above, and to collect, though, once again, their testimonies, following information on spot: i) Each truffle hunter has its own gathering zones, that he keeps strictly secret. These areas, regarded as family heritage, are generally passed down from generation to generation; ii) During dry years, gatherers concentrate their harvests within depressions, humid spaces, and former lakebeds, which retain moisture for longer periods. However, these zones are not systematically productive every year, but they are, despite this, explored annually; iii) Elderly desert truffle hunters are able to distinguish between *Helianthemum guttatum* stands that are favorable for production and those that are not. Plants considered unproductive, having never yielded *Terfezia* despite their presence and regarded as permanently sterile, are locally referred to as "*Teqssis L'Aazri*" or "*Teqssis Dkar*".

Figure 7. Transport containers: a) Plastic bag; b) Plastic bucket; c) Backpack.

Perceptions of desert truffle availability and phenology (Q11 to Q12; Table 3)

Differences between cantons regarding desert truffle availability perception are statistically significant (χ^2 = 17.72, p = 0.0014). desert Truffles are perceived as scarcely available in cantons A and C (55.56 % and 67.74 %, respectively), and as rare in cantons B, D and E (75.00 %, 73.68 % and 70.59 %, respectively). This current perception is reinforced by results of Q_{11b}, where 100 % of respondents stated that desert truffles are less abundant today than they were ten years ago.

Our results show a highly significant temporal diversity in truffle harvesting across cantons (χ^2 = 39.68, p = 0.0001). "March-April" period is most frequently mentioned in canton B (54.17 %), followed by cantons A, C, D, and E (38.64 %, 37.04 %, 35.29 % and 31.25 %, respectively). "Early March-Early May" period is predominant in cantons C, D, and E (59.26 %, 64.71 % and 68.75 %, respectively). Finally, "Late February-Late April" period is more frequently cited in canton A (43.18%) but remains marginal or absent in other cantons B, C, D and E (12.50 %, 3.70 %, 0 % and 0 %, respectively). Some respondents indicated an early start in February and others an extension into May. In *Delastria rosea* case, harvesting occurs from December to January, exclusively in cantons A and B (100 %).

Knowledge transmission modes (Q13; Table 3)

Analysis indicated a significant difference between cantons regarding knowledge transmission modes about desert truffles (χ^2 = 19.55, p = 0.0122). Friends are main source of knowledge transmission in cantons C and E (48.28 % and 41.18 %, respectively), whereas they are rarely mentioned in canton A (13.73 %). Grandparents play an important role in cantons A and B (48.28 % and 44.44 %, respectively). Parents, in general are frequently cited, especially in cantons D and A (55.56 % and 45.10 %, respectively). These results reflect the coexistence of two classical forms of ethnobiological knowledge transmission: i) Horizontal, through friends or neighbors; and ii) Vertical, intergeneration, from parents or grandparents to teenager.

Gathered desert truffle species

The multiple correspondence analysis (Fig. 8) highlights a clear structuring of the factorial space. The first two axes (Dim 1 and Dim 2) alone account for 82.32 % of the total inertia (56.02% and 26.30%, respectively), which ensures a robust interpretation of the main factorial plane.

Along axis 1, a marked opposition emerges between canton C, closely associated with harvesting of *Tuber oligospermum* and a pole dominated by canton D joined by cantons A and B all three grouped around *Terfezia arenaria*, the most frequently collected species in these areas.

Axis 2 reflects a more nuanced differentiation. Canton E is positioned near the modality corresponding to combined harvesting of *Terfezia arenaria* and *Tuber oligospermum*, suggesting a more mixed profile of gathering practices. It is also worth noting that *Delastria rosea* modality was projected in the upper quadrant, in proximity to cantons A and B, confirming the spatially restricted character of its collection. Only a few gatherers reported harvesting this species mobilized by desert truffle vendors operating along roadside selling points between Sidi Taïbi and Kénitra as well as at Laarjat-Sidi Allal Bahraoui.

