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CULTURAL ECOSYSTEM SERVICES PROVIDED BY THE BIODIVERSITY OF FOREST SOILS: A EUROPEAN REVIEW

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Abstract

Soil is one of the most species-rich habitats and plays a crucial role in the functioning of terrestrial ecosystems. It is acknowledged that soils and their biota deliver many ecosystem services. However, up to now, cultural ecosystem services (CES) provided by soil biodiversity remained virtually unknown. Here we present a multilingual and multisubject literature review on cultural benefits provided by belowground biota in European forests. We found 226 papers mentioning impact of soil biota on the cultural aspects of human life. According to the reviewed literature, soil organisms contribute to all CES. Impact on CES, as reflected in literature, was highest for fungi and lowest for microorganisms and mesofauna. Cultural benefits provided by soil biota clearly prevailed in the total of the reviewed references, but there were also negative effects mentioned in six CES. The same organism groups or even individual species may have negative impacts within one CES and at the same time act as an ecosystem service provider for another CES. The CES were found to be supported at several levels of ecosystem service provision: from single species to two or more functional/taxonomical groups and in some cases morphological diversity acted as a surrogate for species diversity. Impact of soil biota on CES may be both direct – by providing the benefits (or dis-benefits) and indirect – through the use of the products or services obtained from these benefits. The CES from soil biota interacted among themselves and with other ES, but more than often, they did not create bundles, because there exist temporal fluctuations in value of CES and a time lag between direct and indirect benefits. Strong regionality was noted for most of CES underpinned by soil biota: the same organism group or species may have strong impact on CES (positive, negative or both) in some regions while no, minor or opposite effects in others. Contrarily to the CES based on landscapes, in the CES provided by soil biota distance between the ecosystem and its CES benefiting area is shorter (CES based on landscapes are used less by local people and more by visitors, meanwhile CES based on species or organism groups are used mainly by local people). Our review revealed the existence of a considerable amount of spatially fragmented and semantically rich information highlighting cultural values provided by forest soil biota in Europe.

Key words: soil biota; forests; soil ecosystem services; Europe

Highlights

Contributes to the understanding of cultural significance of forest soils

Spatial distribution and temporal variations of CES of soil biota has been analyzed.

Highlights use of biodiversity data in soil CES studies

1. INTRODUCTION

The idea of ecosystem services (ES) was originally coined to quantify the benefits that natural ecosystems generate for human society (Westman, 1977). The aim of this effort was to raise the public awareness for the value of biodiversity and conservation of ecosystems. The Millennium Ecosystem Assessment (MEA, 2005) defined four main categories of ES: Supporting, Provisioning, Regulating and Cultural. Of these four, cultural ES probably raise the biggest controversy. Cultural ES (CES) are defined by MEA as "non-material benefits people obtain from ecosystems through spiritual enrichment, cognitive development, reflection, recreation and aesthetic experiences". CES are inherently difficult to identify, evaluate and employ in environmental management and decision making (de Groot et al., 2005), as their benefits are intangible and have "non-use values" for most of them (Burkhard et al., 2014). However, Satterfield et al. (2013) and Fish et al. (2016) emphasized that many cultural phenomena, such as artistic media, architecture, clothes, etc., are not immaterial or intangible and admitted thus that many CES are in principle marketable. Even though CES are not considered an initial driver of political or management decisions (Milcu et al., 2013), many researchers recognize them as one of the most potent arguments for ecosystem conservation (Hernández-Morcillo et al., 2013).

The greatest hindrances in identification of CES and their subsequent employment in management plans are difficulties in the identification of ecosystem elements underpinning CES, identification of beneficiaries of CES, the valuation of the benefits delivered and variation of CES in time and space (Blicharska et al., 2017). Therefore, research on CES mapping and evaluation often employs only the "safest", that is, marketable service groups like recreation and ecotourism (e.g., Maes et al., 2012, 2013). An additional difficulty in CES evaluation is variability of beneficiaries' attitudes towards the same CES depending upon their “mental filter” which is defined by education (Braat, 2014), cultural/societal position (Satterfield et al., 2013) or different national traditions (Daniel et al., 2012). Furthermore, CES categories overlap with each other (Daniel et al., 2012) and with other ES, for example provisioning and regulating services may in many cases also be perceived as cultural (Chan et al., 2012; Schulp et al., 2014). This may strengthen the value of CES (their importance to the beneficiaries), on the other hand, it can complicate the evaluation as double counting could occur. Temporal and spatial changes can further complicate the picture as shown for the use of fish in Swedish mountains (Blicharska et al., 2017), or the uses of wild plants for food and medicine in Eastern and Northern Europe (Luczaj et al., 2012; Stryamets et al., 2015), where the primarily provisioning ES changed in time to largely recreation and ecotourism CES.

Soil is a fundamental component of any terrestrial ecosystem and by itself it hosts a huge biodiversity, both in terms of species richness and functionality. It is estimated that about 25 % of the species on Earth live in the soil (Jeffery et al., 2010). Soils have played an important role in human life by predetermining societal and cultural development even since pre-agricultural societies (e.g., Mortensen et al., 2014) and they contribute to human welfare far beyond food production. Although they undoubtedly provide a number of ES, soils and soil biodiversity are often neglected in mapping and evaluating ES, largely because belowground biodiversity has received insufficient attention for a long time (Pulleman et al., 2012). The lack of appropriate methods to study belowground biodiversity and processes, as well as the cost and complexity of such studies is the main reason for this neglect. We also lack tools to evaluate biodiversity components and CES derived from these components. Noteworthy is how little we understand of CES provided by soils and the biota belowground. Even the most recent papers that review ES provided by soils, state the lack of studies pertaining CES from soils. Iconic or attractive landscapes that are underpinned by different soil types were shown as the only example of CES of soils in the review of Dominati (2013).

