Conservation strategies for *Tuber aestivum*

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Abstract: The genetic diversity of *Tuber aestivum* is a valuable resource that is potentially at risk due to habitat losses, increasing harvest and environmental change. The conservation status of *Tuber aestivum* and legal provisions for the conservation respectively exploitation of this species differ considerably among European countries. Changes in population densities and the underlying driving forcing are still poorly understood. The local apogee and decline of *Tuber aestivum* in the southern Vienna Bassin is tentatively explained by the land-use history of the past 200 years. Conservation strategies for *Tuber aestivum* are proposed, based on the current understanding of the ecology of this species.

Zusammenfassung: Die genetische Diversität von *Tuber aestivum* ist eine wertvolle Ressource, deren Fortbestand durch Habitatsverlust, Nutzungsdruck und Umweltveränderungen bedroht wird. Die Einschätzung der Gefährdung sowie die gesetzlichen Bestimmungen betreffend den Schutz bzw. die Nutzung von *Tuber aestivum* sind in den Ländern Europas sehr unterschiedlich. Die Bestandsveränderungen und ihre Ursachen sind noch unzureichend bekannt. Die ehemals hohe Produktivität sowie der Rückgang der Vorkommen von *Tuber astivum* im südlichen Wiener Becken werden auf die Entwicklung der Landnutzung in den letzten 200 Jahren zurückgeführt. Auf Basis der gegenwärtigen Kenntnis der Ökologie von *Tuber aestivum* werden Schutzstrategien für diese Art vorgeschlagen.

Tuber aestivum (s. l., incl. *T. uncinatum*) is widespread in Europe, but only locally abundant (CHEVALIER & FROCHOT 1997). It is associated with a variety of angiosperm and gymnosperm host trees in various soil types and landscapes (ŁAWRYNOWICZ 1990, CHEVALIER & FROCHOT 1997). Available molecular data revealed a high genetic diversity, much higher than in *T. melanosporum* (PACIONI & POMPONI 1991, MELLO & al. 2002, WEDÉN & al. 2004, PAOLOCCI & al. 2004). Genetic studies further suggest that the species consists of a multitude of clonal or highly inbred lineages (PAOLOCCI & al. 2004). Given the genetic and habitat diversity of *T. aestivum*, it is likely that natural populations are locally adapted to a variety of climates, soils, host trees and other environmental variables. The genetic diversity of *T. aestivum* must be considered an important resource for the sustainability of the cultivation of this species, and, ultimately, for the breeding of cultivars. Surprisingly, the species is hardly ever detected by the meanwhile numerous studies of ectomycorrhizal (ECM) communities, in contrast to the minor white truffles, suggesting that the species is uncommon, at least in those habitats covered by ECM community studies (URBAN, unpubl.).

Tuber aestivum is harvested from wild populations and marketed in important quantities in several European countries. Intense truffle harvest outside the classic truffle producing countries (France, Italy, Spain) is a relatively recent phenomenon, fuelled by the opening of markets, the spread of knowledge and the activities of traders and collectors. The collection of truffles from natural populations generates considerable value and income. The scientific exploration of hypogeous fungi relies to a non-negligible extent on a symbiosis of scientists with amateur or professional truffle searchers. If collection data are recorded, truffle searchers may contribute significantly to the progress of the study of hypogeous fungi.

In certain Central, North and East European countries *T. aestivum* is included in the Red Lists of endangered species, e.g., Austria (3; KRISAI-GREILHUBER 1999), Bulgaria (EN; GYOSHEVA & al. 2006), Germany (CR; BENKERT & al. 1992), Poland (EX; WOJEWODA & ŁAWRYNOWICZ 2004), Slovakia (CR; LIZOŇ 2001), and Sweden (Sweden: VU GÄRDENFORS 2005). In the past decade the conservation status has been revised in several countries due to the availability of new records (e.g., WEDÉN & al. 2004; HILSZCZAŃSKA & al. 2008), and it is likely that *T. aestivum* is more common than previously thought in Germany and other countries.