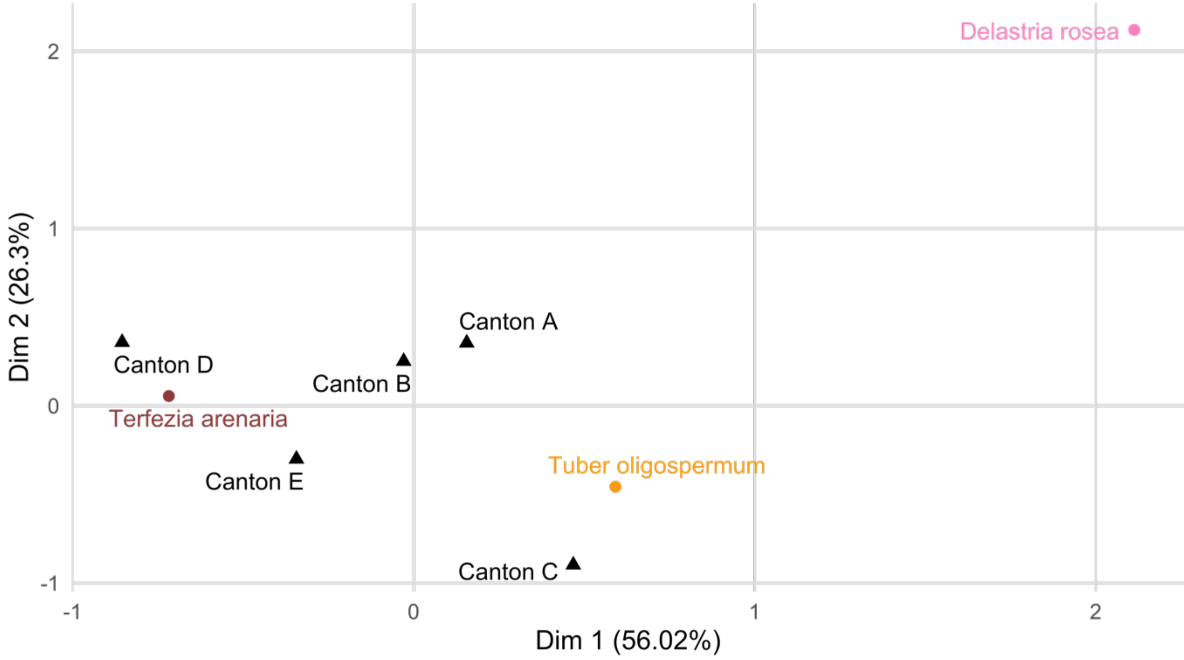

Figure 8. Multiple correspondence analysis of cantons and harvested desert truffle species
Colored points correspond to the active modalities of the species variables (the "Yes" modality);
▲ represent the cantons (A - E) projected as supplementary modalities.

Perceived drivers of decline
Ordination is robust and reliable, as stress value is extremely low (0.034), indicating an excellent two-dimensional representation of dissimilarities among cantons based on reported factors. PERMANOVA ($R^2 = 0.563$, $p = 0.001$) shows that more than 56 % variation in perception of decline causes is explained by differences among cantons. This highlights significant contrasts between cantons regarding factors identification responsible for decline in desert truffle abundance (Fig. 9).

Low rainfall ($R^2 = 0.06$) is mentioned consistently across all cantons. Experienced truffle gatherers affirm that abundance and size of desert truffles belonging to *Terfezia arenaria* depend on a well-synchronized distribution of rainfall across three key seasonal periods: i) Autumn, which promote seeds germination of *Helianthemum*, the host- plant; ii) Late December to early February, period known by local population as "*El-Lyali*" and considered essential for desert truffle spores germination, commonly referred to as "*Truffle eggs*" in local vernacular; and iii) Spring, which sustain ascocarps development and growth, reflect this empirical ecological knowledge, as for examples:

These seasonal markers are recognized and named by elder gatherers based on the traditional lunar calendar, particularly according to the "lunar mansions". Several local proverbs clearly "*I'la ma ṣebtch f Rrasha, e'terfess ma yeṭfa*" (If it doesn't rain during *R'rasha* [lunar mansion corresponding to late September/early October], "desert truffles will not emerge); "*El-berd yerabbi e'terfess*" (Cold breeds desert truffles; this must happen during lunar mansions from *Iklil* to *Saad Belaa* [approximately late January to mid-February]); "*E'terfess ykhrrej f Saad s'aud, w ykemmel f Saad l'Akhbiya*" (Desert truffles emerge between February 22^{th} and March 5^{th} and reache full maturity during March 6^{th} and March 18^{th}); and "*F l'Akhbiya, e'terfess y'terabba*"(During approximately March 6^{th} to 18^{th}, desert truffles raise up.

Low spring precipitation poses a significant challenge for desert truffle hunters, as hardened soil prevents appearance of usual harvesting signs, particularly surface cracks.

Other causes appear to be associated with specific territorial contexts.

Urbanization ($R^2 = 0.28$) is strongly associated with canton A, particularly in villages (*douars*) located between Kenitra and Sidi Taïbi, areas undergoing rapid peri-urban expansion. According to truffle hunters, some desert truffle-producing zones have been converted into urban areas, resulting in loss of natural habitats favorable to desert truffle development.

