Polypore fungi as a flagship group to indicate changes in biodiversity – a test case from Estonia

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Abstract

Polyporous fungi, a morphologically delineated group of Agaricomycetes (Basidiomycota), are considered well studied in Europe and used as model group in ecological studies and for conservation. Such broad interest, including widespread sampling and DNA based taxonomic revisions, is rapidly transforming our basic understanding of polypore diversity and natural history. We integrated over 40,000 historical and modern records of polypores in Estonia (hemiboreal Europe), revealing 227 species, and including Polyporus submelanopus and P. ulleungus as novelties for Europe. Taxonomic and conservation problems were distinguished for 13 unresolved subgroups. The estimated species pool exceeds 260 species in Estonia, including at least 20 likely undescribed species (here documented as distinct DNA lineages related to accepted species in, e.g., Ceriporia, Coltricia, Physisporinus, Sidera and Sistotrema). Four broad ecological patterns are described: (1) polypore assemblage organization in natural forests follows major soil and tree-composition gradients; (2) landscape-scale polypore diversity homogenizes due to draining of peatland forests and reduction of nemoral broad-leaved trees (wooded meadows and parks buffer the latter); (3) species having parasitic or brown-rot life-strategies are more substrate-specific; and (4) assemblage differences among woody substrates reveal habitat management priorities. Our update reveals extensive overlap of polypore biota throughout North Europe. We estimate that in Estonia, the biota experienced ca. 3–5% species turnover during the twentieth century, but exotic species remain rare and have not attained key functions in natural ecosystems. We encourage new regional syntheses on long studied fungal groups to obtain landscape-scale understanding of species pools, and for elaborating fungal indicators for biodiversity assessments.

Keywords: Assemblage composition, Cryptic species, Functional groups, Species pool, Substrate ecology, Wood-inhabiting fungi

INTRODUCTION

The fact that global biodiversity trends are assessed almost without a fungal perspective (e.g., Butchart et al. 2010, IPBES 2018) calls into question how we should integrate scattered mycological knowledge. Historically, regional checklists of fungal biotas have served such aims (e.g., Senn-Irlet et al. 2007), but the rapid advancement of molecular methods and mass data accumulating from ecological assemblage studies challenge such integration (e.g., Peay 2014, Thomson et al. 2018). Thus, molecular biodiversity research is searching its way out of slow nomenclatural procedures (Hibbett 2016); for example, through a concept of species hypothesis based on DNA barcoding (Kõljalg et al. 2013). This causes accumulation of ‘dark taxa’ that lack names or even physical specimens, which cannot currently be used in conventional taxonomy or conservation (Ryberg & Nilsson 2018). For ecological research programs and environmental
management, taxonomic and nomenclatural revisions can be too dynamic or impractical, such as when new species are described without morphologically distinct characters (e.g., Korhonen et al. 2018). As a consequence, ecological studies remain taxonomically heterogeneous, often simplified or of unknown quality (Bortolus 2008, Vink et al. 2012), and may omit taxa of critical conservation importance (e.g., rare undescribed species). Taxonomic descriptions, in turn, include only very basic ecological data and seldom report population- and ecosystem-scale context (Durkin et al. 2020). Conservationists have responded with calls to transform taxonomically accepted species lists into special conservation lists to resolve the administrative problem of taxonomic instability (Mace 2004).

