

OVIDIU COPOT

Relevance of eDNA, citizen science,
and species distribution modelling
for fungal conservation



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LIST OF ORIGINAL PUBLICATIONS

This thesis is the summary of the following papers, which are referred to in the thesis by their Roman numerals **I–V**. The author of the thesis is highlighted in bold.

- I.** **Copot,** O., Lõhmus A., Abarenkov, K., Tedersoo, L., & Runnel, K. (2024). Contribution of environmental DNA toward fungal Red-listing. *Frontiers in Ecology and the Environment*, 22(9), e2791. <https://doi.org/10.1002/fee.2791>
- II.** **Copot,** O., Runnel K., Kohv M., Hagh-Doust N., & Lõhmus A. (2025). Sampling eDNA at outflows from artificial drainage systems: what is the potential to monitor landscape degradation? *Environmental Monitoring and Assessment*, 197, 602. <https://doi.org/10.1007/s10661-025-14047-w>
- III.** Lõhmus, P., Degtjarenko, P., Lotman, S., **Copot,** O., Rosenvald, R., & Lõhmus, A. (2023). “Ready! Set! Lichen!”: a citizen-science campaign for lichens, against the odds of success. *Biodiversity and Conservation*, 32, 4753–4765. <https://doi.org/10.1007/s10531-023-02724-6>
- IV.** **Copot,** O. & Lõhmus, A. Predicting future habitat change for an old-forest fungus: precautionary and best-case interpretations differ. Submitted manuscript.
- V.** **Copot,** O., Runnel, K., & Lõhmus, A. Where to improve the European protected areas network to represent threatened fungi? Submitted manuscript.

Author’s contribution (* moderate contribution; ** high contribution; *** leading role)

	I	II	III	IV	V
Original idea	—	—	—	***	**
Study design	*	*	—	***	**
Performing the work	**	***	—	***	**
Data collection	***	***	—	***	***
Data analysis	**	***	*	***	**
Manuscript writing	*	**	*	**	*

1. INTRODUCTION

1.1. Traditional and modern sources of information on fungi

The fungal kingdom includes an estimated 2.2 to 3.8 million species (Hawksworth & Lücking, 2017). Of this, an estimated 80,000 species are ‘macrofungi’, i.e., fungi that produce structures visible to the naked eye (Li et al., 2018). While fungi form only ca. 2% of total global biomass (Bar-On et al., 2018), they play key roles in ecosystem functioning by forming a symbiosis with plants, decaying organic matter, sustaining soil organic carbon storage, or acting as pathogens (Pérez-Izquierdo et al., 2021; Runnel et al., 2025). Since prehistory, humans have used macrofungi as supplementary food or for medicinal purposes (Schlosser 2021). Fungi have also attracted public fascination, giving rise to modern global communities of fungi enthusiasts (Lemelin & Fine 2013). For more than a century, fungi have been increasingly used in scientific research for applied purposes. New biotechnological advances highlighted their enormous potential beyond food production and fermentation processes into medicine and valuable metabolite production (Meyer et al., 2020).

Despite such ecological and sociocultural importance, fungi have traditionally not been used as targets or model organisms of study to the same extent as plants and animals. This is primarily due to their cryptic lifecycle: they remain hidden in the substrate until they form fruit-bodies – the main macroscopic unit observed by fungal recorders and the sexual reproductive structure in macrofungi. In addition, it is complicated to identify fungal species, as it often requires microscopic investigation. In this context, it is also understandable why most fungal records come from a relatively small subset of species – mainly charismatic, easily identifiable, and commonly found macrofungi (Gautier et al., 2022).

A central concept of fungal data is the ‘fungal record’ – a documented and accessible occurrence information of a fungal species, including the location and time of observation. The location and time also carry ecological information, which may be specially collected in the field or later added based on other, notably spatial data. The opportunities to link records with such other data are most linked with the accuracy of the record location. Notably, the preserved fruit-bodies in Herbaria or Fungaria are usually associated with the description of the habitat and locality but lack geocoordinates (Braga-Neto et al., 2013).

In the past decade, a tremendous amount of fungal records has been made publicly available on a global scale as new technological advancements have allowed the digitization of previously collected records and the uploading of new observations directly into international databases (Andrew et al., 2018a). Nowadays, most fruit-body-based fungal records are curated within international databases, of which the Global Biodiversity Information Facility (GBIF; <https://www.gbif.org/>) is the most important. Other major international databases include iNaturalist (<https://www.inaturalist.org/>), MyCoPortal (<https://www.mycportal.org/>), and several regional ones, such as PlutoF (Estonia; Abarenkov

et al., 2010), SLU Artdatabanken (Sweden; <https://www.slu.se/artdatabanken/>), Artsdatabanken (Norway; Henriksen & Hilmo, 2015), Danish Fungal Atlas (<https://svampe.databasen.org/>), Finnish Biodiversity Information Facility (Finland; <https://laji.fi/>), NBNAAtlas (United Kingdom; <https://nbnatlas.org/>), and French National Fungal Database (FongiFrance; <http://fongibase.fongifrance.fr>). These modern databases have also adopted eDNA-based occurrence information, especially GBIF and PlutoF, and some databases are even specialized in eDNA samples, notably GlobalFungi (Větrovský et al., 2020) and Global Soil Microbiome consortium (GSMC; Tedersoo et al., 2021).

1.2. The information challenge in fungal conservation

In the past decades, increasing efforts have also been directed at protecting fungi as a part of the wider biodiversity, with multiple approaches contributing to this endeavour (**Table 1**). The most important approach to the knowledge base includes the establishment of lists of fungal species of conservation concern. Such lists serve a general aim of focusing conservation attention on particular species, with multiple potential applications in setting land-use regulations or initiating conservation programs that depend on the jurisdiction (Löhmus et al., 2018). Perhaps the most common application is managers' considering local fungal records when establishing or managing protected areas.

A key information for such practical tools is an understanding of the fungal species' extinction risk. The standard procedure for assessing that is the IUCN (International Union for Conservation of Nature) system of Red-listing. Either at a global or regional level, Red-listing combines quantitative assessments of population size, geographical distribution, ecology, and understanding of the threats into a qualitative (Red-list) category (IUCN, 2025; **Figure 1**). Vascular plants and vertebrate animals have been the traditional targets of Red-list assessments, while fungi have received less attention. Even only 15 years ago, almost no fungi had been assessed for the global Red-list (Mueller et al., 2022). By 2022, the Global Fungal Red-list had increased substantially to approximately 600 fungal species, of which almost half have been categorized as threatened (Mueller et al., 2022). The most recent estimate is approximately 1,000 globally assessed fungal species (IUCN, 2025). Such an increase in the assessed number of fungal species has become possible due to consistent knowledge accumulation on fungi around the world, but especially in certain well-sampled regions in Europe, North America, and South America (Andrew et al., 2018b; Mueller et al., 2022). Still, considering that the estimated species richness ratio of fungi to plants is 5:1, the Red-list assessment ratio is 1:60,000.

National Red-lists influence and support the global assessments. Starting in the 1980s, 40 countries had developed national Red-lists of fungi by 2019 (Mueller et al., 2022). For example, in Estonia, the first initiative that included fungi started in 1988. By 2008, the Estonian Fungal Red-list used the official IUCN Red-list criteria, and by 2019, 434 fungal species had been assessed at least once (Saar et al., 2019).

Table 1. Major sources of information for fungal conservation.

Source of information	Description	Records used
Herbarium and fungarium with preserved fungal specimens	Collections of preserved fungal specimens (e.g. fruit-bodies, cultures), usually accompanied by metadata such as observing date, habitat type, and collector information; many specimens awaiting formal description (Yahr et al., 2016)	fruit-bodies
Fungal inventories	Systematic lists of fungal records in a region (e.g. national fungal checklists)	fruit-bodies
Social media	Public photos with fungal content on social platforms (e.g. Instagram)	fruit-bodies
Public databases	Fungal records by professionals and citizen scientists on digital platforms (e.g. iNaturalist, PlutoF, MycoPortal, GBIF), which are in a constant process of curation and are accessible to researchers, policymakers, and the public, usually include a large variety of metadata information (e.g. geocoordinates, date, taxon name, collector, habitat, images, genetic information)	fruit-bodies, eDNA sequences
eDNA databases resulted from sampling projects	Operational taxonomic units (OTUs) lists for soil fungi (e.g., GSMc, Tedersoo et al., 2021)	DNA sequences
eDNA databases resulted from data compilation	Sequence variants of the fungal internal transcribed spacers (ITS) 1 and 2 and samples of soil fungi (GlobalFungi, Větrovský et al., 2020), sequence variants of three barcoding regions (SSU, ITS2, LSU) of arbuscular mycorrhizal fungi (GlobalAMFungi, Větrovský et al., 2023)	DNA sequences
Ecological studies	Lists of species, often supplied with abundances or presence/absence tables, as supplementary files or uploaded files to repositories	fruit-bodies, eDNA sequences, or fruit-bodies and eDNA sequences
Distribution maps	Maps depicting the species's potential distribution as generalizations of records, either at grid cell level or just range delineations	fruit-bodies
Predicted distribution studies	Maps depicting the species' predicted potential distribution in a study area, either as probabilities of presence, binary maps, or habitat suitability classes	fruit-bodies, or fruit-bodies and eDNA sequences
Red-lists and conservation assessments	Key information about fungal species (e.g. Red-list category, ecology, threats, population size, range size and distribution)	fruit-bodies, or fruit-bodies and eDNA sequences

As an important research focus, there have been efforts to adjust the IUCN Red-list criteria to the unique characteristics of fungi (Dahlberg & Mueller, 2011). For example, IUCN criteria calculate the population size of animals as the total number of individuals (IUCN, 2025), while fungal fruit-bodies are not equal to individual organisms. To resolve this problem, Dahlberg & Mueller (2011) coined the concept of ‘fungal functional individual’, referring to all conspecific fruit-bodies growing on a dead wood piece or within a 10-meter radius circle. Such approximations can be further elaborated.

Another central line of Red-list reasoning uses two proxies for species’ geographical distribution: AOO, Area of Occupancy, and EOO, Extent of Occurrence (IUCN, 2025). Their inclusion is based on the assumption that range size and shape are causally linked to the extinction risk (Gaston & Fuller, 2009). AOO is calculated by summing the number of overlapped grid cells over all known records (Marsh et al., 2019), while EOO is calculated in different ways to represent “the area within the outermost geographic limits of the distribution” (Keith et al., 2018). They indicate different spatial processes: EOO is related to range extension and landscape-scale threats, and AOO is related to habitat fragmentation and local-level threats (Keith et al., 2018; Marsh et al., 2023). Methodologically, AOO is more dependent on the sampling effort (Marsh et al., 2023), while EOO is largely scale-independent (Joppa et al., 2015) and better targets poorly recorded species (Marsh et al., 2023).

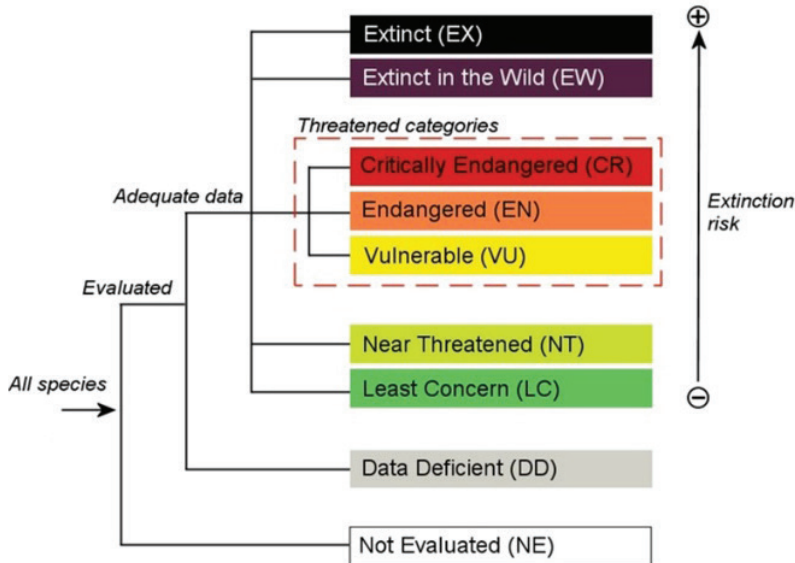


Fig. 1. The IUCN Red-list categories and their subsets, along with the gradient of extinction risk (IUCN, 2025).