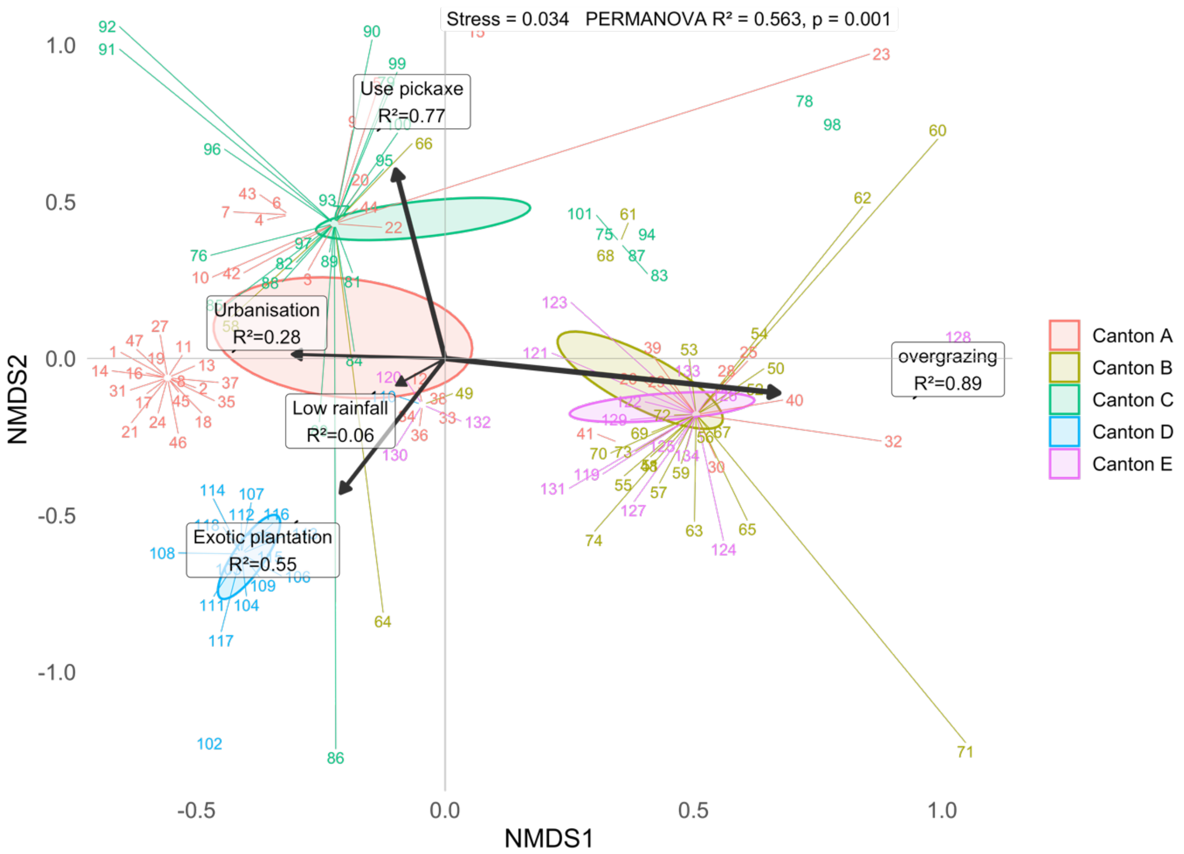

Figure 9. nMDS ordination of cantons with fitted vectors for desert truffle decline factors

Reforestation with exotic species (R^2 = 0.55) is mentioned exclusively in canton D. According to informants, this perception is linked to intensive *Eucalyptus* spp. planting in *Helianthemum* clearings, which is believed to hinder desert truffle development.

Pickaxe use (R^2 = 0.77) , considered as direct threat to soil, host-plant roots, and mycelium, is frequently reported in canton C. This distribution is attributed to wider adoption of this extraction technique, especially by less experienced gatherers, particularly when harvesting truffles under pine trees (Fig. 10a). Hunters are aware of destructive impact of using pickaxes as one informant pointed out: "*We don't look for truffles in areas that have already been dug with pickaxes. Degraded areas no longer produce truffles*".

A high frequency of mentions related to overgrazing (R^2 = 0.89) is observed in cantons B and E, indicating significant grazing pressure in these areas (Fig. 10b). This finding, reinforced by our field observations and supported by truffle hunters' accounts, indicates that livestock directly consume host-plants of *Helianthemum* genus, essential for development of *Terfezia arenaria*.