Nevertheless, local truffle populations remain a valuable resource that should be reserved for propagation in the first place. Other hypogeous fungi are probably much rarer than *Tuber aestivum*, but the economic potential of the species and its emerging exploitation in large parts of Europe call to focus on its conservation. Several questions arise: Is the intensive harvest from natural populations sustainable? Do the different legislations reflect different knowledge bases, or is the status of *T. aestivum* indeed very different in various countries? Is the Red List status in various countries justified? Are current provisions designed to protect *T. aestivum* adequate?

More knowledge about the conservation status and potential management strategies for this species are needed to address these questions. Ideally, conservation and resource management should be based on a solid knowledge of population ecology including biotic and abiotic interactions. Factors such as effective population sizes, population structure and genetics, population growth or decline, the minimal viable population size, reproductive success, changes in predation rates, competition, parasitic or mutualistic interactions and environmental parameters such as climate change need to be taken into account (SOULÉ 1985). Due to the secrecies of the truffle life cycle and due to the hidden nature of the truffle business quantitative data on the productivity of *T. aestivum* populations are scarce, and statistic tools of conservation biology such as Population Viability Analysis (PVA) are therefore hardly applicable. This situation is unsatisfactory, all the more since there has been a nearly complete and poorly understood local decline of *T. aestivum* in its best known habitat in Austria, in the *Pinus nigra* forests of the southern Vienna Basin.

Landscape history and decline of truffle productivity in the southern Vienna Basin

In the lowlands and hillsides of Austria, large surfaces are potentially suitable for the growth of *T. aestivum*, but current land-use patterns seem to disfavour this species.

All available information from the classic region of truffle harvest in Austria suggests that there had been a massive decline during the last century, which can not be explained by climatic change only (URBAN & MADER 2003). On the other hand, new sites of *T. aestivum* were discovered during the last years (URBAN & PLA 2001). Here we will focus on the populations from the southern Vienna basin, which are historically best documented. In these forests, it was possible to recognize truffle beds more easily without dogs than in deciduous forests due to the relatively clear visibility of brûlés (LOHWAG 1932).

The southernmost part of the Vienna Basin is an alluvial plain made up of thick sediment layers of calcareous gravel covered by rendosols. SAUBERER & BIERINGER (2001) hypothesize that this area had not been forested during the most part of the Holocene. First *Pinus nigra* forests were established in the 15th century to create hunting grounds for the emperors. The large-scale conversion of poor arable land, meadows and pasture land to pine forest by local farmers started at about 1790. The main purpose of forestation with *Pinus nigra* was the production of litter for animal husbandry, forestry was only secondary. Later, the collection of resins for the chemical industry became an additional source of income. In the 1880ies the forested area had multiplied compared to the pre-1790 situation, and had approximately reached its current extension. Sheep husbandry became unprofitable in the late 19th century and remaining pastures were converted into arable land. Further regional development resulted in the expansion of settlements, gravel quarries and industrial complexes (BIERINGER & GRINSCHGL 2001).

The spontaneous colonisation of recently established pine plantations by *T. aestivum* followed by a progressive decline parallels the apogee and subsequent fall of *T. melanosporum* harvests resulting from the reforestation of Mont Ventoux in the first half of the 19th century (SOURZAT 2001) and the abundance of *Tuber indicum* in China in mountain areas reforested in the 20th century (I. HALL, pers. comm.). This comparison hints at fundamental similarities of the ecological needs of *T. aestivum* and other truffle species, despite different habitat preferences (climate, soils, forest density, etc.). SOURZAT (2001) mentions the significance of changes in agricultural practices linked to the industrialization and increased specialization and market-orientation of agriculture (e.g., reduced collection of forest litter, soil compaction due to the use of heavy machinery), suggesting that the decline of truffle productivity is a "slow but inexorable process" linked to forest succession and land-use changes resulting in an increase of permanently forested land. If this holds true, the study of the history of truffle producing sites is essential as a shortcut to observing successional processes in real time, in order to identify the manipulations that might slow down this process in natural and managed truffle habitats and help maintaining them.