The Red-list criteria refer to trends in these abundance and distribution proxies, and together with a threats assessment, enable us to assign a Red-list category to a species. The Red-list identifies ‘threatened’ species by the categories Critically Endangered, Endangered, and Vulnerable, which refer to significant risk of extinction in a decades perspective. Near Threatened category is allocated to species that, despite not qualifying as threatened, are very close to being classified as such in the near future (IUCN, 2001). If the species is abundant and widespread and not clearly declining, it usually qualifies as of Least Concern (IUCN, 2001). If the assessment cannot allocate any Red-list category, the species will be categorized as Data Deficient, which is frequent in fungi with up to 9% of the assessments (Mueller et al., 2022). It is essential for fungal conservation to develop and integrate new tools that would rapidly improve our mycological knowledge to provide better categorization to those fungal species of currently unknown status.

Similar information needs emerge from conservation policies. Specifically, in the context of the current thesis, a need to protect fungi and their habitats can be seen as an objective of the EU Biodiversity Strategy until 2030. This strategy explicitly targets 30% of the EU’s land area to be protected, including one-third of this as a strictly protected area (European Commission, 2020). Currently, one-fifth of the European Union is protected by the Natura 2000 network (Jackson, 2018), initially established under the EU Birds Directive of 1979 and Habitats Directive of 1992 (Jackson, 2018; Morán-López et al., 2019). Its purpose is to conserve Europe’s most threatened species and habitats, and it is the world’s largest coordinated network of protected areas (Jackson, 2018).

The strong mandate to expand protected areas area and representativity in the European Union means a reassessment of the existing protected area networks that are (for similar reasons as Red-lists) historically based mainly on plant, animal, and general ecosystem-level assessments. Apparently, numerous species other than those targeted initially are also protected within these protected areas (an ‘umbrella effect’; Morán-López et al., 2019). However, this argumentation is not explicit, and the network has been shown to clearly fail in protecting at least some non-target groups of organisms (Gruber et al., 2012; Hermoso et al., 2015). Importantly for this thesis, the role of the European protected area network in the protection of fungal species remains largely unknown. Two information needs arise from this: (i) a need for fungal populations and distribution to be assessed within the current protected areas network; (ii) a need to expand this assessment beyond the protected areas network and to the future to assess potential consequences of changes in the network combined with the changes in the broader environment.

1.3. Citizen Science and eDNA as emerging sources of fungal data

During recent decades, citizen science (scientific work undertaken by members of the general public) has been evolving toward an efficient tool for mycological research and for informing fungal conservation. By using voluntary work

(potentially reducing direct financial cost), citizen science could provide large amounts of fungal records (occurrences) of many species (Bonney et al., 2009). However, the citizen science records of fungi and lichens are almost inevitably biased toward charismatic, often common, and easily identifiable species. Other known limitations of citizen science data are: (i) it can contain false presences due to incorrect taxon identification and inaccurate geocoordinates; (ii) it can overrepresent a specific type of habitat due to its proximity to access roads or cities (Mair & Ruete, 2016; Koo et al., 2022; Sicacha-Parada et al., 2019). Therefore, citizen science records are recommended to be accounted for despite such limitations, which introduces additional assumptions. Nevertheless, the resulting filtered or corrected data can be used in subsequent analyses like species distribution modelling (Fourcade et al., 2014), Red-listing, and conservation management. Since citizen science promotes public participation (Dickinson et al., 2012), it can also enhance broader environmental awareness (Meschini et al., 2021).

Another recently emerging data source for fungal conservation is environmental DNA (eDNA). Fungi are among the kingdoms most studied for eDNA (Tedersoo et al., 2014). The primary technique in eDNA studies involves direct sampling of the substrate of interest (e.g., soil, wood or water), processing it in the laboratory (through DNA extraction, PCR, and sequencing), and finally, generating a list of OTUs (Operational Taxonomic Units) following bioinformatics. OTUs are an association of a group of sequences to a sequence within an official database (e.g. UNITE). Adding functional assignment to the identified taxa (e.g., FungalTraits, Põlme et al., 2020) further facilitates the use of fungal eDNA data. On a broad scale, recent fungal eDNA databases such as GSMc (Tedersoo et al., 2021), GlobalFungi (Větrovský et al., 2020), or GlobalAMFungi (Větrovský et al., 2023) have significantly improved the gaps in our knowledge of the global distribution and diversity of fungi.

On local scales, which are more relevant for practical conservation, eDNA surveys can surpass expert-led fruit-body surveys in detecting species richness, particularly in soil-inhabiting fungi. This is because eDNA also reveals inconspicuous species – such as microfungi – that are almost impossible to detect through conventional methods. An additional benefit of eDNA is its non-invasive nature: it does not require collecting live organisms, which is especially important for rare and threatened species. Moreover, eDNA is present in a wide range of environmental samples, sometimes more conveniently than sampling the species' typical habitat or substrate. For example, terrestrial fungal communities can be partly detectable by eDNA extracted from river or stream water draining the landscape (Matsuoka et al., 2019, 2021; Yang et al., 2021). Such pervasive presence of eDNA in the environment could significantly reduce sampling costs in large-scale conservation monitoring programs. Specifically, fungal community data obtained from aquatic eDNA might be used to evaluate disturbance intensity or frequency at the landscape level. Several studies have shown that fungal diversity recovered from river eDNA reflects landscape disturbance and can serve as an

indicator of ecosystem degradation (Chmolowska et al., 2023; Osburn et al., 2023; Synková et al., 2024).

One challenge remaining is that a significant amount of eDNA-based fungal records present in public databases have incorrect or insufficient annotations (Nilsson et al., 2006). The sampling may, perhaps simply by chance, miss rare or threatened species (Frøslev et al., 2019). Further, eDNA can reveal dead organisms, leading to false records in terms of species habitat (Roussel et al., 2015) and inflating the assessment of the biodiversity ‘hotspots’ for conservation. Other limitations and biases include: (i) DNA degradation in the environment before the sampling (Barnes & Turner, 2016); (ii) risks of contaminations that can occur during any stage from sampling to DNA extraction and PCR (Goldberg et al., 2016); (iii) quantitative limitations since eDNA abundances do not always correspond to absolute abundance or biomasses (Doi et al., 2015), and finally (iv) PCR and sequencing biases (Piñol et al., 2015).

In the absence of financial resources to carry out detailed expert inventories (Prendergast et al., 1993), both eDNA and citizen science data could thus provide essential information for fungal conservation. When the above-mentioned challenges are understood and adequately addressed, eDNA could promote rapid and cost-effective modern inventories, while citizen science data could complement the eDNA data by providing records of threatened or undescribed species (Irga et al., 2020). Importantly, though, those contributions should be demonstrated in actual studies and conservation situations.

1.4. Possibilities to transform fungal information for conservation: Species distribution modelling as a modelling tool

Understanding species’ geographical distributions and ecological niches is key to biodiversity conservation. The main mathematical tools for that are nowadays organized under the approaches of Species Distribution Modeling (hereafter, SDM), sometimes called Environmental Niche Modelling or Bioclimatic Niche Modeling. In essence, SDMs use species occurrence data (records and, when available, absence data) that are linked to environmental variables (e.g. representing the macroclimate, soil, vegetation, land cover, or pollution) to predict the potential distribution of species across a study area (Elith & Leathwick, 2009).

Zurell et al. (2020) distinguished five significant steps for an SDM : (1) a summary of the model hypothesis, methodology, and study area; (2) a data section covering the biodiversity data preparation and environmental predictors; (3) a model section focused on variable selection, multicollinearity, and model tuning; (4) an assessment phase addressing model performance and predictor–presence relationships; and (5) a prediction step covering post-processing and uncertainty analysis. SDM algorithms fall into three main groups: (i) simple, low-performance models (e.g. BIOCLIM, DOMAIN); (ii) regression-based models (GLM, GAM); and (iii) advanced, non-parametric models with high performance (e.g.

ANN, BRT, MaxEnt, RF). Among these, MaxEnt offers several advantages (**Table 2**) and is the focus of the current thesis.

Table 2. Advantages of MaxEnt compared to other modelling algorithms and implications for the final prediction. The species distribution modelling stage is adapted from Zurell et al. (2020).

SDM stage	Characteristics	Reason
Data	Does not require absences; instead, the user can generate background data or pseudoabsences	Absences are difficult to confirm in the field and rarely targeted in field surveys
Data	Can use a small number of records	Rare species are usually challenging to record due to their inconspicuous nature
Data	Can use both numerical and factorial variables	Allows researchers to identify potential key relationships between a specific class and the probability of presence
Model	Has parametrization that allows users to deal with model overfitting	Overfitting is a major issue in species distribution modelling
Prediction	Prediction values are continuous	Can be used to classify the probability of presence values into classes

Species distribution modelling has already significantly advanced our knowledge about species' ranges and the environmental factors behind species presence (Elith & Leathwick, 2009). Furthermore, a substantial diversification of SDM algorithms has allowed application to specific research questions in biogeography, biology, ecology, and conservation (Elith et al., 2011). SDMs outputs can be tailored to inform a wide range of conservation issues: managing biological invasions, identifying critical habitats, delineating and establishing protected areas, or evaluating the establishment of alternative reserve designs (Guisan et al., 2013; examples for fungi in **Table 3**). The SDM output can be further interpreted to obtain habitat suitability maps (Franklin, 2013), which helps conservationists search for possible unknown populations (Ferraz et al., 2020). Additionally, SDMs can reflect habitat changes to assess the potential impact of climate change (Miller et al., 2015) or landscape transformation on species and communities (Ferraz et al., 2020).

Similarly to Red-lists, SDMs have primarily focused on non-fungal taxonomical groups like insects, mammals, and plants (Kass et al., 2022; Chowdhury et al., 2023; Adde et al., 2024). Fortunately, fungi (and especially macrofungi) have become increasingly used as subjects of distribution modelling in the past decade, some of which have conservation goals such as identifying the species' habitat protection status (Yan et al., 2017), identifying fungal diversity hotspots (Yu et al., 2021, 2023), and identify key environmental predictors that either sustain

or limit the species distributions (Pietras et al., 2021; Kujawska et al., 2021; Yu et al., 2021, 2023).

1.5. Objectives and study questions of the thesis

In this thesis, I evaluate the potential and limitations of three emerging tools in fungal conservation – environmental DNA metabarcoding, citizen science, and species distribution modelling. The dissertation consists of five case studies that explore how these tools can be applied in different conservation contexts. The studies focus on the capacity of eDNA-based data to support fungal (including lichen) population and range assessments (**I**, **III**), biodiversity assessment in degraded ecosystems at the catchment scale (**II**), and broad-scale spatial prediction and conservation planning (**IV**, **V**). The thesis addresses the following questions:

(i) What is the contribution of eDNA and citizen science sampling in informing fungal Red-listing at the national level?

Current fungal data is biased and incomplete, especially for many inconspicuous or rare species. eDNA and citizen science offer possibilities for improvement, but in particular eDNA is not yet used in Red-list assessments. This limits the quality of assessing species threat status.