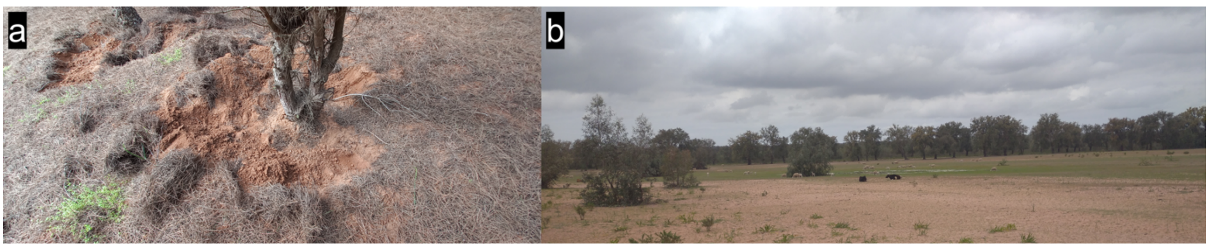

Figure 10. Threats observed in truffle-harvesting areas: a) Deep plowing around pine trees; and b) Overgrazing in a still-productive truffle zone.

Towards sustainable management of desert truffle sector

Field observations carried out during desert truffle gatherers accompaniment in Maamora Forest have revealed a series of problematic practices that threaten long-term sustainability of desert truffle sector. One of the most frequently noted issues is premature harvesting of immature truffles, often collected before they have fully developed (Fig. 11a). This occurs most

commonly during first week of harvest season, which usually takes place in last week of February or first week of March, depending on the year, thus leading to truffle quality decline and hinders their natural regeneration capacity.

Moreover, significant overexploitation has been observed in highly productive areas, particularly in large depressions located near villages. Easily accessible, these microhabitats attract large number of gatherers on a daily basis, especially organized groups of more than fifteen women who carry out intensive and repeated harvesting.

Use of sharp and unsuitable tools such as knives or metal picks has been observed. These instruments, often chosen for their ability to quickly extract truffles, nonetheless cause visible damage to ascocarps (Fig. 11b), thereby reducing their market quality and jeopardizing mycorrhizal associations essential for desert truffles sustainable fruiting.

Increasing desert truffle harvesting misuse by occasional gatherers poses a serious threat to ecological balance of wild desert truffle production in Maamora Forest. During certain outings, inexperienced individuals attracted by sudden rise in market prices are engaged in *Terfezia arenaria* collection without any knowledge of proper detection techniques. These gatherers misuse sticks, striking ground violently instead of probing it gently. This practice results in host-plantuprooting and destruction of natural cracks that serve as essential visual cues for experienced hunters, thereby hindering future detection efforts (Fig. 11c). In other cases, gatherers carry out random digging with spoons causing significant disruption to upper soil layer.

Post-harvest storage conditions also represent a critical issue. In several observed cases, freshly harvested ascocarps are placed in airtight plastic bags and remain there for several hours sometimes up to eight hours before being transferred toanother container at home or sold (Fig. 7a). This storage method promotes moisture accumulation, mold formation and degradation of desert truffle texture. Further down supply chain, compressive plastic mesh bags use by intermediaries and wholesalers exacerbates physical damage which affects not only commercial quality but also desert truffles storage potential (Fig. 11d).

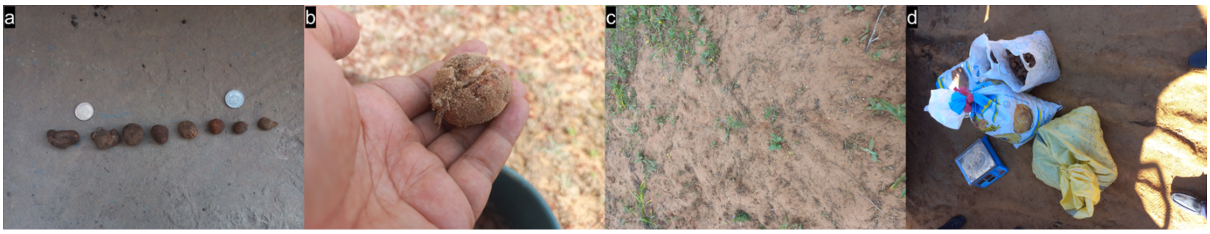

Figure 11. Unsustainable practices affecting truffle quality and regeneration: a) Prematurely harvested ascocarps; b) Ascocarp damaged by a sharp tool; c) Soil degraded by inexperienced gatherers; d) Excessive truffles compression in transport bags.