In other reviews, Dominati et al. (2010), Jónsson and Davíðsdóttir (2016) and Robinson et al. (2009) mentioned soils that are archives of archaeological heritage and spiritual-religious meanings of soils (mostly extra-European examples). Adhikari and Hartemink (2016) demonstrated very generalised CES (human wellbeing) as secondary, derived from another ES provided by soils. However, often CES are neither elaborated or mentioned at all, e.g. in reviews by Lavelle et al. (2006) and Pulleman et al. (2012). Lavelle et al. (2006) even stated that "Soils ... contribute to cultural services although to a rather minor degree...". Thus, perception of CES from soils is rather biased towards abiotic structures and processes contrary to the usual classification and assessment of ES where biota play the main role as a service provider (Van der Meulen et al., 2016). The direct cultural benefits from soil biota are only casually mentioned in the few reviews on soil fauna (e.g., Anderson, 2009; Decaëns et al., 2006; Del Toro et al., 2012) and cultural significance of soils is often attributed to agriculture and agricultural landscapes. Even the iconic cultural symbol, a "handful of dirt" generally refers to agricultural soil. Understanding of CES provided by forest soils as opposed to agricultural soils is particularly unclear.

The aims of the present study were to i) identify the CES of European forest soil biota, ii) highlight the importance of belowground diversity on human culture and well-being, iii) outline the geographical scope of beneficiaries of these CES, iv) contribute to the understanding of temporal changes of CES and their interrelations with other ES. Our findings are intended to ensure more exhaustive evaluations and mapping of ES (including CES) that are provided by forests.

2. METHODS

To compose a list of CES, we used the framework of the Millennium Ecosystem Assessment (MEA, 2005). More than often understanding of different CES overlaps and the same benefits can be attributed to more than one CES (e.g., to spiritual and aesthetic values) (Cooper et al., 2016). Therefore, we added here descriptors to the CES, which we followed when searching for references, so that we could attribute each source to a distinct CES.

Cultural diversity, according to the Universal Declaration on the Cultural Diversity (UNESCO, 2002) includes diversity of languages, traditions, folklore and other national heritage.

For *Spiritual and religious values* we followed definition by De Groot et al. (2002), as use of nature for religious purposes.

Knowledge systems encompass traditional and formal knowledge. According to Karvonen and Brand (2013), formal knowledge is characterised by impersonal and often quantitative precision with a concern for explanation and verification. Meanwhile traditional knowledge is "experimental, local or tacit knowledge arising from personal experience and explorations outside the confines of educational institutions and without strict adherence to the scientific methods" (Karvonen and Brand, 2013).

Educational values can be provided for formal, non-formal and informal education. For further understanding of the education types we followed Dib (1988).

Following De Groot et al. (2002), *Inspiration* derived from ecosystems is defined as cultural and artistic information where nature is employed as motive in books, film, painting, folklore, national symbols, architecture, advertising, etc.

Aesthetic values are the interaction of humans with the environment based on human perceptions and resulting in aesthetic and affective reactions and judgments. According to Cooper et al. (2016), in aesthetic evaluations humans are assessors of natural beauty, rather than recipients of products or benefits.

Sense of place is usually characterised as the emotional bonds formed by people with places, their values, meanings and symbols (Williams and Stewart, 1998), however, lifestyle and traditional use of natural resources also make a part of sense of place, as was shown by Urquhart and Acott (2013).

For *Heritage values* we followed the definition by ICOMOS (Brooks, 2002): "cultural heritage is an expression of the ways of living developed by a community and passed on from generation to generation, including customs, practices, places, objects, artistic expressions and values".

Social relations and human interactions are influenced by ecosystems found in a particular place. Social interdependences connected to ecosystems and their biodiversity may come in various levels (Barnaud et al., 2018).

Recreation and ecotourism encompass opportunities for recreation and tourism that stem from ecosystems and are termed as "free services" of natural capital in providing infrastructure for recreational activities (Clough, 2013).

For definition of *Health and wellbeing* we followed the statement by Sandifer et al. (2015) that apart from the absence of disease, human health is defined as a state of physical, mental and social wellbeing.

Based on these CES types, we evaluated six groups of belowground biota. Many references have demonstrated that cultural significance of organisms and their reflection in human life and perception does not always coincide with biological values or grouping of biota. Therefore we did not strictly follow the usual biotic groupings, as in, e.g., Jeffery et al. (2010) or Briones (2014), though our grouping comes close to that suggested by Orgiazzi et al. (2016). We grouped soil biota as follows:

- *Roots* (in a broad sense) included all belowground parts of vascular plants;

- *Fungi* encompassed all trophic groups (mycorrhizal, saprotrophs and pathogens). We included all references mentioning belowground mycelium and fruit bodies of macromycetes (encompassing sequestrate and semi-sequestrate (truly belowground) and emergent (above-ground) fruit bodies);
- *Microorganisms* included bacteria, protozoa and algae;
- *Mesofauna* included nematodes, collembolas and acari;
- *Macrofauna* included earthworms and burrowing macroarthropods;
- *Megafauna* included burrowing mammals (we restricted to the true burrowers only).

To avoid analysis of too extensive material, we limited search only to Europe and its forests. However, based on our search principles, methods and the keywords employed, similar reviews can be carried out in any part of the world.

For the literature analysis, we conducted a reference search at two levels. Firstly, we performed a comprehensive search of Clarivate Analytics Web of Knowledge using the search terms Cultural ecosystem service × organism group or subgroup, for example, recreation × fungi or recreation × mycorrhizal in the title, key words and abstract. The search was conducted from December 2015 until April 2016. After the screening of results for subject relevance, the search was finalized with 41 articles that were identified as relating to forest soil biota and CES in Europe. Moreover, the major part (29) of these papers dealt with only one group of organisms (fungi). As a second step, we made queries based on a system of better adapted keywords for each case, e. g. “roots + ethnography”, (full keyword list provided in Supplementary material 1) in English, French, German, Dutch, Spanish, Italian, Czech, Slovenian, Slovak, Norwegian, Polish, Russian and Lithuanian languages. Thus, wider reference range in ethnobotany, ethnozoology, ethnology, mycology, toxicology, archaeology, palaeontology, literature and art research, linguistics, sociology and medicine, was covered. The queries were performed using Google Scholar, in September, 2016 – February, 2017.

This procedure was necessary as Milcu et al. (2013) noted that a large part of the CES research is published in non-peer-reviewed journals. Moreover, Harrison et al. (2014) indicated that, using a relatively new term “ecosystem service” as a keyword, will lead to inadequate numbers of relevant papers, which is especially consequential for culture-related issues, because many papers were published before the term came into wide use. In addition, a large part of data is found either in publications of non-ecological research with the CES term not mentioned (Braat, 2014) or a significant portion of information on biodiversity and human culture interactions is found in “grey literature” and in the sources published in national languages.