I hypothesize that integrating eDNA with fruit-body records will significantly expand the known ranges of fungi, especially for threatened and near-threatened species (**I**). Similar results are expected from integrating citizen science and expert data for epiphytic lichens (**III**). If confirmed, these additional data would affect assessing the species threat status.

(ii) What is the potential of eDNA and citizen science sampling for detecting disturbance-induced effects on fungal diversity in forests?

Fungal diversity is difficult to map due to its hidden nature and different ecologies of species. While eDNA and citizen science sampling may enable the improvement of the data coverage, their capacity to reflect environmental disturbance-induced effects on fungal diversity is unclear.

As a landscape approach, I expect that eDNA sampled from ditch freshwater can capture the biodiversity across different scales and seasons and reflect drainage intensity at the landscape level (**II**). At the local scale, I hypothesize that citizen science records of lichens on forest trees can help reveal patterns in species occurrence associated with forest management (**III**). Overall, these approaches could support rapid and large-scale disturbance monitoring.

(iii) How can flexible species distribution modelling reveal conservation gaps and restoration needs in Europe?

Conservation planning often ignores fungi, and consequently, there is no clear understanding of how well protected areas protect fungi. Moreover, the effects of climate change on fungal protection status are poorly understood.

I expect that species distribution modelling (SDM) can identify major gaps in the current protected area coverage of fungal habitats (IV, V). Specifically, I examine whether the existing protected area network overlaps with predicted fungal habitats (IV, V) and how it may ensure the protection of fungi and their habitats under future climate change (IV). I also anticipated that conservation responsibilities would vary nationwide, revealing a need for differentiated strategies (V). Lastly, I expect that protection gaps will reveal different patterns of conservation needs across fungal trophic groups, reflecting the historical biases in European protected areas designation (V).

1.6. Thesis setup

The case studies have been organized to answer the study questions as follows. Study I focuses on **complementary records from fruit-body surveys and eDNA**, considering that (i) the data used to assess the species' populations and range sizes are variably biased and often insufficient; (ii) eDNA metabarcoding provides vast amounts of records that are not integrated into Red-list assessments; while (iii) Red-listing should be based on all the relevant data available (IUCN, 2001). By putting together comprehensive sets of data on soil fungi in Estonia, I measure how much eDNA-based records increase the range size and population estimates of fungi that are based on fruit-body records. I expect especially important contributions in species that are inconspicuous by nature (e.g. hypogeous) and in rare and threatened species.

Study II explores **alternatives to traditional ecological surveys of drained forest-peatlands**, considering that (i) the profound ecosystem changes induced by drainage warrant rapid multi-taxon assessments, which are difficult to achieve through traditional surveys; (ii) although freshwater eDNA samples can capture nearby land biodiversity, there is no study confirming this from outflow ditches; (iii) drainage intensity (as measured from ditch densities) is not necessarily related to the impact severity. In a study in nine forest catchments in Estonia, I expect that ditch eDNA samples collected at outlets can capture the ditch catchment biodiversity, which varies along with the drainage intensity.

Study III addresses similar scientific questions but used **citizen science to record lichens in Estonian forests**. Current lichen data are collected by (few) experts, which clearly limits their extent. However, the effectiveness of using citizen science is unclear since most lichens are inconspicuous. I explore how many people will participate in a lichen survey campaign and how many records (i.e. photos of lichens) they supply according to the required sampling methodology. Notably, I expect that these records will increase the range size estimates of both common and rare lichens in a country. As a test of capturing lichen diversity, I study whether CS can provide data comparable to expert surveys in assessing the value of retention trees in silvicultural practice (in comparison with surrounding forest trees).

Study IV uses **SDM to assess potential climate change effects on fungi**. SDM-based habitat suitability maps are prone to multiple errors (sampling biases, environmental data, modelling parametrization, etc.), and their outputs are typically fixed ‘current’ habitat suitability maps. This may mislead species protection strategies that rely on current habitat quality distribution within protected area networks. By modelling a well-known threatened species, I expect that predicted habitat suitability changes follow not only climatic scenarios but also depend on how alternative models are summarized for practical conclusions. Specifically, I explore how much the assessment of future habitat changes depends on whether multiple scenarios are interpreted based on their worst outcome (leading to a “cautionary” conservation approach) or possible improvements (“optimistic” approach).

Study V expands the **SDM use to assess the protection of fungi in the protected area network in Europe**. European regions have different conservation histories, which impacts future protection options in the EU Biodiversity Strategy for 2030 framework, and there is no consensus about each country’s responsibility in protecting wider biodiversity, including fungi. Furthermore, the majority of fungal SDM predict the species’ bioclimatic envelope, while habitat quality is a key component in Red-listing and conservation planning. I expect that the current European PAs network is not protecting the fungal species’ habitat according to the representation targets and that there are significant regional differences in PAs coverage gaps and options. In addition, I explore whether certain groups of fungi are less protected than others.

2. MATERIAL AND METHODS

2.1. Target species

The studies targeted different fungal groups and ecosystems. Studies **I**, **IV**, and **V** targeted only macrofungi, while study **III** targeted lichenized fungi – symbiosis of fungi and algae. Study **II** targeted all eukaryotes but also had a special focus on micro- and macrofungi. Forest assemblages were best represented, both in Estonian (**I**, **II**, **III**) and European perspectives (**IV**, **V**), but landscape-scale sampling (**II**) and species in grasslands or anthropogenic habitats were also included (**V**). In terms of ecosystem functions, studies **I**, **IV**, and **V** focused on ectomycorrhizal and saprotrophic fungi from soil, litter, and dead wood, while study **III** focused on epiphytic lichens growing on bark.

Threatened and Near Threatened fungal species were the key subjects in studies **I**, **III**, **IV**, and **V**. Study **I** included the broadest set: 1,570 fungal species belonging to *Basidiomycota* and *Ascomycota* that were Red-listed according to the Estonian (Saar et al., 2019; Runnel et al., 2021) or Finnish assessment (Hyvärinen et al., 2019). Study **V** focused on 33 threatened fungi proposed by Dahlberg & Croneborg (2006) to be included in the Bern Convention Annex, and study **IV** was based on an example species on their list (*Antrodia albobrunnea*).

2.2. Study region

Studies **I–III** were carried out in Estonia, in hemiboreal Europe (**Figure 2**), while studies **IV–V** are based on data from the whole Europe (**Figure 3**).

Estonia is located in Northern Europe, has a surface of 45,335 km², and its land cover is mainly split between forests (51.5%), agricultural lands (27%), wetlands (5%), bodies of water (5.8%), and built areas (5.7%) (Estonian Environment Agency, 2025). The forests in Estonia are dominated by boreal tree species – *Picea abies*, *Pinus sylvestris*, *Betula* spp., with some inclusion of temperate broad-leaved species such as *Quercus robur*, *Tilia cordata*, *Fraxinus excelsior*, *Ulmus* spp. (Poska et al., 2022). These forests are estimated to host up to 20,000 species of plants, animals, and fungi (Lõhmus & Soon, 2004), including over 227 documented polypore species alone (Runnel et al., 2021). In terms of mycological interest, Estonia has a strong tradition of amateur and expert mycologists, in particular being one of the countries with the most intensive soil-based fungal eDNA sampling in the world (Tedersoo et al., 2021).

The studies addressing the whole of Europe obtained data from all countries on the European continent except Moldova, Ukraine, Russia, Belarus, and Iceland. To avoid introducing artificial distribution limits, the study area exceeds the borders of the European Union (the initial target for the EU Biodiversity Strategy for 2030) as much as enabled by the availability of environmental data. Thus, I attempted to follow the general recommendations to model the species distribution for the entire species range (Raes, 2012). Still, the study area does not represent the entire European distribution range of the species modelled in

studies **IV** and **V**. For example, *Anthoporia albobrunnea* is known to rely on Scots pine, while the distribution map for this tree host was not available for Russia and Ukraine.

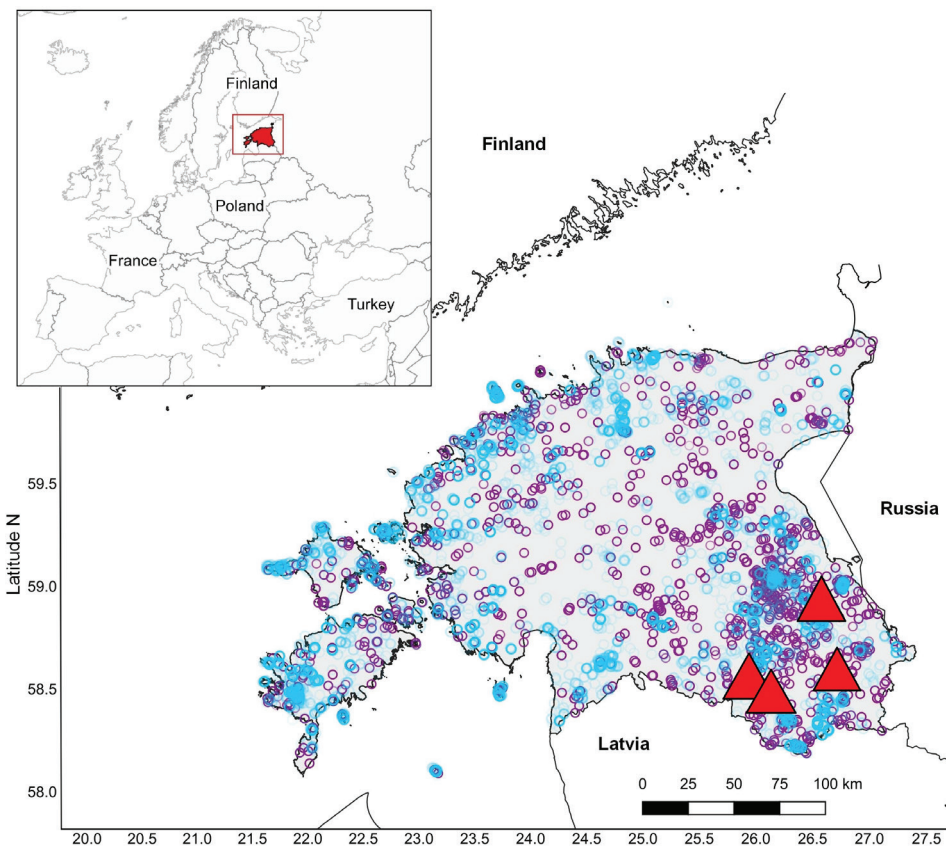


Fig. 2. Distribution of fungal fruit-body (cyan) and eDNA records (purple) in Estonia (**I**). Red triangles denote the drained catchments sampled in southeastern Estonia (**II**).

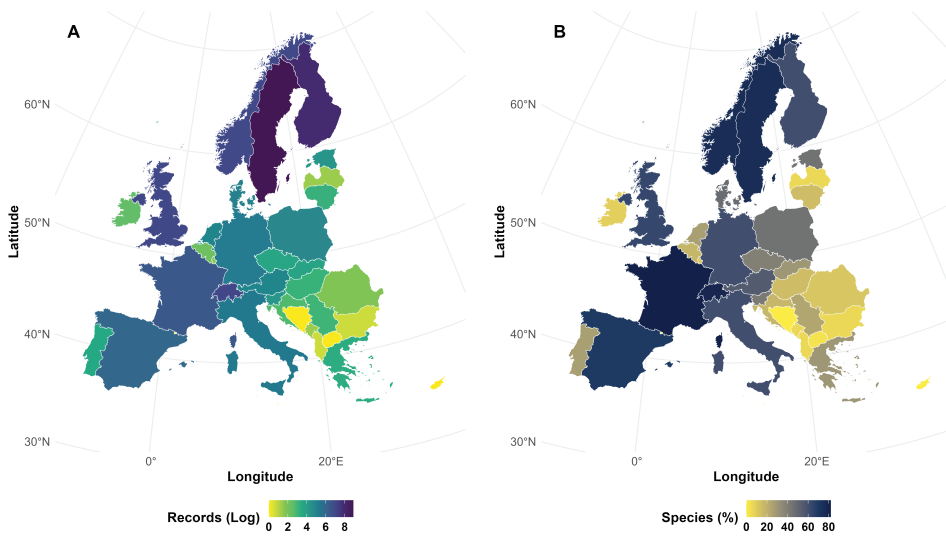


Fig. 3. Distribution of records (A) and species (B) of 33 threatened fungi in Europe (The target species of studies **IV**, **V**).