With a broader aim to reintegrate disciplines for monitoring fungal diversity, this study provides a new regional synthesis of polyporous fungi (Agaricomycetidae: Basidiomycota; hereafter: polypores) – a conspicuous and well-studied fungal morphogroup. Polypores are distinguished based on poroid hymenophore and mostly lignicolous lifestyle; they inhabit forests on all continents. In recent overviews for Europe and North America, the number of polypore species was assessed at 400 and 492, accordingly (Zhou et al. 2016, Ryvarden & Melo 2017). Historically, all polypores were included into a common family, Polyporaceae, within the order Aphyllophorales (Fries 1874). This higher classification based on basidiome morphology was refined by several mycologists in the twentieth century, most notably by Singer (1944), Donk (1948, 1964, 1971), and Jülich (1981), but has been largely/rejected since the introduction of molecular systematics. The name Polyporales now only refers to one of at least 12 orders within Agaricomycetidae that include fungi with polyporoid basidiomes (Hibbett et al. 2014). Polyporous ‘morphogenera’ are increasingly replaced by molecularly supported clades that may be closely related to, or even comprise, non-polyporoid fungi (e.g., Miettinen et al. 2012; Runnel et al. 2019). Molecular data have also revealed extensive undescribed species diversity, including morphologically indistinguishable (cryptic) taxa (e.g., Korhonen et al. 2018). Despite these changes in taxonomy and systematics, polypores continue to be treated as a morphogroup in local and regional studies (e.g., Dai 2012, Zhou et al. 2016, Ryvarden & Melo 2017), and in ecological and conservation research. The reasons for that include acceptance by conservationists and educational values.

Functional significance is a major reason why polypores remain a distinct object of research, especially in the fields of forest ecology and conservation. These fungi constitute important decayers, specifically of the huge woody biomass and its lignin component in forests (Floudas et al. 2012). Their mycelia and basidiomes attached to wood provide forage or microhabitat for diverse assemblages of saproxylic invertebrates (e.g., Birkemoe et al. 2018). A subset of polypore species parasitize live trees, some bearing significant economic and social costs for production forestry and arboriculture through root-, butt- and heart-rots (Schwarze et al. 2013). Ecologically, however, heart-rots are key processes in the formation of tree cavities supporting forest fauna (Remm & Löhmus 2011), while root- and butt-rots promote tree uprooting and trunk breakage (Honkaniemi et al. 2017) that create diverse microhabitats in forests. Several polypore genera include mostly mycorrhizal species, some of which form basidiomes on dead wood (e.g., among Sistotrema; Nilsson et al. 2006, Di Marino et al. 2008). Polypores are best studied in North and Central Europe where intensive forest management has been threatening their diversity – this has facilitated their use for assessing forest conservation values and planning the management (Junninen & Komonen 2011, Halme et al. 2017). Linked with these practical issues has been theoretical interest in polypores as model taxa for metapopulation and assemblage models applicable to dynamic habitat patches (e.g., Övaskainen et al. 2010; Ramiadantoa et al. 2018).

To explore the perspectives of this flagship group for fungal diversity assessment, we synthesize diverse information from Estonia – a North European country in the hemiboreal (boreo-nemoral) vegetation zone. The first reliable data on Estonian polypore biota were published in the overview by Dietrich (1856, 1859). Local surveys, with an emphasis on (forest) pathology, were initiated by Elmar Lepik (Leppik) in the late 1920s; he also re-checked and summarized the previously collected material from Estonia (e.g., Lepik 1931, 1940). The forest pathology research direction soon focussed on a few economically significant taxa: Heterobasidion species causing butt-rots in conifers (e.g., Karu 1953, Hanso & Hanso 1999) and Phellinus tremulae causing heart-rot in European aspen (Populus tremula) (reviewed by Tamm 2000). A wider research perspective on polypores, accompanied with taxonomic work, was developed in the second half of the twentieth century by Erast Parmasto (Parmasto 2012). Parmasto (2004) published a monograph that quantitatively summarized all the distribution data on the 211 species then known, their main habitat types and host trees. In the 1990s, Parmasto focused on species sensitive to loss of old-growth forests (Parmasto & Parmasto 1997, Parmasto 2001); this research line has been recently re-assessed based on ecological sampling (e.g., Runnel & Löhmus 2017). Overall, there has been a large increase in polypore data since 2004 from ecological studies, including the development and testing of the survey methods (Runnel et al. 2015, Löhmus et al. 2018a). Also species’ distribution mapping has
continued, notably through monitoring protected species and in protected areas. However, this new knowledge has remained scattered among projects, and the historical data have not been taxonomically updated.