Additional literature and, in some cases, examples from other sources (internet sites, movies, fiction books, etc.) were found by snowball search (tracking down cited references within sources examined for their content) and expert suggestions (other sources suggested through discussions with fellow scientists at meetings during the process of the study).

For each publication, we checked element (organism group), spatial range of the benefit/service and temporal scale, type of impact on CES (direct, indirect, positive, negative or unclear (controversial or mentioning both positive and negative impacts)) and, possible beneficiaries and interaction with other CES or ES. As the collected data could not be quantified, the analysis is largely descriptive. In the text below, when the references are cited as examples of a benefit, in cases where there were more than three papers dealing with the benefit in question, only the number of references is indicated instead of a full citation.

3. RESULTS AND DISCUSSION

3.1. General results of literature analysis

The combination of both searches resulted in 226 papers (peer-reviewed and non-peer reviewed articles, conference abstracts, thesis, book chapters and books) which were further reviewed. The list of all reviewed references is provided in Supplementary material 2. It has to be noted that sometimes it was impossible to identify whether given organism or organism group was exclusively related to forest soils (i.e., some burrowing mammals, earthworms, etc. are able to inhabit both forest and non-forest habitats).

The number of references found for the soil organism group contributing to the analysed CES and the type of impact of organism group on CES are presented in Table 1. The detailed results of the reference analyses are presented in Supplementary material 3. In a number of cases one paper covered more than one organism group or more than one CES, or both, therefore total numbers of references in Table 1 and Supplementary material 3 is higher than in Supplementary material 2. Of the total of analysed papers, 61 were pertaining all (or almost all) European countries, or had universal cultural significance. The rest of the references could be identified to the relevant country. The resulting distribution of the found references showed spatial unevenness across Europe, the western Mediterranean region providing the largest amount of available literature data (Fig. 1).

Soil organisms contributed to all CES, although their weight (expressed as numbers of references found) differed for individual CES and individual organism groups (Fig. 2). Based on reviewed literature, the highest impact was found for cultural diversity (in total 108 references, 24 % of all references) and the lowest for aesthetic values (in total 8 references, 1.8 % of all references) (Fig 2a). Of all soil organisms, fungi had the highest impact on CES, while microorganisms and mesofauna had the lowest (Fig 2b). Inadequacy between the different organism groups (“smaller” organisms versus vertebrates in their case) on CES in comparison to the impact on most other ES was demonstrated by Norris et al. (2011, table 4.2). In their study, vertebrates were shown to play a significantly higher role in CES provision than the rest of the biota. These “cultural divisions” found by Norris et al. (2011) and in our review as well, can be largely explained by the fact that the major part of the CES is based on folk perception of nature, ethnobiology and folk taxonomy, i.e., cultural recognition of biological taxa. Cultural recognition of biota is governed by the salience of different taxa, which was classified by Hunn (1999) into phenotypic, perceptual, cultural, and ecological. Following this grouping, folk recognition of organisms is based on: i) economical salience (economically important species or species used in everyday life); ii) morphological/behavioural salience (species with outstanding morphological and/or behavioural traits, often culturally important species); iii) ecological/geographical salience (species encountered in the area and the more frequent species); iv) size salience (larger species, notwithstanding organism group – microscopic species are „invisible“ and therefore non-existent). Size was also recognized by Harrison et al. (2014) as an important attribute affecting species-based CES provision (recreation in their case).

3.2. Cultural ecosystem services and disservices provided by soil biota

3.2.1. Cultural diversity

According to the references, benefits to cultural diversity were shown to be provided by four groups of the reviewed organisms (roots, fungi, macrofauna and megafauna) (Table 1). The largest part of relevant references (75) dealt with local or national traditions of use (medicinal, edible and other) and traditional attitude towards target groups of soil biota, a benefit that supplies a base for other benefits related to cultural diversity. In many European languages, linguistic diversity is reflected by vernacular names, idioms and language forms for plant roots, fungi, and, to lesser extent, for soil fauna (25 references). Notably, linguistic diversity related to fungi was mainly reported in the references from eastern and southern Europe (Estonian, Hungarian, Lithuanian, Romanian, Spanish and Slavic languages), while only few references (Haga, 2001; Molitoris, 2002; Rätch, 1998; Yamin-Pasternak, 2011) mentioned several folk names for fungi in German, English and Friesian languages. This imbalance of information on linguistics related to fungi between different parts of Europe was well explained by Casebeer‘s (2002) admission that “...mushrooms play no significant role in many Western lives, which is why most of us have no folk biological knowledge of their different varieties...“. Folklore based on belowground biota is mentioned in 19 references. As in most of CES, references mentioning fungi also prevailed for Cultural diversity (Table 1). This can be explained by two reasons. Firstly, the history of using fungi is long (Dugan, 2008) and secondly, the attitudes towards fungi differ greatly among various countries, regions and nations of Europe (Hawksworth, 1996; Wasson and Wasson, 1957). This attitude difference influences many cultural phenomena. Only in the references on folklore, the number of papers referring to invertebrate fauna and roots was equal to the number referring to fungi (6 references each). Geographically, the reviewed references included most of Europe, except for the plant roots in folklore where they were limited to France, Lithuania and the Mediterranean area in general. Similarly, references that describe the tradition of use of vertebrate megafauna, were all (except one) related to European rabbit (*Oryctolagus cuniculus*) and were largely limited to the Mediterranean region.

3.2.2. Spiritual and religious values

Impact of belowground biota on spiritual and religious aspects of human life originates from the World Tree or Cosmic tree, an ancient Indo-European archetype present in many myths and religions of Indo-Europeans. Plant (especially tree) roots, burrowing mammals and earthworms are attributed to the chthonic world, or roots of World Tree (Gamkrelidze and Ivanov, 1995; Vėlius, 1987) which is reflected in various manifestations of spirituality. We found 30 relevant references where plant roots, fungi, invertebrate macrofauna (earthworms and ants) and megafauna made the base of a considerable number of beliefs, taboos, superstitions, rituals, symbols and mythology of various countries and nations which largely, at least in some forms, exist to the present time as a part of spiritual life in Europe. Sailors' beliefs connected to rabbits (Houseman, 1990) are an example of such still surviving spiritual tradition. Ivancheva and Stantcheva (2000) mentioned rituals employed by local healers to strengthen the impact of medicinal plants. Referowska-Chodak (2015) and Džekčioriūtė-Medeišienė (2016) showed superstitions connected to mushrooms that still exist in Poland and Lithuania: pregnant women shouldn't collect mushrooms and that it is dangerous for humans to see how a mushroom grows.