2.3. Data sources and processing

Studies **I**, **III**, **IV**, and **V** were based on fungal fruit-body and DNA records in different public databases (**Table 3**). The taxonomy of the fungal records downloaded from these sources was harmonized based on Index Fungorum (<https://www.indexfungorum.org>). Additionally, the records were filtered according to the following criteria: (i) time frame (from 1960 to 2024; **IV**, **V**); (ii) geolocation certainty (records with unlikely/incomplete georeferences removed; **IV**, **V**); (iii) location (only the most recent record per 1×1 km grid cell was kept; **IV**, **V**). To reduce spatial autocorrelation, a minimum nearest-neighbor distance of 10 km was used (**IV**, **V**).

Table 3. Databases used for fungal fruit-body and eDNA records in studies **I**, **III**, **IV**, and **V**. In study **III**, also datasets from Lõhmus et al. (2006) and Lõhmus & Lõhmus (2019) were used.

Database	Reference	Record type	I	III	IV	V
Artportalen	https://artportalen.se	fruit-body				
Artsdatabanken	https://artsdatabanken.no	fruit-body				
Danish Fungal Atlas	https://svampe.databasen.org	fruit-body				
Estonian Nature Observations Database	https://elurikkus.ee/collectory/public/showDataResource/dr18	fruit-body				
FongiFrance	https://fongibase.fongifrance.fr	fruit-body				
GBIF	https://gbif.org	fruit-body				
iNaturalist	https://inaturalist.org	fruit-body				
MyCoPortal	https://www.mycportal.org	fruit-body				
PlutoF	Abarenkov et al., 2010	fruit-body				
Grzyby	https://grzyby.pl	fruit-body				
GlobalFungi	Větrovský et al., 2020	eDNA				
GSMc	Tedersoo et al., 2021	eDNA				

The environmental variables used in modelling studies **IV** and **V** were downloaded in raster format from different GIS databases for soil physical and chemical characteristics (SoilGrids, <https://soilgrids.org>), topography (Fick & Hijmans, 2017; Hengl & Parente 2021), vegetation (i.e. probability of distribution of tree species; Achille et al., 2022; vegetation period, <https://lifewatch.eu>; habitat heterogeneity, Tuanmu & Jetz 2015; tree height, Turubanova et al., 2023), land cover (Corine Land Cover, Buchhorn et al., 2020; old-growth forests, Sabatini et al., 2018), protected areas (ProtectedPlanet database, protectedplanet.net/region) and bioregions in Europe (www.eea.europa.eu). Bioclimatic variables were downloaded for the current scenario (WorldClim 2.0; <https://worldclim.org>; Fick & Hijmans, 2017) and, for future predictions in **V**, for two Shared Socio-economic Pathways (SSPs; i.e. SSP2-4.5 and SSP5-8.5) of the CCSM4 model for the year 2070.

The environmental and bioclimatic variables were checked for their multicollinearity to avoid model biases (Dormann et al., 2013). To select the most meaningful predictors in study **IV**, I used the Variance Inflation Factor metric. In study **V**, I used partial merging of correlated variables into Principal Components. However, variables essential for understanding the distribution of specific fungal species were maintained (e.g. probability of host tree presence for specialized species). I used a slightly different approach for variable selection in studies **IV** and **V** due to their different aims: in study **IV**, I explored the main

factors for the prediction, so I kept the original variables, while study **V** was focused on prediction quality rather than the effects of particular factors.

Comparison between fruit-body and eDNA datasets was performed by calculating specific Red-list metrics (i.e. population size, AOO, EOO, **I**) for each species in each dataset. To test how much the fruit-body-based range size estimates increase for threatened and near-threatened species by adding soil samples, we performed a simulation by randomly adding a fixed number of eDNA samples (e.g. 10, 100, 1000).

Study **II** was based on my original field data. The sampling was performed in four forest-peatland landscapes (a subset of the study system described in Tomingas et al., 2025) in south-eastern Estonia, containing nine catchments. The water samples were collected at three locations along the main outflow from each catchment in spring and autumn. These samples were sequenced on the PacBio Sequel II platform. First, DNA was extracted according to the extraction kit protocols, followed by amplicon sequencing using the primer pair ITS9mun (forward) and ITS4ngsUni (reverse). This primer pair is meant to sequence the whole ITS region (covering ITS1, 5.8S and ITS2) for all eukaryotes, including fungi (Tedesoo & Lindahl, 2016). Bioinformatic processing was performed using the NextITS v.0.5.0 pipeline. Chimera sequences were compared against the UNITE v.9 database chimera (Nilsson et al., 2019). Good-quality sequences were clustered at a 98% sequence similarity threshold and curated using LULU (Frøslev et al., 2017). Taxonomic assignment of OTUs was performed using BLAST +2.11.0, using the UNITE v.9 reference database. FungalTraits (Põlme et al., 2020) was used to divide fungal species between functional groups. This study also used elevation data from the Estonian Land Board (<https://maaamet.ee>) and climatic data from local weather stations.

In the assemblage study **II**, the statistics included: (i) Species accumulation curves construction to test how sampling effort affect the number of OTUs per sample; (ii) Kolmogorov-Smirnov test to assess of whether non-fungal and fungal OTUs accumulation curves differ significantly at the waterbody level; (iii) non-metric multidimensional scaling to assess fungal and non-fungal community variation; (iv) three mixed-effects PERMANOVA models, that elaborated each other to explain how the fungal community variation is explained by broad-scale conditions and sampling effort, water identity, and landscape-and-location-level characteristics; (v) Jonckheere-Terpstra test to detect if the community variation is explained by drainage intensity. The same study computed summaries of OTUs distribution by kingdoms and fungal trophic levels for each waterbody.

Study **III** used citizen data gathered during a publicly announced one-year campaign by hundreds of volunteers, whose main task was to find the largest trees in forests and retain trees on clear-cuts. On these trees, the task was to photograph the most lichen-rich spot on the bark. Expert lichenologists identified the lichens from uploaded photographs and created a dataset of lichen species, morphotypes and genera, and the tree characteristics. For processing, the data was split into two datasets: (i) ‘distribution dataset’ compiling these citizen scientist records and records for the same test species from the local biodiversity database

(PlutoF); (ii) ‘forest vs retention tree dataset’ representing records from spatially close (maximum 10 km) pairs of forest vs. retention trees, which could be compared with previous professional studies using ANOVA.

2.4. Species distribution modelling and prediction map analyses

To predict the species distribution range in SDM studies **IV** and **V**, I used the MaxEnt machine learning algorithm (Muscarella et al., 2014; Valavi et al., 2022), implemented within the R software (R Development Core Team; **IV**, **V**). For study **IV**, I modelled the species distribution using all filtered variables in a single model, but for study **V**, I modelled the bioclimatic distribution separately from the landscape distribution. To avoid model overfitting, I used model parametrization features, regularization multipliers, and model performance metrics for both **IV** and **V**, as well as a step-by-step variable removal technique for **IV**.

The species distribution maps were transformed into habitat suitability maps with the classes (non-habitat, marginal, and suitable habitat). In particular, by introducing the class “marginal”, I was able to explore the size and spatial distribution of less-suitable habitats and assess how they overlap with the current protected area network in Europe. In study **V**, I combined the bioclimatic and landscape maps to obtain one habitat suitability map depicting these three classes. In study **IV**, I combined the habitat suitability maps in two different ways: according to the “cautionary” scenario with future optimal and stable habitats in focus and according to the “optimistic” scenario with a focus on potential new habitats in the future. These scenarios were compared to the current habitat predictions, resulting in four habitat change maps (two approaches × two shared socio-economic pathways; **Figure 4**).

Marginality interpretation	GCM1	GCM2	GCM3	GCM4	GCM5	Suitability interpretation	Process	Cautionary	Optimistic
No marginal	Non-habitat	Non-habitat	Non-habitat	Non-habitat	Non-habitat	No suitable		Non-habitat	Non-habitat
Some marginal	Marginal	Marginal	Marginal	Non-habitat	Non-habitat	No suitable		Non-habitat	Marginal
Complete marginal	Marginal	Marginal	Marginal	Marginal	Marginal	No suitable		Marginal	Marginal
No marginal	Non-habitat	Non-habitat	Non-habitat	Suitable	Suitable	Some suitable		Marginal	Marginal
Some marginal	Marginal	Marginal	Marginal	Suitable	Suitable	Some suitable		Marginal	Suitable
No marginal	Suitable	Suitable	Suitable	Suitable	Suitable	Complete suitable		Suitable	Suitable

Fig. 4. Schematic view of the dual approaches (i.e. cautionary and optimistic) for defining the future suitability maps (**IV**), where GCM1 to GCM5 are the five global climatic scenarios. Each row exemplifies a different combination of habitat qualities from the scenarios.

As a next step, habitat suitability maps were used to compare the potential distribution of the fungal species with the current European protected area network (**IV**, **V**). For each species in each European country, suitable habitat areas (in km²) currently under strict or less strict protection were calculated (Protected Planet portal – <https://www.protectedplanet.net/region/EU>). Using these habitat and habitat protection maps, I identified tentative gaps in the protection of the 33 threatened fungal species in Europe (**V**). For this, I calculated species representation targets for each species in each country – the habitat area that has to be

protected in line with the EU 2030 Biodiversity Strategy. Comparing the representation target with the current protected area provided the protection gap. To elaborate on this target, I further identified the cases when the area was bioclimatically suitable and the species was present, but the habitat area was insufficient. This would constitute a tentative restoration target in the country. Finally, I compared the protection gaps among countries both within and across the species, with the aim of understanding the need for international coordination to optimize the protection efforts for the 33 species of fungi.

The analyses and graphical outputs were performed with R v. 4.4.0 (R Core Team 2021, **I–V**) and Statistica v 6.0 (StatSoft 1984–2001, **III**), while some of the GIS processing with QGIS v. 3.36 (QGIS Development Team 2025, **III–V**).

3. RESULTS

3.1. Obtaining records and range estimates for fungal Red-listing (I, III)

In Estonia, the eDNA and fruit-body data represented altogether 1,583 soil-inhabiting macrofungal species that had been assessed for their Red-list category (I). Of these species, 79.2% were detected as fruit-bodies, while 70.8% were detected as eDNA. In total, the majority of records (77.4%) were based on eDNA. However, 34% of threatened species were documented exclusively as fruit-bodies (compared to 18% documented only as eDNA).

For most soil fungi species, the fruit-body-based range estimates (AOO and EOO) differed from those that were based on eDNA (**Figure 5**): the range estimates based on eDNA were mostly larger. In particular, eDNA-based AOO was often disproportionally larger than when calculated based on fruit-bodies (**Figure 5A**). The species range estimates also depended on their characteristics. For example, *Amanita muscaria* and *Cantharellus cibarius* (charismatic species; both Least Concern) were the soil fungi with the largest range estimates in Estonia according to fruit-body records, while *Amphinema byssoides*, *Tomentela stiposa* (difficult to identify macromorphologically) had huge ranges based on eDNA records. Interestingly, eDNA revealed much larger ranges for several species with hypogeous fruit-bodies (e.g., *Tuber rufum*, *Melanogaster ambiguus*) or litter-inhabiting millimetric apothecia (e.g. *Hymenoscyphus immutabilis*) than previously known.