Discussion

Molecular identification and vernacular nomenclature

In our study, three desert truffle species were identified as being harvested in the five cantons of the Maamora Forest. In addition, phylogenetic analyses confirm the identification of our samples as *Tuber oligospermum* and *Terfezia arenaria* and reveal a strong genetic affinity with previously described populations, originating from the same Moroccan forest for *T. oligospermum* (Boutahir et *al.* 2015) and from Portugal for *T. arenaria* (Santos-Silva *et al.* 2021). However, the literature also reports the collection of other species, such as *Terfezia leptoderma*, which appears before *Terfezia arenaria* and signals its fructification, and *Tuber asa*, which shares the same habitat as *Tuber oligospermum* (Abourouh 2020, Khabar 2002).

Concerning vernacular nomenclature**,** the naming criteria used by desert truffle hunters in the Maamora Forest are similar to those reported in other parts of the world (López-García *et al*. 2024; Oso 1975). The "**al-kamah''** holds deep religious significance in the Muslim world. An authentic hadith reported by Sahih Muslim states that the Prophet (peace and blessings be upon him) said: "**al-kamah** (the truffle) is a type of manna, and its juice is a remedy for the eyes" (Khalifa *et al.* 2019). A similar observation regarding vernacular terms without specific meaning was made among local communities in Western

Ghats, India (Karun and Sridhar 2017). Many of the recorded names correspond to those reported in the literature (Abourouh 2020, Bokhary 1987, Thomas *et al.* 2019). However, other vernacular names, such as "**al-faga'a**", "**asqal**", "**afateeh**", "**bidat el-ardh**", "**banat ober**", "**nabat al-rahd**", "**soil daughter**" or "**sand truffles**", are not used in the Maamora Forest but are cited in the literature (Thomas *et al.* 2019, Zambonelli *et al.* 2014), further highlight the richness of desert truffle-related lexicons in various regions of the world.

Overall, the names attributed to wild desert truffles reflect a close relationship between the Maamora local population and these fungi, demonstrating an ingrained knowledge.

Hunters socio-demographic characteristics

The predominance of women among desert truffle hunters can be explained by their strong attachment to traditional knowledge and practices and by the fact that desert truffles enable them to earn money, obtain essential goods, and meet their family's nutritional and health needs. These findings confirm observations of Claridge *et al.* (2014) in Aboriginal Australia. However, several surveys indicate that desert truffle hunting is predominantly carried out by men in many countries, such as Turkey (Akyüz *et al.* 2017). Similarly, the strong representation of older informants among desert truffle gatherers aligns with previous studies, as many researchers have documented significant engagement of elderly people in traditional desert truffle gathering practices (Pieroni 2016).

Regarding education level, the high proportion of illiterate desert truffle hunters contrasts with that reported by Mandeel and Al-Laith (2007) in Bahrain, where 60.5 % of gatherers held a secondary level or university level degree.

In terms of occupation, the overrepresentation of unemployed desert truffle hunters contrasts with the findings reported by Bradai *et al.* (2015), who highlighted a wide range of professional backgrounds among desert truffle gatherers. In terms of monthly income, the predominance of desert truffle gatherers reporting no monthly income suggests that desert truffles provide an important source of income and livelihood support for individuals who are unemployed or have low monthly incomes (Fellaki *et al.* 2025, Owaid 2018, Therville *et al*. 2013).

The higher engagement of married individuals can be explained by several factors. Firstly, as heads of households, married individuals have the responsibility to guarantee their family's food security and increase their income. Secondly, they often prepare traditional remedies to help them avoid expenses of visiting doctors and purchasing medications. Such results are consistent with those reported in Cameroon by Teke *et al.* (2018).

Ethnomycological knowledge and practices

The predominance of regular gatherers and the often family-based nature of the activity can be explained by the fact that the desert truffle harvesting season generates strong engagement, motivated by a threefold function: economic, medicinal and culinary, as highlighted by our previous study (Fellaki *et al.* 2025). The high share of desert truffle gatherers with more than 16 years of experience supports the idea that desert truffle harvesting requires experience accumulated over time, as emphasized by Bradai *et al.* (2015). In other contexts, collection is not necessarily a daily activity but is organized around extended stays in gathering areas. This is also case in Algeria, where Bradai *et al.* (2015) reported that respondents spent one to two weeks per trip searching for desert truffles. Moreover, the collective nature of gathering observed in the Maamora has also been reported elsewhere. For instance, Mandeel and Al-Laith (2007) describe desert truffle hunting in Bahrain as a family-oriented and collective practice involving all household members.

Our field observations, gathering generally begins between 6:30 and 7:00 a.m. and ends between 2:00 and 4:00 p.m. This schedule is considered practical, as gatherers report that it allows for better visibility of signs on the ground (Bokhary 1987). Moreover, distances covered during the season can be also substantial. Mandeel and Al-Laith (2007) indicate that in Bahrain, desert truffle gatherers may cover up to 1 000 km per season.