Jürgenson (2000, 2005) and Yamin-Pasternak (2011) showed that the attitude towards fungi may be connected to the professed religion. Intrinsic values of every species are mentioned by Decaëns et al. (2006) (soil fauna in their case), as giving a base to ethical consideration of nature conservation and moral obligation of humans to protect nature.

3.2.3. Knowledge systems

In total, 69 references were found related to the CES knowledge system, and majority of them showed that biodiversity in soil has a positive effect on the establishment of new knowledge. Data obtained from all groups of soil organisms contributed to the formal knowledge in wide fields, such as general ecology, soil science, ecotoxicology, evolutionary science, paleoecology, archaeology, ethnology and forensic science. In traditional knowledge, only roots, fungi and invertebrate macrofauna were reflected in the relevant references as a source of folk medicinal (medicinal and poisonous plants and fungi), food and non-food everyday uses, as well as folk phenology (23 references). Soil organisms were also a source of controversial formal knowledge, such as use of fungi as bioindicators. Egli (2011), for example questioned use of fruit bodies of mycorrhizal fungi as indicators of tree health by demonstrating that decrease of ectomycorrhizal mushroom production not necessarily coincide with visibly deteriorating tree health. Meanwhile, Halme et al. (2017) analysed limitations of a widely used conservation concept of fungi as biodiversity surrogates. Steup (1915) and Referowska-Chodak (2015) showed persistent erroneous traditional knowledge concerning poisonous fungi which may have adverse effects on human health. Two papers demonstrated the connection between traditional and formal knowledge: Vogl et al. (2013) described the use of traditional Austrian medicinal plants (including roots) in formal pharmacology, while Money (2016) analysed diverse mushroom species, used in traditional medicine, and questioned their medicinal values.

3.2.4. Educational values

We found 11 references showing that all groups of soil organisms are used or proposed to be used in formal, non-formal or informal educational activities for various ages and professional levels. Earthworms and fungi can be considered as good tools to stimulate general interest in natural and environmental sciences (Blouin et al., 2013; Halme et al., 2017). Anderson (2009) demonstrated the intrinsic educational values of soil fauna as a tool to stimulate children‘s interest in natural studies. Picot (2013) gave examples of education programs for children and adults, which employ plant roots. There are many websites which employ belowground organisms as educational objects: roots (McNear Jr., 2013), badgers (Badgerland, http://www.badgerland.co.uk/education/education.html) and earthworms (L'Observatoire Participatif des Vers de Terre, https://ecobiosoil.univ-rennes1.fr/OPVT_accueil.php), etc. Decaëns et al. (2006) also cited an educational website which introduced children to soil biodiversity. Mushroom exhibitions can be used as tools of public education (Jürgenson 2005). Importance of public education was discussed by Eren et al. (2010) who stated that teaching about mushrooms is essential both for general public and medical personnel in order to decrease the mortality from mushroom poisoning. Ramesh (2016) discussed uses of fungi to attract students to mycological studies. Belowground biota were also employed for general educational purposes: Stonkuvienė (2000) mentioned ants used as an example of moral education of children and Brink (1990) showed the use of fungi from *Amanita* genus in teaching children arithmetics.

3.2.5. Inspiration

The majority of the reviewed soil organisms – roots, fungi, macro- and megafauna are popular objects depicted in art, literature, cinematography, post stamps, crafts etc., as was shown in 34 references. In eastern and central Europe, fungi and mushroom gathering was a common topic in adult and children's literature, especially in classical prose and poetry, such as short stories by Alexander Pushkin (Russia) or poems by Adam Mickiewicz "Sir Thaddeus" (Poland) and Antanas Baranauskas "The Forest of Anykščiai" (Lithuania). Earthworms, ants and burrowing mammals are commonly depicted in children's literature. Representatives of burrowing fauna are characters of the worldwide-famous Kenneth

Grahame‘s “The wind in the willows“ and Hans Christian Andersen‘s “Thumbelina“. Furthermore, fungi, mushroom gathering, invertebrate soil macrofauna, rabbits and their hunting, fishing with earthworms as a bait are depicted in many popular movies, such as “Lord of the Rings“, “Lady Hawk“, “Alice in Wonderland“ and “Midsomer murders“.

3.2.6. Aesthetic values

Only eight references, all related to invertebrate macrofauna and fungi, discussed the organisms from an aesthetical point of view. Some fiction literature directly described aesthetic values of fungi, such as the above-mentioned poems by A. Mickiewicz and A. Baranauskas. Similarly, aesthetic values of burrowing vertebrates are indirectly reflected by illustrations for children’s books (e.g., Woodland folk series by Tony Wolf). In the reviewed references, aesthetic values of fungi vary. They may be positive, perceived as an addition to the-aesthetic perception of forest (Meiresonne and Turkelboom, 2012) or even as the “flowers of forest“ (Lubienė, 2015). In a negative perception, fungi are seen as monsters or as a metaphor of death and decay (Kiernan, 2010). Meanwhile, earthworms are perceived as aesthetically controversial or negative: either as symbols for Victorian aesthetics of death and decay (Sax, 2001) or outright as the objects of disgust (Cooper et al., 2012).

3.2.7. Sense of place

Fungi were the only group contributing to patrimonial values: mushrooms and mushroom picking being an important part of lifestyle mainly in Eastern Europe (9 references). Cultural identity (sense of place) in literature pertaining CES (also CES from soil) is usually associated with landscapes (e.g., Dominati 2013), but in case of fungi, benefits provided by mushroom picking shape cultural heritage, identity, social life and, subsequently, the sense of place similar to the cultural and patrimonial contribution of fish and fishing in coastal communities shown by Urquhart and Acott (2013).