Among the sampled soil-inhabiting macrofungal species that had been assessed for their Red-list category, 10.8% (172 species) were threatened or Near Threatened. I simulated whether and how much eDNA data from each added soil sample would expand the fruit-body-based range estimates of such species. I found that, on average, eDNA from ten soil samples expanded the known distribution range of 12 threatened and Near Threatened species with 18 grid cells (2-km × 2-km grid). When scaled up, data from 500 soil samples expanded the known distribution range of 78 species by 895.5 grid cells. Additionally, incorporating eDNA data from ten soil samples revealed, on average, three previously undetected threatened or near threatened species by fruit-bodies, while 500 samples uncovered 32 additional species (I).

In the lichen study **III**, the citizen science observations provided data and improved range estimates mostly for common species, while species of conservation concern (those nationally protected, threatened, or indicators of forest key habitats) were only recorded in a relatively small number of samples (5.6% of all photographed trees). The range size increased for only one out of four specifically targeted lichen species of conservation concern (*Lobaria pulmonaria*). Out of common species, the citizen science project improved the former range estimates of microlichens on average more than those of macrolichens (15.2% vs 11.5%).

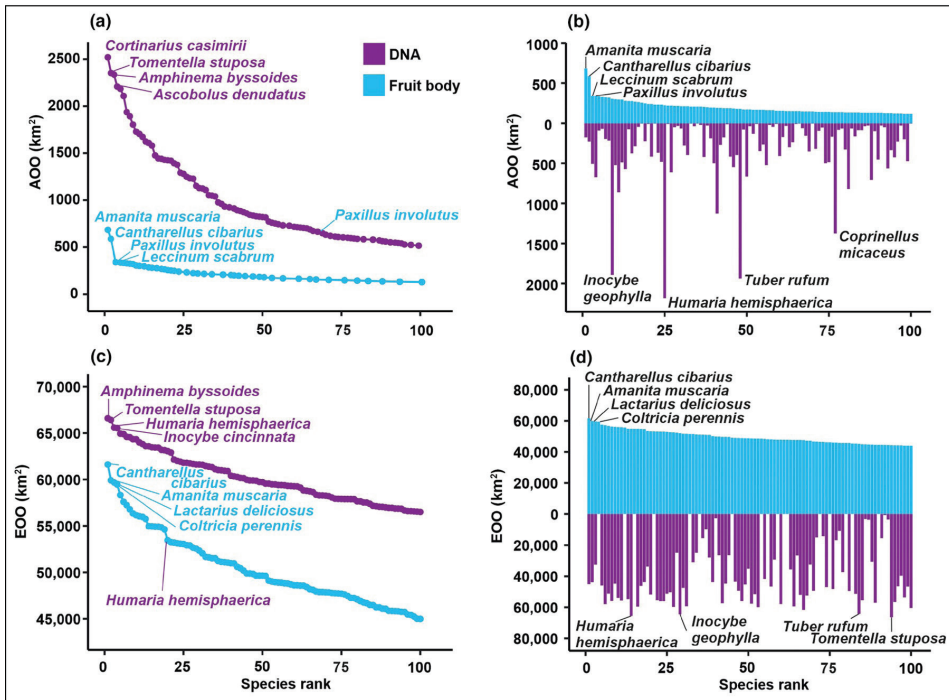


Fig. 5. Rank abundance curves calculated based on the range metrics AOO (A, B) and EOO (C, D) for fruit-body (blue) and eDNA (purple) datasets (I). AOO (Area of Occupancy) is calculated as the number of grid cells which contain records, while EOO (Extent of Occurrence) is usually calculated as the minimum convex polygon of records.

3.2. Describing fungal diversity under environmental change (II, III)

In the nine drained forested catchments, I recorded 5,900 OTUs (~ 1,000,000 reads) from freshwater eDNA samples, among which 49.5% were fungi (II). The 10% of most abundant OTUs comprised 89.6% of all the reads and were also mostly fungi, e.g., *Physalospora scirpi*, *Pucciniastrum areolatum*, and *Flagellospora curvula*. However, the most abundant detected OTUs belonged to the order Cyclopoida (microinvertebrates).

Along with the freshwater sampling, OTU accumulation curves showed faster accumulation in fungi than in non-fungi, although the curves from none of the waterbodies (catchments) reached asymptote. Total, non-fungal, and fungal community variation was significant between the waterbodies (>25%) and between seasons (<10%). The fungal and non-fungal communities were more distinct between than within the waterbodies, although the variation within the communities was high (Figure 6; II). Between-catchment variation was significantly related to drainage intensity, which was partly related to different water properties (i.e. pH, electrical conductivity). Considering trophic guilds individually, only

the abundance of animal parasitic fungi significantly increased with drainage intensity. In general, intensively drained landscapes were characterized by a high genus richness of soil saprotrophs, wood saprotrophs, animal parasites, and plant pathogens (II).

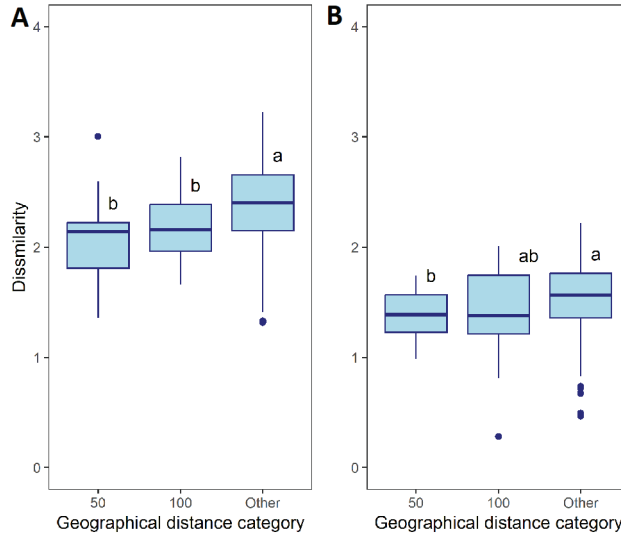


Fig. 6. Community dissimilarity in non-fungi (A) and fungi (B) identified from freshwater eDNA along with the distance between samples (50 m and 100 m – within the same waterbody, Other – between waterbodies, II).

In the lichen citizen-science study (III), the participants took photos of forest trees nearly four times more often than of retention trees, despite clear instructions to sample the largest two trees in both forests and closeby cutovers with retention trees. Despite such bias, the photos revealed lichen cover differences between the forest and retention trees, as well as different species of trees, which were comparable to those previously established in expert surveys.

3.3. Species distribution modelling for fungal habitat protection (IV, V)

Distribution modelling for the old-growth polypore fungus *Antophoria albobrunnea* predicted its current distribution in Northern Europe (93% of total habitat) and a discontinuous habitat range in Central Europe (IV). Of an estimated 555,000 km² of habitat, 41% was identified as suitable, and its main host (*Pinus sylvestris*) was the most important factor explaining the distribution. However, only 7.2% of *A. albobrunnea*'s predicted habitat in Europe is currently protected, including 6.3% of suitable habitat being strictly protected (IV).

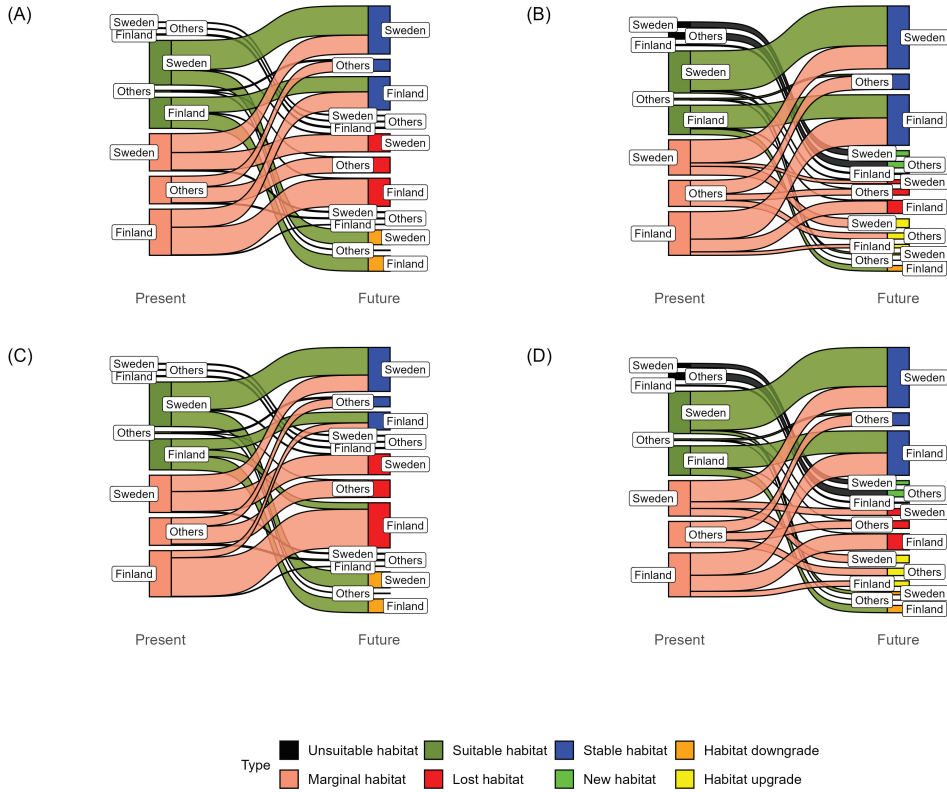


Fig. 7. Sankey diagram of predicted habitat suitability change in *Anthoporia albobrunnea* in Europe by 2060: A, cautionary interpretation of SSP2-4.5 scenario; B, optimistic interpretation of SSP2-4.5 scenario; C, cautionary interpretation of SSP5-8.5 scenario; D, optimistic interpretation of SSP5-8.5 scenario. The habitat area is separately shown for the two main host countries (e.g. Sweden and Finland), while the other countries are pooled (IV).

Both the moderate (SSP2-4.5) and strong climate-change scenario (SSP5-8.5) decreased the total predicted habitat of *A. albobrunnea* in Europe and reorganized the distribution in its core range (**Figure 7**). The habitat loss extent ranged from a mere 6% for an optimistic interpretation of SSP2-4.5 scenario to 43% for a cautionary interpretation of SSP5-8.5 scenario, and an optimistic assessment even suggests that the suitable habitat will increase by 16% in both climatic scenarios (the cautionary assessment predicted 36%–43% decrease). Of the marginal habitat, 22% to 43% was predicted to become unsuitable depending on the climatic scenario and the assessment. However, the predicted marginal habitats had a consistently higher proportion of (recently) persistent forest area and higher host probability than suitable habitats. Overall, the strictly protected suitable habitat would change only slightly in any scenario.