Given the considerable time-spans concerned it is hardly practicable to test this hypothesis directly. However, long-term experiences from managed truffle plantations and truffle productivity restoration trials may additionally support some of the main assumptions of this hypothesis (truffles grow well in pioneer forests if edaphic and climatic conditions are favourable; the accumulation of litter and acidification of forest topsoils favour other ectomycorrhizal species, mostly basidiomycetes). Other questions linked to the rapid spontaneous expansion of truffle populations accompanying the (re-)forestation of unforested land remain enigmatic. Where did the source populations come from? Was the spread of inoculum mainly accomplished by natural vectors or intentionally or unintentionally assisted by human practices? At which speed were truffles successful in colonizing the new habitat? Concerning the southern Vienna Basin, we hypothesize that the source populations were located in the adjacent hillsides and, possibly, in gallery forests along the main rivers crossing this plain. According to our experience, *T. aestivum* is present even though not common in the forested hillsides adjacent to the Vienna Basin. We estimate that currently there are more viable populations in the hillsides than in the pine forests of the plains. Nothing is known about the past condition of the hillside populations and about their interactions with landscape development. Given the potentially highly efficient dispersal by animal vectors it may be the case that few source populations were sufficient to colonize the plains, once the forest was expanding. *Tuber aestivum* populations in near-climax vegetation (old growth forest, typically mixed forest with *Quercus* spec.; URBAN & PLA 2001) are probably less abundant and productive than well developed populations in habitats with strong anthropogenic impact such as the pine plantations invaded by truffles, but the populations in more natural habitats might be more stable and more likely to guarantee long term persistence of the species. Therefore we think that it is useful to introduce the concept of primary and secondary truffle habitats, even though this distinction can only be gradual in the cultural landscape. We think that primary habitats are particularly important for the protection of the species and its genetic diversity. More data about the potential correlation of habitat characteristics and the genetic diversity of *T. aestivum* are needed.

Conservation strategies for *Tuber aestivum*

The key objectives for the conservation of *T. aestivum* may be defined as (1) the preservation of the genetic diversity of the species; (2) preservation and creation of habitat diversity; (3) preservation of the extent of the distribution area; (4) preservation of production levels sufficient for natural reproduction facilitated by natural vectors, including the recolonization of anthropogenic habitats; (5) facilitation of natural or anthropogenic processes that create new truffle habitats; and (6) improved understanding of the fundamentals of truffle biology and conservation. Different actions may be necessary to achieve these goals (Table 1).

Probably the most detrimental factor for *Tuber aestivum* is habitat loss respectively the lack of new habitat, due to a combination of anthropogenic and natural factors: lack of pioneer forests in climatically favourable areas, replacement of traditional agricultural practices by intensive agriculture, land management reducing the extent of primary and secondary successional states, habitat loss due to (sub-)urbanization. The influences of environmental changes such as the spread of invasive non-host trees, immissions, particularly nitrogen deposition, and climatic change are certainly important. Inappropriate truffle search may be detrimental, too. Careful truffle searchers avoid cutting the roots of symbiont trees with unsuitable tools (spade, knife) and take care that the truffle mycelia are not exposed to desiccation by filling up the holes in the ground resulting from truffle search. Intense harvest may decrease the natural reproduction of the species. The organisation of truffle searchers in associations may be important in spreading good practice and mitigating damage caused by truffle searching (BRATEK 2008).