3.2.8. Heritage values

Soil biota have an impact on cultural heritage, both intangible and tangible, as was shown by 35 references. The influence of soil organisms on tangible heritage can be direct or indirect. Indirect impact is provided by the depiction of fungi and megafauna in heritage artefacts (5 references). Direct effect on tangible heritage is the impact of soil biota on archaeological objects. Soils are termed to be an archive of archaeological heritage (Robinson et al., 2009), and a positive impact of soil fauna has been registered: for example earthworms bury artefacts and, thus, conserve them (Blouin et al., 2013). However, there are more reports on damage of archaeological layers caused by bacterial and earthworm decomposition or earthworm-induced bioturbation of organic archaeological layers, both directly by their own activity and indirectly, as a prey to wild boars and moles which turn over soil and stones and thus assist root penetration into the organic layers (Louwagie et al., 2005). Badgers have been known to reveal hidden artefacts (Killgrove, 2016) but they also damage archaeological sites (Mallye, 2007). On the other hand, the impact of soil biota (earthworms, burrowing mammals, fungi and plant roots) on intangible heritage was positive in all cases: they underpin national folklore, tradition and crafts. Fungi are important in traditional cuisine of “mycophilous“ nations (7 references), while rabbits are widely used in traditional cuisine of southern Europe (Amaral et al., 2014; González Redondo et al., 2007).

3.2.9. CES Social relations

We found 34 references demonstrating that belowground biodiversity influenced social relations at various society levels: from family and local community to the state level. Gathering of fungi and plant roots include common activities with family members and generates knowledge transfer (13 references). At a community level, the impact of plant root and mushroom gathering may be positive (socio-economic) (Sisak et al., 2016; Stryamets et al., 2015) but also negative, in case of conflicts between the gatherers (Boa, 2004; Karvelytė and Motiekaitytė, 2013; de Román et al., 2006). Fungi, vertebrate burrowers and invertebrate macrofauna function as an incentive for activities of various interest groups, for example mycological societies, insect gatherers, nature photographers, public scientists and conservation movements (7 references). Laws which specifically regulate gathering of plants (including roots) (Picot, 2013) and mushrooms (Peintner et al., 2013; de Román et al., 2006; Wright, 2010) and rabbit hunting (Ricci, 2008; Rödel and Dekker, 2012) function in many countries. Four references mentioned existing or potential conflicts with law in the case of mushroom gathering.

3.2.10. Recreation and ecotourism

A total of 23 references showed impact of belowground biodiversity on recreation and ecotourism, and the impact may both be indirect or direct. Indirectly, mesofauna and fungi may aid in the maintenance of the quality of recreational areas when used as monitoring tools (Barico et al., 2012, Blasi et al., 2013). Niemi et al. (2014) showed a case where forest soil and its fungi aided in faster conversion of landfill sites into urban green spaces. Direct benefits are provided by plant (roots) and especially by mushroom gathering, which is a popular recreational activity in many countries (9 references). Burrowers (predominantly rabbits) are objects in recreational hunting (6 references), earthworms are used as a bait for fishing (Blouin et al., 2013; Tripodi et al., 2012; Ulicsni et al., 2016) and are important as food for game (Decaëns et al., 2006), while burrowing mammals are common objects for nature observation and photography (Macmillan and Phillip, 2008).

3.2.11. Health and wellbeing

We found 55 references showing that soil biota influence human health and wellbeing in different ways. Plant roots and fungi had highest number of references (13 and 7 accordingly) showing their positive effect on human health, mainly as medicinal sources or healthy food. Use of fauna – earthworms and badgers in folk medicine was also mentioned (4 references). Bere and Westersjo (2013) and Stryamets et al. (2015) demonstrated that activity of mushroom and wild plant (including roots) gathering helps to fight obesity and improves the general health. Temraleeva et al. (2011) showed that soil algae diversity can be used as indicator of soil pollution that may be hazardous for health. However, 25 references indicated negative impacts of fungi and plant roots on human health: toxicity to humans and their pets was described in 16 references and high contents of trace elements in edible mushrooms as a hazard to health was indicated in 9 references. Marfenina et al. (2011) mentioned that presence of opportunistic fungi in urban forests may have adverse effects on human health as a source of potential pathogens and allergens. Tripodi et al. (2002) described a rare case of allergy caused by earthworms used as bait. Effects of vertebrate fauna on human health were shown as largely negative: five references dealt with burrowers as vectors and sources of known and emerging zoonotic diseases.

3.2.12. Disservices

Cultural benefits provided by soil biota clearly prevailed in the total of the reviewed references, but there were also negative effects mentioned in six CES for all organism groups, except mesofauna (Table 1). Highest number of references indicating negative effects were noted for Health and wellbeing CES, largely through plant roots and fungi (adverse effect of use) and megafauna (as vectors of zoonotic diseases), and for Cultural heritage CES (damage to archaeological sites caused by various soil organisms). The largest controversy was found on the effect of vertebrate fauna, especially its diversity, on human health. Woolhouse et al. (2012) stated that "…biodiversity probably has little net effect on most human infectious diseases but, when it does have an effect, observation and basic logic suggest that biodiversity will be more likely to increase rather than decrease infectious disease risk…". This statement was, however, contradicted by Levi et al. (2015), Morand et al. (2014) and Salkeld et al. (2013) who opposed that even if biodiversity were a source of pathogens, general biodiversity loss in ecosystems but not the richness of ecosystem biota may be associated to an increase in zoonotic and vector-borne disease outbreaks. A review by Sandifer et al. (2015) demonstrated that this controversy has no unambiguous answer and requires further research on a case-by-case basis.

Fungi were the only organism group which provided benefits to all CES, but also the one that provided disservices in most of the CES. Their disservices for Spiritual and religious, Knowledge systems, Social relations and Health and wellbeing CES are discussed in corresponding subchapters.

The same organism groups or even individual species may have negative impacts within one CES and at the same time act as an ecosystem service provider (ESP) (fide Kremen, 2005) for another CES: e.g., toxic plant roots and poisonous fungi impact negatively on Health and wellbeing CES but positively on Inspiration CES when used by the authors of fiction literature and movies, as in the examples provided by Iwicka (2015) and Trestrail III (2000).