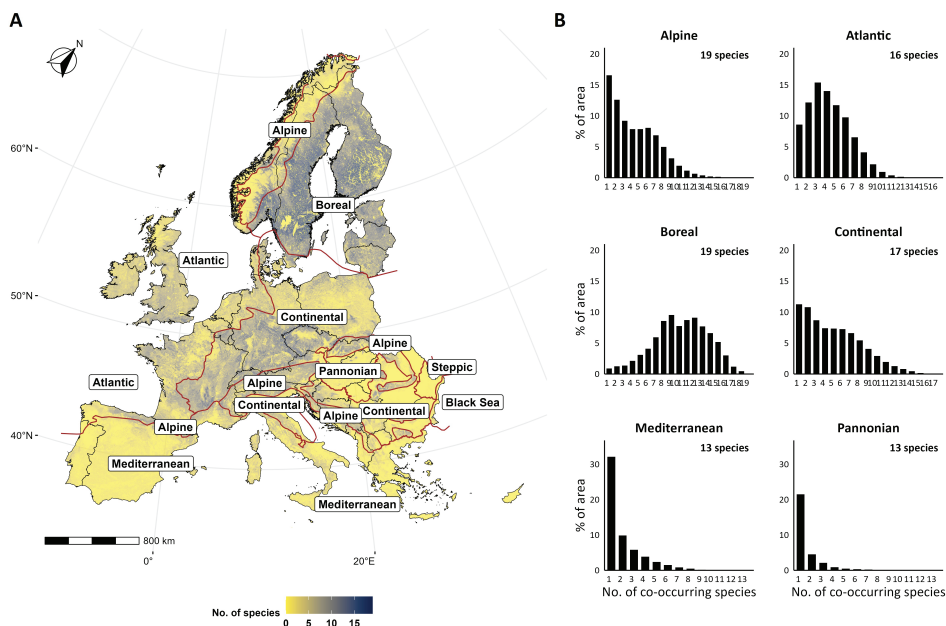


Fig. 8. Numbers of threatened fungal species co-occurring at 1×1 km scale in Europe (A) and the habitat area of the shared number of species for each bioregion (B). (V)

By modelling the distribution of 33 threatened fungal species in Europe, I established highly variable habitat areas (ranging from 61.500 km² to 1.790.000 km²; V). On average, 13% of the habitat area was predicted in countries where actual species records were lacking. Joint species distributions highlighted potential ‘hotspots’ of co-occurrence in boreal, southern continental, and Alpine bioregions (**Figure 8**). On the opposite, the Mediterranean and Pannonian bioregions had the least co-occurrence among species, although their total richness was comparable with the top bioregions. Across the species, the models indicated that, on average 47% of the habitat area as ‘suitable’ and 53% as ‘marginal’ (V).

The predicted habitat of none of the 33 Red-listed species met the EU’s biodiversity goals of 30% overall protection or 10% strict protection. However, when compared with the minimum national target of 2,000 km², all the species had at least one country where this goal was achieved. Protected area gaps calculated by each country individually would accumulate to 39%–71% of species’ habitat to be protected and consistently place the main burden on specific countries (usually the better-studied and most forested ones, mostly the Scandinavian countries). By allowing for coordinated protection, individual responsibilities would become more equally allocated among countries. Additionally, for 24 species, habitat restoration responsibilities were highlighted (usually in 1–2 countries).

4. DISCUSSION

4.1. eDNA metabarcoding and citizen science for Red-listing of fungi

Environmental DNA (eDNA) is increasingly used to assess fungal biodiversity in both scientific studies and national monitoring programmes (Kelly et al., 2014), but not in the Red-listing practices – the cornerstone of conservation planning. My study (I) showed that eDNA data significantly improved species range estimates for soil fungi in Estonia. In addition, new species were discovered that had not been previously reported by fruit-bodies in the country. However, many threatened species remained undetected by eDNA alone, highlighting the need to retain fruit-body surveys, especially for the species that produce easily identifiable fruit-bodies. Thus, eDNA should be seen as a complementary rather than a replacement method.

In the fungal fruit-body data, the species with the largest estimated ranges (specifically, AOO) were typically morphologically easy to identify, charismatic, and well-known (e.g. *Amanita* and *Cantharellus*; I). As a result, Red-list assessments are clearly more accurate in such conspicuous species, while cryptic or taxonomically challenging taxa (e.g. *Tuber*) remain difficult to evaluate. To this end, eDNA provides crucial data that can fill the gap in many species assessments, significantly increasing both AOO and EOO estimates. These eDNA-based estimates may lead to a changed (lowered) Red-list category; however, rare and previously undetected species with small ranges (high category) are also likely to be added. In both cases, the identifications must be cautiously considered as current sequencing methods or bioinformatics protocols can provide false positive observations. Based on my results (I), eDNA metabarcoding should be incorporated into large-scale national sampling schemes (Niskanen et al., 2023) with careful protocols for sampling density, spatial arrangement, and record interpretation to address gaps left by fruit-body surveys and previous smaller eDNA metabarcoding studies.

Importantly, eDNA sequences should be submitted to global databases (i.e. GBIF or PlutoF), so that an end user (distribution modeller or a Red-list assessor) can use them. Following up, the recording process should be enhanced towards user-friendly to avoid the necessity of bioinformatic expertise (Větrovský et al., 2020). Importantly, the value of eDNA data depends on the quality of reference databases used for sequence comparison (Blackman et al., 2022). The reference databases such as GenBank and UNITE, compile sequences derived from sequenced, taxonomist-identified fruit-bodies (Benson et al., 2012; Kõljalg et al., 2019). Thus, continued fruit-body sampling along with high level species identification is essential to match the rapid growth of eDNA datasets.

Diversified survey approaches could also be developed for fruit-body surveys, notably those with public involvement. Even in the generally inconspicuous lichens, a citizen-science project presented a clear potential to record overall

lichen diversity, although its specific contribution to species of conservation concern was modest (III). The results emphasized the importance of taxonomic expertise for traditional sampling and the necessity of validating records in public databases. This aligns with the current trend in fungal recording, where only records with sufficient metadata and taxonomic identification pass quality checks and are accepted into dedicated international databases (Haelewaters et al., 2024). An important result was the high capacity of the “blind photography” methodology to capture microlichens, which are almost always neglected by amateurs (III). However, while this eased the contribution of volunteers to the project, it required considerable effort and attention from taxonomists to investigate those photos. Still, the lack of physical material did not enable the microscopical and chemical identification needed for many species, which limits the use of such data for species Red-listing. This is a fundamental issue in lichens-related datasets as taxonomic identification accuracy is often compromised due to lichen’s taxonomic complexity (McMullin & Allen, 2022).

4.2. Environmental impact on fungal diversity

Through different methodological approaches in the case studies, different threats to fungal diversity were investigated at local (III), landscape (II), and continental scales (IV, V). These approaches also illustrated the trade-offs between gaining a full local fungal diversity assessment with much random noise in the data (II) versus obtaining a causal but simplified understanding at the level of a species’ range (IV). Furthermore, the citizen science project showed that balanced ecological sampling by volunteers might not be achievable in the case of clear instructions; in this study, the clear cuts were simply not attractive for sampling (Bliss, 2000) to properly compare with the reference system (forest trees) (III). The behaviour is similar to that of berry-pickers (Remm et al., 2018), but it has traditionally also characterized lichen experts (Löhmus & Löhmus, 2009). To understand the distribution of fungal diversity, such biases need to be targeted by sampling towards less sampled habitats and species.

On the other side, the citizen-science information gathered on the range size of common species is of great value since these species weigh more in ecosystem functioning (Gaston, 2010) (III). And, despite biased samples, the citizen-science project was able to reveal several general lichen diversity patterns on which the current understanding of retention trees as lichen diversity ‘lifeboats’ in fragmented managed forests is based on (Löhmus & Löhmus, 2010; Lundström et al., 2013; Hämäläinen et al., 2014).

In the drained forested peatlands study, I found that eDNA metabarcoding captured a high taxonomic diversity of fungi that broadly also reflected the effect of drainage intensity (II). The fact that fungal diversity was best captured may be due to the primers used. This means that primer choice is essential for target-organism studies and that primers have to be researched towards specific groups at the same time with less costly sequencing (Scibetta et al., 2019).

However, with limited sampling effort, there remained a high community variation within waterbodies and an overwhelming proportion of taxa (OTUs) were found rarely (**II**). The high within-waterbody variation indicates that individual eDNA samples are capturing a ‘very local diversity’, perhaps affected by sample quantity and substrate flexibility (water flow). Also, seasonal turnover was confirmed, which highlights the importance of seasonal sampling (Matsuoka et al., 2021). Most likely, this is due to: (i) the community’s annual cycle, including spore release cycles; (ii) broad ecological phenology (e.g. litter accumulation in water in late summer and autumn); (iii) drainage maintenance during summer (e.g. ditch cleaning increasing soil disturbance nearby streams, thus releasing fungal hyphae fragments or fungal spores).

While the capacity of eDNA sampling to rapidly detect biodiversity change is thus not obvious, it can indicate ecosystem risks by detecting particular taxa, as demonstrated by repeated discovery of pathogens and invasives in freshwater samples (**II**). For example, the detected strong association of soil saprotrophs and entomopathogenic fungi with intensively drained water catchments is ecologically plausible. Disturbance can lead to a decrease in ecosystem resilience (Ennos, 2015) due to increased permeability to invasion of new species and the already-present obligatory pathogens’ proliferation and facultative pathogen activation in stressful conditions. Rapid pathogen vectorization is an important characteristic of successful pathogen invasions and spread (Suarez & Tsutsui, 2008). Artificial ditch network (whose characteristics often mimic true streams) can enhance their linear transportation of propagules, either by water (Jansson et al., 2005; Nilsson et al., 2010) or air (Wubs et al., 2016). Besides this, a heavily impacted drained system may allow an increase in surface water flow during rain, but this issue has yet to be studied. Additionally, the identification of particular soil and dead wood inhabiting organisms in freshwater may indicate enhanced transport into the ditch system under disturbance, with possible implications on litter decomposition, sedimentation, and propagule spread.

In contrast, the potential negative interaction of climate change with habitat degradation (Travis, 2003) was best illustrated by the habitat modelling study on a single species, *Anthoporia albobrunnea* (**IV**). This study used multiple sources to obtain records, and another study confirmed that larger samples provide better models (**V**). Importantly, the main metric (spatial and directional change of habitat) highly depended on how multiple scenario results were interpreted (**IV**). For this species, Northern Poland, Scania, and Swedish Lapland could be expected to host suitable habitats in the future. However, it is unclear how probable such colonization of new habitats is, and especially whether conservation strategies should rely on it. Thus, scientists should promote field studies of these processes and test the feasibility of the introduction of propagules (Nordén et al., 2020).

4.3. Species distribution modelling of protection gaps

Species distribution modelling, combined with conservation-oriented analyses, revealed the current and future habitat distribution of threatened fungal species and their protection in Europe (IV, V). Even in a polypore species primarily found in Northern European natural forests, *A. albobrunnea*, the existing network of protected areas appears to safeguard only a small fraction of its habitat (IV). This study also revealed that, in a future perspective, the degradation of marginal habitats deserves more attention since marginal habitats for *A. albobrunnea* appeared ecologically even more stable than its currently most suitable habitats. This finding is important because conservation efforts typically focus on core populations, even though peripheral ones may be equally vital for species conservation (Channell, 2004). In countries that do not protect high-quality habitats for specialized polypores, I thus recommend prioritizing the protection of additional natural habitats predicted to provide stable conditions in the future, as it has been shown that such species can successfully recolonize boreal old-growth forests within protected areas network (Ruete et al., 2016; Runnel et al., 2020).

Elaborating on this methodological framework (i.e. combining the marginal-suitable habitat dichotomy and habitat protection overlap analysis), I found that (i) none of 33 well-known threatened fungal species meet the EU' Biodiversity Strategy targets for 2030; (ii) particularly soil-saprotrophic species are clearly unprotected; (iii) protection status of fungi across Europe is unevenly distributed, and countries can be grouped based on their conservation involvement (V). The high variability of predicted range sizes across Europe was anticipated, given the diverse ecological and biogeographic backgrounds involved. Our findings align with a study on approximately 1,900 macrofungal species (Yu et al., 2021), which identified the boreal bioregion as the richest, corresponding in our case to locally high species co-occurrence.