Tuber aestivum can be regarded as a moderately synanthropic ECM fungus, an integral element of the `traditional´ European cultural landscape, that may benefit from gardening activities, like watering, mowing, superficial soil tillage and the application of lime and organic manure, since it prefers half-open habitats and tolerates certain properties of many agricultural soils and garden soils, such as narrow C:N ratios of about 10-12 and low levels of organic matter. Most of the Austrian agricultural landscape is currently unsuitable for truffle growth due to the intensification of agriculture and due to a lack of host trees. Gardens and other non-agricultural anthropogenic landscape elements may be among the most promising potential truffle habitats. *Tuber aestivum* can grow spontaneously in gardens, if suitable host trees and soil conditions are present.

Table 1. Strategies for the conservation of *Tuber aestivum*; objectives: (1) preservation of genetic diversity, (2) preservation and creation of habitat diversity, (3) preservation of the distribution area, and (4) preservation of production levels, (5) habitat creation, (6) improved understanding of truffle ecology and conservation.

Actions	Objectives	Probability of realisation	Stakeholders
Planting truffle orchards (shift from gathering to cultivation)	(1), 3, 4, 5	high	farmers, landowners, regional development agencies
Research on the reasons for decline, exchange of information	(1-5), 6	medium	scientists, truffle collectors and growers
Protection of truffières in natural near-climax habitats	1, 2, 3, (6)	low	scientists, nature protection agencies
Revitalization of declining wild truffières?	1-6	low	landowners, scientists
Corridors for genetic exchange between populations	1-5, (6)	low	nature protection agencies, scientists
Research on population genetics	6	medium	scientists
Nature reserve management to enhance truffle production in protected landscapes	1-6	medium	nature protection agencies, scientists
Sanctuaries in highly productive areas (rotating?)	1-5	medium	nature protection agencies, truffle collectors
Close seasons	1, 4	high	nature protection agencies, truffle searchers, market offices
Education of truffle searchers, truffle associations	1, 3, 4, 6	medium	scientists, truffle collectors
Improve potentially favourable anthropogenic habitats, such as suburban gardens or cemeteries	2, 5	medium	landowners, scientists
Keeping truffle sites secret	1, 4	high	truffle collectors

The spread of *T. aestivum* in parks, gardens and similar urban and suburban environments could be favoured by planting suitable host trees, or, in a more targeted way, by planting mycorrhized trees. Gardens and truffle plantations might provide truffle habitats outside formally protected land, connect natural populations and buffer protected areas. If truffle orchards are established in conservation relevant areas, the use of local truffle inoculum would be highly desirable. Whether truffle facilitation and cultivation will alleviate or increase resource-use pressure on natural truffle habitats is difficult to predict. Truffle populations on public land are likely to experience the tragedy of the commons, i.e. the depletion of a shared limited resource (HARDIN 1968). Secrecy is a common and partially successful strategy to avoid competition for publicly accessible truffières, but it hampers scientific progress, and when competition increases, other forms of regulation are necessary. Limited collection licences, the association of collectors in federations and the designation of close seasons and sanctuaries are possible solutions. Privately owned truffières are typically actively defended, e.g., by fencing, which may cause conflicts with other stakeholders, particularly with hunters.

Apart from serving the survival of truffle species in a changing cultural landscape, truffle orchards may create valuable habitat for many other species, like traditional mixed fruit orchards. This potential role needs further study and can not be covered here.

Conclusions

The study of the ecology and demography of wild truffle populations is fundamental for conservation biology but lags behind recent insights into truffle genetics and physiology. Details of the past and current evolution of wild truffle populations are highly uncertain. Dealing with uncertainty is a common issue in conservation biology. Further study and international information exchange on both truffle plantations and wild truffle populations are necessary to improve and test hypotheses relevant for truffle conservation.

In Austria the major historic truffle habitat became increasingly sterile, probably due to land use changes. New habitat for truffles is most likely to be found in anthropogenically transformed areas, particularly gardens and truffle plantations. Remaining truffle populations in near-natural habitats should be used for propagation purposes in first place in those countries where truffles are rare.

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