3.3. Organism groups, species diversity and key species as providers of CES

The CES were found to be supported at several levels of ESP: single species, two or more species, a single functional/taxonomical group, two or more functional/taxonomical groups. Mostly, the providers for CES were entire taxonomic/functional groups, such as collembolas (e.g., Urbanovičová et al., 2014), ants (e.g., Del Toro et al., 2012), earthworms (e.g., Blouin et al., 2013), plant roots (e.g., Picot, 2013) or fungi (e.g., Gyozo, 2010). In some cases, CES were facilitated by one or several species: roots of mandrake (primarily *Mandragora officinarum* s. lat.) (e.g., Carter, 2003), European badger (*Meles meles*) (e.g., Griffiths and Thomas, 1997), fly agaric (*Amanita muscaria*) (e.g., Brink, 1990), several species of a fungal genus *Psilocybe* with psychotrophic properties (e. g., Stamets, 1996). Tradition of collecting wild food and the CES related to this tradition was based on two functional groups – fungi and plant roots (e.g., Łuczaj et al., 2013, 2015). None of the CES were found to be supported by only one-level service providers, with the exception of hunting-based recreation and tourism CES which was mainly facilitated by the population of one species, European rabbit (e.g., Delibes-Mateos et al., 2009). In the cases of taxonomic/functional groups as ESP, the importance of species diversity varied: e.g., in most papers earthworms are treated as one entity, due to the fact that earthworm species are usually not recognised in folk taxonomy. According to Sax (2001) in human understanding, "…With facial features that are difficult to see, earthworms are hard to distinguish from one another…", therefore, their species diversity does not play any role in folk taxonomy-based CES. In the case of fungi and plant roots, diversity of the species involved as ESP varied depending on regions and countries, and the involvement was determined not only by presence/absence of the species but rather by local tradition (Schulp et al. 2014). As an example, mandrake roots provide direct cultural benefits in Western Europe and the Mediterranean where the plant grows naturally or has been introduced (Carter, 2003; Picot, 2013). Meanwhile, the widespread species of the fungal genus *Suillus* are traditionally used in Eastern Europe but not in Spain, even though they are common in this country (Blanco et al., 2012).

In CES such as Inspiration, Aesthetic or Heritage values, morphological diversity often acts as a surrogate for species diversity: i.e., root motifs based on form but not the species are depicted in paintings, artefacts, children's books and cinema (e.g., book by Sybille von Olfers "Etwas von den Wurzelkindern", artwork by Walter Williams, Vincent van Gogh, Caspar David Friedrich, Akseli Gallen-Kallela, etc.).

Regardless of how many species function as ESPs in a single taxonomic group, the reviewed contributions suggest that the general richness of biota is important when it comes to cultural benefits and their diversity. People have to encounter different organisms considerably frequently in order to gain cultural benefits through their use or observation. However, human activity in forests has already led to a significant decline in biodiversity and its homogenisation (Newbold et al., 2015; Van der Plas et al., 2016) thereby restricting the encounter of humans with many species, including the biota living in soil. Climate change also affects biodiversity and has a negative impact on the CES it provides, as the example of fungi and mycotourism in Spain has shown (Büntgen et al., 2017).

3.4. Impact of soil biota on CES – direct and indirect

Previous reviews referring to CES provided by soils considered them as derived from the soil as a whole, that is, a mixture of abiotic and biotic parts. Therefore, cultural benefits rendered by soil were either generalised (soils as an archive for archaeology) or only indirectly related to the soils per se (Robinson et al. 2009, Dominati et al. 2010, Adhikari & Hartemink 2016). Our review shows that the impact of biota-based CES from soils may be both direct – by providing the benefits (or dis-benefits) and indirect – through the use of the products (i. e., folklore, books, artefacts) or services (monitoring of environment with the help of soil organisms, use of earthworms as a bait in fishing-based recreation, etc.) obtained from these benefits (Supplementary material 3). Indirect impact may be shown as transition of the intangible CES (Cultural Diversity, Inspiration, Heritage values, Knowledge systems) into tangible CES by bringing revenue from e.g., tourism (folklore festivals, mushroom picking festivals, ecotourism with local tradition included, restaurants serving local cuisine that uses wild food, thematic souvenirs, etc.) or cultural consumption, i.e., books, cinema and art. Indirect impact may also be created by a cascade of benefits: e.g., the iconic book by K. Grahame “Wind in the willows”, largely inspired by burrowing mammals, has led to the foundation of the book fans’ society and to the creation of the tourist attraction Henley River and Rowing Museum (Kenneth Grahame Society, https://www.facebook.com/Kenneth-Grahame-Society-320770334685402/). In an on-going discussion what is to be evaluated as CES, Daniel et al. (2012) stated that some historical cultural values (historical buildings, paintings, etc.) have little dependence on ecosystems, and Blicharska et al. (2017) proposed to disaggregate ecosystems into biotic, abiotic and anthropogenic objects. Our review, however, indicates that a number of artefacts were created under inspiration provided by soil organisms, and impact of these art objects on humans has a connection to the present biodiversity – through educational and aesthetic values related to recognition of the depicted natural objects.

3.5. Interactions of CES provided by soil biodiversity

Given that ecosystems are multifunctional, they provide multiple ES which often appear together in time and space, thus creating ES supply bundles (Berry et al., 2016). In the case of CES provided by soil biota, almost all of them interact with at least one other CES; in 27 cases with Provisional ES, in two cases with regulating ES and three cases with supporting ES (Supplementary material 3). However, not all cases can be regarded as bundling, because of the temporal value fluctuations in CES and a time lag between direct and indirect benefits. For example, mushroom gathering activity in eastern and southern Europe has developed from primarily provisional ES (losing its value in the course of time) to largely recreational CES (gaining value in the course of time). Hence, the provisioning service of food evolved to CES such as cultural heritage (cuisine, traditions, folklore), which, in turn, further cascaded into recreation and ecotourism CES, knowledge systems (traditional knowledge), sense of place and social relations. However, mushroom gathering had an element of recreation even when being mostly provisional ES (as shown for instance in the above mentioned poem by A. Mickiewicz) and thus these two ES make a bundle together with Cultural heritage and Knowledge (traditional) systems CES. Time-lags between value changes and cascading services make the bundling definition complicated.

3.6. Beneficiaries of CES

Individual beneficiaries of ES (including CES) understand and value the benefits they receive from ecosystems in different and subjective ways (Braat, 2014; Fish et al., 2016). Therefore, for valuation, all possible beneficiaries have to be identified for any specific service provided.