The regional discrepancy revealed by the gap analysis can be explained by Europe's land-use history and the development of its protected areas network. Mediterranean societies adopted agriculture early in Europe's history (Bogucki, 2002), while Northern and Eastern Europe experienced a delayed transition in land use (Zvelebil & Dolukhanov, 1991). This contributes to the lower degree of habitat fragmentation within the protection network in Eastern and Northern Europe compared to Western Europe (Lawrence et al., 2021). Also, North European countries have a strong conservation legacy demonstrated by the early establishment of national parks in the 20th century and a history of scientific and cultural movements that advocated awareness for biodiversity protection (Elbakidze et al., 2013; Niemelä & Ruuskanen, 2019).

As expected based on the niche breadth-range size relationship (Gaston et al., 1997; Slatyer et al., 2013), the two species with the smallest predicted habitat areas in Europe – *Fomitopsis officinalis* (Alps) and *Hohenbuehelia culmicola* (Atlantic coast) – are both associated with narrow ecological settings (e.g. subalpine larch forests and sparsely vegetated coastal dunes, respectively). Despite their different ecological characteristics, both are listed on the Global

Fungal Red-list as Vulnerable and Endangered, respectively, due to their shared reliance on unique fragmented and dispersed habitats (IUCN, 2025). A global meta-analysis of plants and animals found that narrow-range species tend to be less abundant in disturbed ecosystems, opposite to wide-ranged species, placing the former at higher risk of extinction (Newbold et al., 2018). Moreover, species with small ranges and narrow niches are more susceptible to range contractions, a vulnerability that is amplified in highly transformed landscapes like those in Western Europe (Botts et al., 2013). Study V exemplifies *H. cumicola* as a representative case, suggesting that without prompt conservation action, the species cannot upgrade its Red-list status from VU (Vulnerable; IUCN, 2025). Since seminatural landscapes are expected to be prioritized in achieving the EU 30% protection target (Müller et al., 2020), their improvement potential for narrow-range species should be considered.

Gaps in protected area representativity are generally well acknowledged (Secretariat of the Convention on Biological Diversity, 2020), but these are rarely calculated for inconspicuous biodiversity (see Chowdhury et al., 2023). The current status of fungi highlights the need to expand Europe's protected areas to include fungal habitats, especially for soil saprotrophs (**Table 5**). The gap analysis also revealed that country-level representation targets often imply disproportionately large habitat protection requirements, especially for a few countries with extensive habitats left (typically well-forested countries). To account for this, conservation responsibilities could be politically rearranged at the regional scale among all countries hosting the habitat (whether marginal or suitable). Furthermore, countries with bioclimatically suitable but landscape-limited habitats (usually lost due to land use) should aim to restore and protect at least 2,000 km² of fungal habitats (equivalent to the minimum habitat area at which a species is categorized as threatened by Red-list criteria).

Study V extended its geographical scope outside the EU border despite its applied aim being mostly related to the EU's Biodiversity Strategy for 2030. This broader approach improved the species modelling process and provided a context for assessing the protection status of habitats. Specifically, the fungal data from the UK, Switzerland, and Norway contributed significantly to the species modelling process due to a large number of records and probably resulted in enhanced identification of habitats not only in those countries but for the whole model prediction.

Table 5. Main conclusions of the protected area gap analysis by fungal functional groups.

Group	Main conclusion	Potential causes	Potential solutions
Mycorrhizal fungi	Protected areas poorly cover high-quality habitat.	Land cover competition of natural habitats (where fungi usually grow) with agricultural fields (see Sweden, Komonen et al., 2016). Environmental pollution (Arnolds, 1995).	Special attention can be paid to fungi that have keystone roles in ecosystem functioning (Hawksworth, 2003). Identification of soil fungal-rich hotspots (Guerra et al., (2021), i.e. unmanaged grasslands, old-growth forests). Implement agroforestry.
Soil saprotrophs	Suitable habitat is especially poorly represented despite a high number of records.	Soil saprotrophs' habitats are not included in EU' protected areas. Fruit-body recorders are targeting high-quality habitats, omitting more marginal habitats.	Financially support low-input farming practices in soil fungal-rich 'hotspots'. Advocate for inclusion of soil fungi in national biodiversity strategies.
Wood-inhabiting fungi	Land cover-linked conservation status (i.e. forested countries better protect this group of fungi).	Natural habitats are historically protected. Better recording cover in these countries.	Protection can extend in production forests (equivalent to the marginal habitats of fungi); This is in agreement with the fact that habitat marginality plays an important role in biodiversity (Neves et al., 2017).

4.4. Final thoughts on the data needs in fungal conservation

This thesis highlights the various data sources and habitat prediction tools that can enhance our understanding of fungal conservation gaps and opportunities. However, each of these approaches also has its limitations (some shared, others specific) that require ongoing attention. On top of methodological issues (such as overestimation of threatened populations or their habitats due to data accumulation over a long time or lack of habitat-specific data for modelling), there are also issues of data accessibility (digital data sources; eDNA) and public awareness. Real-world conservation must select its data sources, especially in relation to unpopular conservation-led effects (e.g. removing land from economic use or increasing protection restrictions).

Importantly, conservation addresses a ‘moving target’ of continuously changing environmental and socioeconomic context (Groom et al., 2006). The pathogen detections in drained forests (II) suggest that land management shifts and drainage intensity changes may alter fungal pathogen communities. Such shifts confirm that fungi, due to their sensitivity to disturbance gradients and their status as visible links to soil biodiversity, can serve as indicators of ecosystem processes (Heilmann-Clausen et al., 2014). Similarly, while the increase in suitable habitat under climate change should be considered as a possible response, it was restricted to one particular (optimistic) scenario interpretation only (IV). Managing such change requires simultaneous consideration of other possibilities and other boreal polypores for which new habitats may remain unsuitable. The same study suggested major declines in marginal habitats, which may lead conservationists to neglect those. It is unclear whether the loss of marginal habitats should prompt the adoption of additional measures that support fungal survival in the degraded habitats and which measures might be feasible.

The contrasting habitat suitability interpretations reinforce the need for multiple conservation strategies and highlight the importance of clearly defining conservation objectives that consider multiple outcomes (IV). It is essential to investigate the mechanisms behind the species’ responses to environmental changes so that different management practices can be developed and applied. Long-term monitoring in different environmental setups (e.g. across various habitat types and disturbance regimes) is essential to validate models and refine conservation measures. Integrating experimental research, citizen science, and eDNA metabarcoding offers a powerful strategy to monitor the environment for habitat changes and species responses, thereby improving our understanding of fungal conservation (Halme et al., 2012; Niskanen et al., 2023).

5. CONCLUSIONS

In this thesis, I investigated the contribution of different data inputs (including environmental DNA and citizen science data) and species distribution modelling for informing fungal conservation in Estonia and Europe. The main findings can be combined into the following practical conclusions for fungal conservation:

1. **Integrate fungi into biodiversity planning and policy.** When developing national and European-level protection networks (e.g. Natura 2000), fungi, particularly soil saprotrophs, should be prioritized as the current networks may not suffice for protecting threatened fungi. Predicted hotspots of fungal distribution provide guidance when designing the protection areas.
2. **Use fungal monitoring techniques of different types.** Combine freshwater and soil eDNA sampling with fruit-body surveys to complementarily capture fungal diversity. Use eDNA to detect microfungi, inconspicuous macrofungi and fruit-bodies to detect rare and threatened macrofungi.
3. **Use machine learning techniques to fill data gaps and guide spatial conservation.** Species distribution modelling can provide useful assessments of habitat suitability and detect locations potentially impacted by climate change. Use predicted species distributions as an information source to assess fungal species in both national and global Red-listing processes.
4. **Encourage fungal data collection and improve awareness of fungi through citizen science.** Develop online tools that train and support non-specialists in fungal recording, particularly to target macrofungi and forest lichens. Support professional fungal monitoring (e.g., in protected areas or old-growth forests) with citizen-collected data on fungal species' phenology, distribution, and habitat preferences.

SUMMARY IN ENGLISH

Relevance of eDNA, citizen science, and species distribution modelling for fungal conservation

The ongoing biodiversity crisis makes conservation efforts urgent, yet fungi – despite their fundamental ecosystem functions – remain largely overlooked. Growing survey efforts, including new data from citizen science and DNA metabarcoding, and modelling approaches such as species distribution modelling are beginning to offer promising insights for fungal conservation. The primary focus of this doctoral thesis was to synthesize such data and approaches through practical case studies to improve the current knowledge on fungal conservation.

Traditionally, the understanding of fungal species' distribution and habitats has been obtained from fruit-body observations, thus also informing Red-list assessments and guiding conservation priorities. However, fruit-body surveys are limited by seasonality in fungal fruit-body production, detectability issues, and high effort needed. Environmental DNA (eDNA) offers complementary advantages: being sampled directly from substrates such as soil or wood, it may detect fungal presence year-round and capture a broader spectrum of fungal diversity, including cryptic or yeast-like species that rarely form fruit-bodies. Given the accelerating impacts of climate change and habitat loss, eDNA could be useful for monitoring fungal community change across ecosystems under disturbance or protection. Alongside eDNA, emerging digital tools such as machine learning now enable modelling fungal species distributions and relate these to environmental drivers. Together with additional observational input from citizen science, these approaches open new opportunities to advance fungal conservation efforts – through improved Red-list assessments, better integration of fungi into protected area planning, and a clearer assignment of conservation responsibilities across international biodiversity strategies.

To explore how eDNA could improve knowledge of the population status of soil fungi, I comparatively analyzed fruit-body observations and eDNA data from ca. 2000 soil samples in Estonia (**I**). Out of approximately 1,650 species assessed for their Red-list category, a significant share was exclusively present as eDNA. eDNA expanded range-size estimates for Near Threatened and threatened species by an average of 0.18% and contributed up to 0.3 new species detections per additional soil sample. Despite such clear contributions, 34% of Near Threatened or threatened species were only detected by fruit-body observations. This indicates that both eDNA and traditional methods have their distinct strengths and limitations, suggesting a need for integrated approaches in fungal conservation assessments.

I also investigated the use of eDNA to detect changes in fungal communities in response to ecosystem change, focusing on drained forested peatland catchments in Estonia (**II**). I collected freshwater samples from the catchment outflows and analyzed how eukaryote communities (dominated by fungi) varied with drainage intensity, both between and within water catchments. Our results revealed

high variability between samples taken along the same ditch and in different seasons, but differences in the fungal communities between catchments were also detected and could be linked with drainage intensities.

The potential of citizen science for biodiversity monitoring was studied based on a public campaign where over 1,700 photos from more than 1,100 large trees were submitted all over Estonia (III). Species experts identified 119 morpho-species and lichen-forming species in these photos, including 55% microlichens and 5% species of conservation concern. This underscores that, for lichens, citizen science has the most value in monitoring common species. In terms of Red-list assessments, it refers to estimating the species' trends, as common species are often ignored in expert surveys.

I further explored how data from all these sources can inform the planning of Europe's conservation area networks (IV, V). The European Union Biodiversity Strategy for 2030 targets protecting 30% of the land, with one-third under strict protection, but fungi are largely absent from the current conservation planning. I used MaxEnt species distribution modelling for 33 representative threatened fungal species across Europe. Comparing the predicted habitat distributions with the protected area network indicated that none of the species met the protection targets, and the overall representation of the species was close to random. By calculating individual protection responsibilities for each country, it was demonstrated that regionally coordinated improvement in protection and habitat restoration is required (V).

Regarding climate change-induced threats to fungi, the species distribution models were further developed to predict the current and future ranges of a northern polypore, *Anthoporia albobrunnea*, associated with natural and near-natural Scots pine forests. The results showed that suitable habitat is declining and shifting northward, but careful interpretation of habitat suitability predictions is critical for effective conservation planning. Instead of relying on a single prediction outcome, an approach with two combined alternatives was introduced: one interpretation focused on core habitats and avoidance of the worst scenario, while the other highlighted emerging and marginal habitats that may become important under future climates.