The current study revealed that the inhabitants of the Maamora Forest use visual and tactile detection methods, which depend heavily on soil characteristics, gatherers' experience, and surface signs left by desert truffle. Tactile technique using a stick to probe soil is common, particularly when visual signs are minimal. In many regions of the world, gatherers rely on presence of host plants as biological indicators to locate desert truffles. Genus *Helianthemum* is most cited in this regard (Díez *et al.* 2002; Hashem *et al.* 2018). In Maamora Forest, *Tuber oligospermum* is primarily associated with *Pinus pinaster* var. *atlantica*, alongside *T. asa* and *Delastria rosea* (Kaddouri *et al.* 2024).

Beyond host-plant cues, observing fissures or cracked mounds observation is widespread method in arid regions for locating desert truffles. This practice has been described in various geographical contexts (Trappe *et al*. 2014). Additional behavioral indicators have also been reported, as for example certain birds appearance may signal truffle development (Akyüz *et al.* 2017, Bokhary *et al.* 1990). In European and North American countries, olfactory methods dominate truffle searches. Trained dogs are favored for their effectiveness in detecting deeper and more mature truffles, while being less destructive than pigs (Thomas and Kothamasi 2025). This method has also found resonance in Morocco, where Laqbaqbi (2020) highlighted effectiveness of dogs in detecting black truffles (*Tuber melanosporum*), in truffle fields established in Debdou and Imouzzer Kandar regions.

Differences in extraction tools may reflect local constraints and adaptations. The High use of manual extraction for *Terfezia arenaria* in canton B may be explained by a looser substrate or easier desert truffle accessibility, making tools less necessary. In many cases, especially among female gatherers, this method is carried out with gloves for protective purposes. Conversely, the use of mixed tools in some cantons likely reflects adaptation to more difficult soil conditions, requiring a more forceful technique. According to their testimonies, the exclusive use of a pickaxe for pine desert truffles is necessary either because signs of desert truffle presence are often hard to detect whether due to forest litter or to lack of experience, or efficiency this practice offers in collecting large quantities quickly.

In parallel with these practice-related aspects, a decline in desert truffle availability is perceived across all cantons, and 100% of respondents stated that desert truffles are less abundant today than they were ten years ago. This reduction over time has been reported by Abourouh *et al.* (2022) and Khabar (2002) in Maamora Forest. However, desert truffle production decline is not specific to area. But has been highlighted in various regions of the world (Büntgen *et al.* 2012; Morte *et al.* 2021).

This period variability may be explained by specific climatic conditions of each canton. Kaddouri *et al.* (2024) and Thomas *et al.* (2019) highlight that most hypogeous desert truffles in Maamora Forest exhibit spring fruiting. This trend is likewise observed in other arid regions, notably in Spain (Tejedor-Calvo *et al.* 2021) and Saudi Arabia (Bokhary *et al.* 1990) where key fruiting period also occurs between March and April. In Iraq, harvesting begins as early as January indicating an early winter fruiting (Owaid 2018). In other parts of the world, such as Australia and the Kalahari fruiting occurs later in the year. In Australia, it shifts toward autumn and extends from late April to September (Trappe *et al.* 2008), while in the Kalahari it occurs from March to July (Trappe *et al*. 2014).

Our results are consistent in part with those of Mandeel and Al-Laith (2007) which point out that knowledge is mainly acquired from parents and grandparents. Claridge *et al.* (2014) also describe knowledge intergenerational transmission related to use and collection of desert truffles, perpetuated through oral way and collective practices.

Perceived drivers of decline

The central role attributed to rainfall in the decline of desert truffle abundance is consistent with other studies, as shown by Akyüz *et al.* (2017), whose study reports that 97.8 % of desert truffle gatherers consider rainfall to be the most important environmental factor influencing yield. Studies by Büntgen *et al.* (2012), Morte *et al.* (2021) and Thomas and Büntgen (2019) report that desert truffle yields show a strong positive correlation with rainfall. Although, Akyüz *et al.* (2017) emphasizes that desert truffles productivity depends not only on rainfall amount received but also on its distribution throughout year. This relationship is explained by fact that, under water deficit conditions, *primordia* abort and young ascocarps are damaged (Thomas and Büntgen 2019; Trappe *et al.* 2010). Water scarcity also affects host plants and symbiotic fungi, disrupting nutrient exchanges necessary for sporocarp formation (Büntgen *et al.* 2012). Furthermore, precipitation plays a crucial role in growth and desert truffles maturation as well as in development of their *Helianthemum* spp. host-plants (Thomas and Büntgen 2019).