For example, a study in the Sierra Nevada showed that farmers and tourists attributed highest values to different groups of ES provided by the same landscape (Iniesta-Arandia et al., 2014). For example, collecting mushrooms or plant roots and the CES related to these activities are influenced by income, age, gender and cultural factors (Schulp et al., 2014, and the literature cited therein) which indicates that beneficiaries belonging to the same society may put different values on the same CES. Plieninger et al. (2013) have shown that one person's cultural benefit provided by an ecosystem may be a dis-benefit for another person. The references we have reviewed showed similar results, for example, Sisak et al. (2016) showed that increase in mushroom picking-based recreation may lead to legislative restrictions for forest owners. Moreover, it is obvious that a benefit may turn into a dis-benefit to the same person in changed societal conditions, as was demonstrated by an example of mushroom picking by Lithuanian immigrants (recreation and patrimonial values benefit) that resulted in a clash with British law (Džekčioriūtė-Medeišienė, 2016).

In identifying beneficiaries, distances between the ecosystem with its ecosystem service providers (ESP) and the beneficiaries of ES are important. In previous reviews pertaining soil, CES were mostly viewed from a landscape scale and, thus, the beneficiaries were seen largely as users of aesthetic values, recreation and ecotourism CES. This fact has obviously led to the statement by Burkhard et al. (2014) that for CES there is a strong spatial discrepancy between ESP and ecosystem service benefiting areas. However, when CES is provided by organisms (soil biota in our case), the benefits, especially the direct ones, are primarily used by local inhabitants, as shown by the examples of the wild food use tradition (Schulp et al., 2014), that is, immediate benefiting areas are mainly situated close to the occurrence of ESP's.

Accessibility and quality of forests and their biodiversity in the soil are part of the CES supply to the beneficiaries. Forest area in Europe accounts for about 50% of theland area, which varies from 1.9 % (Iceland) to 75.7 % (Finland) (FOREST EUROPE/UNECE/FAO enquiry on pan-European quantitative indicators, https://www.foresteurope.org/docs/SoeF2015/OUTPUTTABLES.pdf). However, many of them are managed forests with low biodiversity, while only 6.3% of European forests currently serve to protect biodiversity (Halkka and Lappalainen, 2001). Gray et al. (2016) has shown that species richness and abundance within protected areas were higher than outside, meaning that visiting a managed local forest means less frequent encounters with biota and less diversified forest. Specific surveys on forest soil biota do not exist, but surveys dealing with the demand of cultural benefits provided by forests generally show that a large proportion of the population frequently visits forests for recreation , harvesting forest products andand observing nature. In Slovenia, for example, almost 100% of the population visited forests, the frequency of visits varied from daily (16% of the interviewed persons) to 1–2 times a month (27.7%). Recreation, relaxation and well-being, nature observation and forest product picking were identified as main reasons of the visits by Slovenians (Bogataj, 2009; Žižek and Pirnat, 2011). In Iceland, where forests occupy a negligible part of the country's area, 78.3% of the interviewed population visited forests on average 14.7 times per month (Curl and Jóhannesdóttir, 2005). The reasons for the visits were categorized as purely cultural: recreation (52.2%), enjoyment of nature (13.4%), well-being and relaxation (11 %), etc. A small percentage (1.8%) of the interviewed persons in Iceland were involved in collecting forest products (mushrooms and berries). When asked about the importance of the forest, the Icelandic interviewees put the highest values of the cultural benefits as well: recreation (91.8% of the interviewed persons), knowledge production (research) (88.3%) and education (84.7%). However, targeted interviews and surveys should be carried out in order to identify beneficiaries' attitudes and values to forest soil biota (CES demand).

3.7. CES values, their temporal and geographical scale

According to the classical Maslow's pyramid of needs, whose basis, notwithstanding wide critique of the concept itself, largely remains unchanged (Kenrick et al., 2010), spiritual and cultural benefits increase in value only after physiological, safety and security needs are fulfilled. Following Guo et al. (2010), human dependence on CES increases along with economic development of the society, while dependence on substitutable provisioning ES decreases. The increased value of CES relative to provisional ES is also due to the fact that the increase in provisional services is achieved at the expense of decreases in regulating and cultural services (Carpenter et al., 2009), cultural benefits from ecosystems becoming rarer and more valuable commodity. Hence, value of CES is generally considered to be highest in richer societies (Satterfield et al., 2013), as can be seen in the increase of interest in wild food in many regions of Europe which is considered mainly as a cultural phenomenon (Schulp et al., 2014). Poorer societies or society members use more provisional ES from forests in the form of wild food and source of pharmaceuticals or as a secondary source of income (e.g., Boa, 2004; Karvelytė and Motiekaitytė, 2013; Łuczaj et al., 2012; Stryamets et al., 2015), making them more closely associated to nature and the CES from biota of forests and their soils, such as traditional knowledge, cultural heritage, etc. This is in contrast to modern industrial societies where the mental distance between humans and nature is increasing (Braat, 2014).

Even with economic development of rural societies or in the-cases when the members of these societies migrate to richer countries, tradition of picking wild plants and mushrooms is maintained as a form of sense of place or "birth right" (e.g., case of Lithuanian immigrant explaining her right and need to pick mushrooms in UK, shown by Džekčioriūtė-Medeišienė

(2016)). Tipping points between rural and industrial societies may be especially difficult periods for valuation of CES connected to wild foods and pharmaceuticals because in some cases their value may decrease, while increasing for others (Stryamets et al., 2015). Besides, access to the benefits (including the cultural ones) provided by ecosystems in communal ownership or use (and forests are mostly such) is more important to the poorer societies or society members than to the rich (Carpenter et al., 2009). Notwithstanding economic power of the society, some provisional ES have already become entirely cultural with time: e.g., historical sites of tar production from pine roots and stumps became archaeological heritage (Hjulström et al., 2006), former commercial collection of ant eggs in Slovenia became a source of inspiration and is reproduced in literature (short story by A. Ingolič “Collectors of ant eggs” (Slovenia)). When it comes to the values of indirect cultural benefits provided by soil biota, a time-lag exists between a product of Inspiration CES and Recreation and ecotourism CES which has cascaded from it (see the examples in the subchapter 3.4 (K. Grahame’s book “Wind in the willows”) and 3.5 (mushroom picking). Therefore, the time aspect is important when it comes to CES valuation.