This doctoral thesis provides a case-study-based insight into the practical use of new information tools (specifically, eDNA sampling, citizen science data and species distribution modelling) to tackle urgent conservation challenges. Building on these findings, I propose key future directions: (i) integrating eDNA data into Red-list assessments; (ii) refining eDNA sampling procedure for landscape-scale monitoring; (iii) expanding the use of citizen science approaches; (iv) expanding species distribution modelling to a larger number of potentially threatened (including Data Deficient species); and (vi) developing new approaches for using habitat predictions in setting conservation targets and evaluation procedures.

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SUMMARY IN ESTONIAN

Keskkonna-DNA, kodanikuteaduse ja levikumodelite olulisus seente kaitses

Käimasolev elurikkuse kriis, mida põhjustavad peamiselt muutused kliimas ja maakasutuses, seab looduskaitsele uusi suuri ülesandeid. Seentel on lagundajate ja sümbiontidena keskne roll ökosüsteemide toimimises, ent looduskaitse planeerimisel neid organisme eriti ei arvestata. Selle põhjuseks on seente peiduline eluviis, millest omakorda tulenevad ebapiisavad teadmised nende elurikkuse ja leviku kohta. Neid vajakuid võiks oluliselt leevendada uued infoallikad: harrastusteadlaste kasvav huvi seente vastu ja avalikud seenevaatluste andmebaasid, üha suurenev hulk keskkonna-DNA (eDNA) andmeid ning masinõppe meetodid liikide leviku modelleerimiseks.

Siinse doktoritöö põhieesmärgiks oligi hinnata, milliseid võimalusi ja uusi teadmisi erinevad andmeallikad ja analüüsimeetodid seente looduskaitse planeerimisel pakuvad. Töö koosneb viiest originaaluuringust, mis jaotuvad kahte ossa: esimene käsitleb vaatlusandmestike täiendamist ja teine ruumiliste looduskaitseliste prognooside tegemist.

Traditsiooniline viis seente leviku ja mitmekesisuse kohta ülevaadet saada põhineb viljakehade vaatlustel ja kollektsioonidel. Niisuguste andmete kogumine on aga töömahukas ning andmed ise ebatäielikud, sest seened moodustavad viljakehi olenevalt keskkonnatingimustest ning viljakehad võivad olla lühiealised. Sellega võrreldes on näiteks eDNA-l põhineval andmekogumisel mitmeid eeliseid: see võimaldab tuvastada seeni erinevates keskkonnatingimustes ja aasta-aegadel, hõlmates ka liike, kes viljakeha ei moodustagi. eDNA proov võetakse otse seente kasvukeskkonnast (kogutakse väike pinnase-, puidu-, vee- või õhu-proov), millele järgneva laboritöö, sekveneerimise ja bioinformaatika tulemusena saadakse proovis esinenud seente DNA järjestused ja liigimäärangud. Seega on eDNA väärtuslik tööriist seente (sh ohustatud, ökoloogiliselt või majanduslikult oluliste liikide) seireks erinevates kasvukeskkondades ja maastikes, kuid seente looduskaitse planeerimisel on seda potentsiaali seni väga vähe rakendatud.

Andmetöötlusliku uuendusena saab seente leviku mõistmiseks praegustes ja prognoositavates keskkonnatingimustes kasutada masinõppet põhinevat modelleerimist. Niisugused praegustel elupaigaseostel põhinevad ja teadmislünki siluvad levikumudelid võiksid aidata seeni paremini arvestada näiteks kaitsealade planeerimisel, sh jagada looduskaitselist vastutust just suurtes mastaapides (nt erinevate riikide vahel). Ka sellised võimalused on seente looduskaitse planeerimisel seni alarakendatud.

Uuringus I analüüsiti, millist lisainfot annavad eDNA-põhised leiud liikide ohustatuse hindamisel, mis on liigikaitse keskne tööprotsess. Ohustatuse hindamine on seente puhul seni peaaegu täielikult põhinenud viljakehavaatlustel. Töö põhines kahel ulatuslikul Eestist kogutud andmestikul mullaseente kohta: mulla-eDNA andmestikul (1135 mulla-proovi) ja avalikes andmebaasides leiduvatel

seenevaatlustel (ligi 15,000 vaatlust). Nendest andmestikest tuvastati 1570 mulla-seeneliiki, mille ohustatust on Eestis või Soomes hinnatud. Leiti, et 21% neist liikidest olid Eestis esindatud eDNA, kuid mitte viljakehade põhjal. Kahe andmestiku põhjal erinesid oluliselt ka liikide asustatava pindala (AOO) ja levila ulatuse (EOO) hinnangud, mis on ohuhinnangute olulised sisendid. Iga täiendava mullaproovi kohta laiendasid eDNA andmed ohustatud ja ohualähedaste liikide hinnangulise levila piire keskmiselt 0,18% võrra ning liiginimekirja lisandus ka 0,06–0,3 ohustatud või ohualähedast liiki.

Need tulemused näitavad eDNA andmete väärtust seente ohustatuse hindamise ja liigikaitse ruumilise planeerimise jaoks. Samas ainult eDNA põhiste andmetest ohustatuse hindamisel ei piisa: isegi nii ulatuslik eDNA andmestik nagu Eestis ei võimaldanud tuvastada suurt hulka seeneliike (sh ohustatud ja ohualähedasi liike), kes viljakehavaatluste põhjal Eestist teada olid (**I**).

Traditsioonilised vaatluspõhised meetodid on peamised ka lihheniseerunud seente (samblike) elurikkuse hindamisel. Töös **III** hinnati harrastusteaduse potentsiaali samblike elurikkuse andmete täiendamisel. Koostöös Eestimaa Looduse Fondiga läbiviidud kampaania käigus koguti harrastusteadlastelt 1700 samblikufotot enam kui 1100 puult Eestis. Eksperdid määrasid nendelt fotodelt 119 samblikuliiki ja morfoloogilist üksust, millest 55% olid mikrosamblikud – rühmad, mida nende vähemärgatavuse ja keerulise määratavuse tõttu samblike seires sageli eiratakse. Umbes 5% vaatlusi hõlmas looduskaitseolulisi liike, ent võrreldes ekspertide kogutavate andmetega jäi nende hulk väikeseks. Küll aga osutus harrastusteadlaste panus väärtuslikuks tavaliste liikide dokumenteerimisel: selliseid liike liigiekspertid sageli ei jälgi ning seetõttu on nende ohustatuse hindamine (mis põhineb arvukuse või levila trendidel) olnud raskendatud.

Koosluste tasemel uurisime töös **II** seda, mil määral võimaldab veeproovidest tuvastatud eDNA tuvastada häiringu (kuivenduse) ökoloogilist mõju kõdusoometsades. Kuivendussüsteemide väljavoolust kogutud veeproovides olid eukarüootide, sh seente, kooslused ühe kraavi piires väga varieeruvad, kuid erinesid uuritud maastike vahel. Need mustrid seostusid kuivenduse intensiivsusega vaid mõõdukalt, kuid teatav potentsiaal võib sellistel andmetel maastike jälgimiseks olla. Seente mitmekesisus oli neis proovides märkimisväärselt suur ning eriti väärtuslikud olid eDNA andmed raskesti tuvastatavate patogeenide kohta.

Doktoritöö teises osas keskenduti ruumiliste mudelite kaudu seente elupaikade kaitsele Euroopas. Euroopa Liidu elurikkuse strateegia üldesmärgiks on aastaks 2030 kaitse alla võtta 30% maismaast, sh. 10% range kaitsereežiimiga. Senine kaitsealade loomise praktika ja teadaolevad plaanid kaitsealade laiendamiseks aga seemi ei hõlma.

Töös **V** modelleerisin 33 hästituntud ohustatud seeneliigi elupaikade levikut Euroopas, kasutades masinõppel (MaxEnt) põhinevaid mudeleid. Need mudelid seovad liigi leiukohtade biokliimaatilised ja maastikulised elupaigatunnused elupaiga sobivuse hinnanguteks, mis prognoositakse kogu käsitletavale alale. Nõnda hinnati töös elupaikade sobivust 38 Euroopa riigis (sh 27 EL liikmesriigis) 1 × 1 km võrkruudustikus kolme kategooriaksse (sobiv, piiripealne, sobimatu).

Edasi uuriti, kui palju sobivatest ja piiripealsetest elupaikadest paiknesid olemas-olevas kaitsealade võrgustikus. Tulemused näitasid olulisi puudujääke seente kaitstes: vaatlusalustel liikidel oli keskmiselt vaid 3,9–29,8% sobivast elupaigast kaitsealadel ja vaid 2,4% rangelt kaitstud. Seega ei vastanud ükski liik seni EL 2030 kaitse-eesmärkidele. Kuigi eri riikidel on kaitse parandamisel mõnevõrra erinev vastutus, ei ole otstarbekas neid puudujääke igas EU riigis eraldi lahendada; pigem tuleks kaitset ja elupaikade taastamist koordineerida.

Viimaks käsitleti kliimamuutuste mõju seente elupaikadele – teema, mida on seni enamasti käsitletud taimede ja loomade puhul. Modelleeriti jämedaid männi lamatüvesid asustava ohustatud torikseeneliigi pruunistuva korgiku (*Anthoporia albobrunnea*) elupaigamuutusi kahe erineva kliimastsenaariumi puhul. Kummagi puhul viit erinevat kliimamudelit kasutades koostati kaks interpreteeringult erinevat järelduskäiku tulevase elupaigasobivuse kohta: ettevaatlik prognoos, mis tähtsustab praegusteid optimaalseteid tingimusi ja halvimat tulevikuvarianti, ning optimistlik prognoos, mis arvestab võimaliku leviku laienemisega. Mudelid ennustasid 6–43% ulatuses praeguste elupaikade kadu, eriti Lõuna-Skandinaavias, kuid ka uusi sobivaid alasid Põhja-Skandinaavias ja Poolas. Keskne tulemus oli aga see, et isegi samu algandmeid ja mudeleid kasutades sai liikide leviku tulevikuprognoose looduskaitsealiselt väga erinevalt tõlgendada.

Kokkuvõtlikult näitavad doktoritöö tulemused, millised on kaasaegsete andmeallikate ja analüüsimeetodite (eDNA andmed, harrastusteadus ja liikide leviku modelleerimine) võimalused ja puudujäägid looduskaitseliste küsimuste lahendamisel. Töö tulemuste põhjal tuleks seente kaitse informeerimiseks järgmiste samudena:

- (i) integreerida eDNA andmed seente ohustatuse hindamisse;
- (ii) täiustada eDNA proovivõtumeetodeid ökosüsteemide ja maastike seisundi ja muutuste uurimiseks (sh luues uusi seirekeeme);
- (iii) soodustada harrastusteadust, et saada parem ülevaade sagedaste liikide populatsioonide trendidest;
- (iv) modelleerida suurema arvu ohustatud seeneliikide levikut Euroopas, selleks et;
- (v) paremini määratleda nende elupaikade kaitse ja taastamise vastutused riikide ja regiooni mastaabis.

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- Copoț, O., Lõhmus, A. & Runnel, K.** Assessing European Union's 2030 target for fungi: species distribution within the protected areas network. *ISME19 (International Symposium on Microbial Ecology)* (poster presentation), 18–23th August 2024, Cape Town, South Africa.
- Copoț, O., Lõhmus, A., Abarenkov, A., Tedersoo, L. & Runnel, K.** Usefulness of the environmental DNA for fungal Red-listing. *CEESME2023 (Central and Eastern Europe Symposium on Microbial Ecology)* (oral presentation), 12–15th September 2023, Budapest, Hungary.
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