The importance of urbanization as a perceived driver of decline among gatherers in canton A is consistent with documented land transfers and ongoing urban expansion in the area. Ttoba (2015), for example, reports several transfers of collective lands for urbanization purposes: 180 hectares in Sidi Taibi between 1994 and 2004 for Kenitra urban commune benefit. Urban expansion has also reduced areas suitable for desert truffle production, as reported in several studies, including Shavit and Shavit (2014) and Therville *et al.* (2013).

Changes in vegetation cover, notably reforestation with *Eucalyptus* species, reported exclusively by desert truffle gatherers in canton D, constitute a significant threat to desert truffle habitats. These forest species are also known to absorb large amounts of water and contribute to depletion of groundwater resources, a phenomenon exacerbated by persistent drought observed in Maamora Forest. According to Ttoba (2015), structure of this forest has been profoundly altered by succession of management plans, particularly in cantons B, C, and D. Safeguard Plan (1918-1950), Vidal Plan (1951-1971), and Danish Plan (1973-1992). All promoted massive planting of fast-growing species, such as eucalyptus, acacias, and pines, mainly in clearings, open forest gaps, and low density cork oak stands.

The impact of pickaxe use observed in our survey is consistent with Abourouh *et al.* (2022), who noted that raking and digging practices in Maamora Forest represent a major threat to desert truffle habitats. By destroying nutrient mycelium and roots, this practice permanently degrades productive areas, transforming them into mycological deserts.

Ultimately, the perceived role of overgrazing is coherent with the literature describing strong grazing pressure in Maamora. According to Ttoba (2015), livestock farming constitutes main economic activity in the region. Maamora Forest is home to an estimated herd of approximately 336,500 sheep and 90,600 cattle. Same author notes that overgrazing, which is common in open areas, puts intense pressure on vegetation, reducing herbaceous cover and promoting invasive or toxic plant species emergence. Moreover, livestock trampling leads to soil compaction, which reduces aeration and disrupts underground fungal structure, conditions that are unfavorable for desert truffle development. Several studies have shown that mycelial growth can decrease by up to 90 % in compacted soils (Ciesla 1998). Overgrazing also disrupts desert truffles dynamics in Australia (Claridge *et al.* 2014).

Towards sustainable management of desert truffle sector

Premature harvesting of desert truffles, observed in the Maamora Forest, is a key concern, as it leads to a decline in their quality and may hinder natural regeneration. As noted by Donnini *et al.* (2013), when ascocarps are entirely harvested without leaving spores behind, natural regeneration of species is compromised. It is therefore essential to raise awareness among gatherers about need to leave behind specimens that are too old, damaged, or unmarketable. In addition, Honrubia *et al.* (2014) recommend leaving at least 10 % of desert truffles in place to ensure their regeneration. This requires limiting harvesting season and quantities to be harvested. Persistent overharvesting poses a serious threat to this resource as highlighted by Hashem *et al.* (2018) in Saudi Arabia. This situation echoes concerns expressed by forest managers in Maamora Forest for whom desert truffle overharvesting represents critical risk. According to Abourouh (2020), it could lead to a significant decline in future production.

Tool-related damage and soil disturbance may jeopardize desert truffle sustainability in production areas. According to Abourouh (2020), intensive harvesting by raking and digging causes direct biotopes degradation and indirectly a gradual depletion of desert truffle resources. Disorganized interventions damage host-plants roots, break mycorrhizal associations and may also harm mycelium of other fungal species be coexisting in the same microhabitat. These elements underscore urgent need to reconsider desert truffle harvesting modes in the Maamora and to introduce targeted measures for regulation, awareness and ecological restoration.

Beyond individual practices, a coordinated management approach must be considered at territorial level. Organizing awareness raising workshops in each canton, in collaboration with local stakeholders, would help build desert truffle gatherers capacity and foster their involvement in sustainable desert truffle exploitation. Supporting creation of local cooperatives could further encourage development of short supply chains and enhance high-quality harvests value. Active forestry services involvement in training, regulation and monitoring is essential to support this transition. In the literature and in several European regulatory frameworks, for example in Italy (Gualandi 2025; Viccaro *et al.* 2021) and Hungary [Ministry for National Economy (Hungary) 2016, Cseh *et al.* 2022], sustainable desert truffle harvesting relies on territorial governance that combines: (i) harvester training/qualification and a permit/authorization system; (ii) technical rules that minimize impacts on soils and habitats; (iii) spatio-temporal regulation (harvesting seasons and specific restrictions); and (iv) monitoring, enforcement and traceability involving competent authorities. In parallel, collective organizations are often highlighted as key levers to structure the value chain, promote short supply chains, enhance the value of high quality harvests and strengthen harvesters' commitment to sustainable practices.