Spatially, the values of reviewed CES varied: for most part, the benefits provided by soil biota were similar throughout Europe (Supplementary material 3). However, even in these continent-wide cases, regional differences between the species that were ecosystem service providers (ESP) were obvious, or the strength of CES values differed from region to region. For example, tradition of mushroom picking and use involved different sets of species in individual countries or regions (examples in Gyozo, 2010; Łuczaj et al., 2013; 2015; Stryamets et al., 2015; etc.). Collecting wild plants and especially mushrooms in different countries of Europe varies from less than 3 % of population to “nearly everybody”, according to Schulp et al. (2014). Consequently, such CES as Health and wellbeing, Recreation and ecotourism, Knowledge systems (traditional knowledge) that are provided by fungi or plant roots will have higher value in the countries where higher percentage of the society keeps to this tradition. Some ESP's and their benefits were strictly regional: e.g., wild rabbits are providers of various CES only in the areas of their natural occurrence or introduction, that is they will have little or no value in northern and eastern areas of Europe where they are not found. Meanwhile indirect benefits (literature, cinema and art inspired by soil biota) may influence a wider geographical area than the actual distribution range of the species. While evaluating the CES provided by soil biota, in both temporal and spatial perspective, human migration must also be accounted for. Interaction of migrants and local inhabitants in exchanging knowledge and traditions is known since the time of Roman Imperium (e.g., see Allen and Hatfield, 2004). Likewise, historical interchange of traditions by European migrants and indigenous people in North America (Turner and von Aderkas, 2012) or Northern Asia (Yamin-Pasternak, 2007) is well documented. Studies of recent migrations within Europe have shown that the usage intensity of wild food and pharmaceuticals, traditional knowledge, attitude and species selection flows rather from migrants to the local inhabitants. Di Tizio et al. (2012) and Pieroni and Gray (2008) stated that migrants tend to collect the species they are used to gather in their home countries more than the species common in the country they immigrated to. Blanco et al. (2012) and Yamin-Pasternak (2011) indicated that immigrants also transfer knowledge on edibility and uses of previously ignored mushroom species to the local residents. In any case, immigration tends to increase CES values provided by soil biota, plant roots and mushrooms in particular.

4. Conclusions

The provision of CES is essential for human wellbeing as shown by an incredible wealth of literature. However, CES as any other ES are in danger of decreasing due to the impoverishment of natural ecosystems. In particular, soils are under considerable threat: they are degraded by human activities such as urbanization, pollution, industrial and development activities, unsustainable agriculture and forestry and overexploitation by tourism. To prevent the loss of the soil's natural capital, valuation of ES provided by soils has been undertaken (Jónsson and Davíðsdóttir, 2016) and even an attempt to define the value of soil biodiversity in providing ES (Pascual et al., 2015). None of these included CES due to the missing studies on the cultural value of soils. Not only are such studies non-existent for soils, but studies on CES in general are largely based on landscapes or ecosystems as a whole. Harrison et al. (2014) has shown that of the two cultural services they have found in the references they reviewed, the first (Aesthetic values) was provided at the community/landscape level and the second one (Recreation) was at the species level, due to species-based recreation (salmon fishing in their case). Although Milcu et al. (2009) have noted the importance of other sciences (economics, social, humanities) in the study of CES and that a significant proportion of the data is published in non-peer-reviewed papers, still most of the reviews are limited to the Web of Science publications, with very few exceptions such as Schulp et al. (2014). Large parts of information pertaining organism groups and their links to various cultural aspects are published in non-English references. Our combined search through multilingual and multi-subject literature (ethnobiology, ethnology, mycology, toxicology, archaeology, palaeontology, literature and art research, linguistics, sociology and medicine) revealed the existence of a considerable amount of information showing cultural values provided by soil biota just in one type of ecosystem, forests. However, we admit that even our extensive search did not cover all existing literature in all European languages. In some European countries, we found a deficiency of literature that allows a link between ecosystems (in our case, forest soils) and human culture (Fig. 1). Therefore, spatially explicit information across Europe is problematic. It is rather fragmented and has the character of a scientific artifact, depending on the search methods we used, the availability of references as Internet resources, but also research activities, research policy, subjects studied in different countries, etc. This lack of existing or widely available data can also become an obstacle to communication with local stakeholders in those countries where relevant research is lacking, as the impacts of soil biodiversity on CES may not be well documented or at least systematic.

To summarize our findings on CES provided by forest soil species or species groups the following should be highlighted:

1) Information pertaining to CES provided by forest soil biota in Europe is considerable, though spatially fragmented.

2) For CES in general, there are many overlaps between individual CES and other ES provided by soil biota.

3) Especially strong spatial and temporal fluctuations were recorded in biota-based CES.

4) We show clearly expressed regionality of CES: a same organism group or species may have a strong impact on CES (positive, negative or both) in some regions while no, minor or opposite effects in others.

5) Contrary to the CES based on landscapes, in the CES provided by soil biota, the distance between the ecosystem and its CES benefiting area is shorter. Landscape-based CES is less used by locals and more by visitors, while CES based on species or groups of organisms is mainly used by locals.

6) When CES are based on species/organism groups, there is no danger that benefits provided by the objects of anthropogenic origin (e.g., buildings in the cases of aesthetic landscapes) or objects of abiotic origin will be included in CES valuation. Species may be depicted in artefacts or appear in objects of tangible and intangible heritage, but in these cases not the

artefact itself is included in CES but the species impact on creation of the object and subsequent appreciation by the public.

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Fig. 1. Reference-based importance of forest soil biota for cultural ecosystem services. Intensity of colour refers to the number of relevant references we have found: darkest shade – over 20 references, lightest shade – no literature data. References pertaining to all European countries, or dealing with universal cultural significance of soil biota were not included

Fig. 2. Distribution of references according to (a) cultural ecosystem services (CES) and (b) organism groups. Acronyms of CES are as follows: CultDiv – Cultural diversity, SpirRel – Spiritual and religious values, KnowSys – Knowledge systems, EduVal – Educational values, Insp – Inspiration, AestVal – Aesthetic values, SocRel – Social relations, SensPl – Sense of place, CultHer – Cultural heritage values, RecEc – Recreation and ecotourism, HealWell – Health and wellbeing