Abourouh *et al.* (2022) propose desert truffles partial domestication as a priority strategy for conservation and sustainable production, supported by a multidisciplinary experimental protocol. This approach aims to move from random harvesting to controlled and sustained production through management of existing natural sites, host-plants sowing, the addition of spore and mycelial inoculum and implementation of appropriate cultivation practices (such as mycorrhization, irrigation, mulching, fencing, etc). Morte *et al.* (2021) emphasize that desert truffle yields can fluctuate markedly from one year to the next, and that the factors underlying this variability are still poorly understood. These limitations are similar to those reported for *Tuber* plantations, where production remains highly heterogeneous due to an incomplete ability to manage the biological and cultivation requirements (Sánchez *et al.* 2025). Key limitationsinclude quality control and certification of mycorrhized seedlings, as well as appropriate site and soil selection (Andrés-Alpuente *et al.* 2014; Murat 2015).

This strategy also aims to restore degraded environments and to valorize unproductive areas of Maamora Forest. These orientations are consistent with those of Morte *et al.* (2021), who report successful cultivation experiments of *Terfezia arenaria*, based on mycorrhized seedlings production, controlled irrigation and adaptation to poor soils under arid and semi-arid conditions. Similarly, spatial modeling carried out in Murcia region (Spain), using GIS tools, has enabled identification of areas potentially suitable for desert truffle cultivation. By integrating *Helianthemum* species distribution, soil types and bioclimatic data and precipitation patterns, this mapping provides a strategic tool to guide ecological restoration and sustainable management of arid zones (Honrubia *et al.* 2014).

Conclusion

This study made it possible to analyze knowledge diversity, including vernacular nomenclature, ethnoecological and ethnophenological data, as well as desert truffle harvesting practices across the five cantons of the Maamora Forest. Analysis considered the sociodemographic profiles of truffle hunters, local dynamics of knowledge transfer and truffle availability perceptions, in order to identify inter-cantonal variations and potential levers for sustainable management of this resource.

Results show that desert truffle harvesting in Maamora Forest is not merely an economic activity, but also represents a deeply rooted cultural practice, particularly among women and older individuals. Vernacular names richness and specific indicators use to locate truffles illustrate existence of dense and still largely undocumented local knowledge. However, the study also reveals signs of ecological pressure and unsustainable practices that threaten the conservation and long-term viability of this valuable forest resource.

These findings are consistent with those reported in other arid regions of North and South Africa, Middle East (notably Bahrain, Iraq, and Syria), Western Asia (such as Turkey), as well as in Mediterranean Europe (Italy, Spain and France) and Australia, while also bringing new insights into local knowledge systems, vernacular nomenclature, ethnophenological knowledge and harvested truffles species. Study thus provides original data that enrich ethnomycology field and highlights urgent need to implement sustainable management strategies adapted to local realities.

Nevertheless, growing threats to truffle habitats have been identified, including overgrazing, excessive use of unsuitable tools, reforestation with exotic species, and increasing urbanization. These pressures, compounded by climate change, in particular as a result of persistent drought affecting Morocco since 2019, could jeopardize truffles natural regeneration and lead to irreversible scarcity in certain cantons.

Future research could focus on quantifying truffle productivity in Maamora Forest and identifying favorable pedological and climatic conditions for their development. Promoting local cooperatives, organizing training on sustainable harvesting practices and exploring partial domestication strategies could help reconcile conservation objectives with the socio-economic needs of local communities.

Declarations

Ethics approval and consent to participate: This study was conducted under an institutional authorization issued by Ibn Tofail University (Kenitra, Morocco), in the form of an official certificate signed by the Vice-Dean of the Faculty, authorizing fieldwork activities and requesting the support of the competent local authorities. Participation of collectors was entirely voluntary. Before each interview and during each field outing, the objectives of the study were explained and prior oral informed consent was obtained. No personally identifiable data were collected, and responses were recorded anonymously.

Restrictions on knowledge / Benefit-sharing: Traditional knowledge was used exclusively for academic research and scientific publication; benefit-sharing was non-monetary and included acknowledging participants and sharing useful information, with no commercial use intended.

Consent for publication: Oral informed consent was obtained from the individuals concerned for the publication of any personally identifiable data.

Availability of data and materials: We now state that anonymized data and the codebook are available upon reasonable request

Competing interests: The authors declare that they have no competing interests

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Author contributions: A.F: Writing -review & editing, Writing -original draft, Investigation, Conceptualization. M.A: Writing -Review & Editing, Visualization, Supervision, Conceptualization. H.E: Supervision, Conceptualization. A.E: Writing -Review & Editing. A.R: Supervision, Conceptualization.

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