Our synthesis of the diversity and ecology of Estonian polypores serves three broad aims: (1) We characterize the country-scale species pool in a regional perspective, including taxonomic uncertainties. We do not omit unresolved material; instead, we combine and present molecular phylogenies and habitat data of ‘difficult’ specimens to address the primary aim of describing (full) biodiversity. (2) By critically comparing the updated checklist with Parmasto (2004), we distinguish actual long-term changes in the biota from the advancement of knowledge. And (3) we pool all ecological data to quantitatively analyse compositional similarity of Estonian polypore assemblages and niche characteristics of species. At the ecosystem scale, we assess correspondence between polypore assemblages and the habitat type, specifically in relation to soil conditions, tree composition and stand age. This addresses the ‘Cajanderian’ approach to boreal forest typology, which is based on stable site types rather than temporary conditions (e.g., Frey 1973, Lahtı & Väissänen 1987). The practical importance of our ecological analyses is to provide a basis for land-cover or substrate-type proxies for conserving polypore diversity (termed ‘coarse-filter’ and ‘mesofilter’ approaches in conservation biology, respectively; Hunter 2005, Cushman et al. 2008).

MATERIAL AND METHODS

Study region and ecosystems

Estonia has a total land area 45,339 km², of which ca. 10% encompasses its western archipelago in the Baltic Sea. The country is situated in the European hemiboreal vegetation zone (Ahti et al. 1968); the natural land cover in the absence of human impact would comprise ca. 85% forest, 8% open wetlands and 5% lakes (Laasimer 1965). The mean air temperature is 17 °C in July and -4 °C in January and the average precipitation is 600–700 mm yr⁻¹. The topography is mostly of glacial origin. Lowlands (post-glacial flooded plains reaching less than 50 m above current sea level) cover nearly half of the territory, and are the dominant land-forms in West-Estonia. The bases of two erosional and three accumulative uplands are 75–100 m above sea level; four of these uplands are in southern Estonia.

Western and eastern Estonia are separated by a borderline of post-glacial landscape history, climate conditions, and land-use patterns (Ahti et al. 1968; Raukas et al. 2004). The last ice sheet retreated ca. five thousand years earlier in the east (Raukas et al. 2004), which now has a more continental climate with isotherm differences up to 4–5 °C compared with western Estonia (Jõgi & Tarand 1995). This border can be also recognised in the distribution of biodiversity, such as plants (Laasimer 1965) and epiphytic lichens (Jüriado et al. 2003).

Forests, the main ecosystem hosting polypores, currently cover 51% of Estonia but, after a long history of land use, only 2% of this is old natural stands (Raudsaar et al. 2018). Forest conversion to agriculture reached its maximum by the 1930s when ca. one-third of the country had woodland cover (Meikar & Uri 2000). Subsequent afforestation mostly took place due to the abandonment of small agricultural fields and wetland drainage for forestry. Timber harvest intensities were relatively low in the second half of the twentieth century, but rapidly increased after the country regained independence: from 2 to 3 million m³ in 1991–1993 to 10–12 million m³ in 2000–2001 where the volume stabilized, after a temporary decline, since 2011. In the same period, strictly protected forest reserves were expanded from ca. 3 to 13% of forest land (Lõhmus et al. 2004, Raudsaar et al. 2018). The forest management has been based on native tree species and, to a significant extent, on natural regeneration (‘semi-natural forestry’), but following the even-aged (clear-cutting based) silvicultural system and including planting (mostly conifers), thinning, and artificial drainage. Such a mixture of approaches maintained commercial forests in a relatively favourable state for wood-inhabiting species (Lõhmus et al. 2016, Runnel & Lõhmus 2017). However, recent developments to lower rotation age, increase cut-block size, subsidized planting, and (in private forests) ditching threaten forest biodiversity in a longer perspective (e.g., Lõhmus et al. 2018b).

Based upon edaphic and hydrological factors, nine natural and two anthropogenic forest site type groups (drained peatlands; reclaimed areas), comprising at least 27 forest site types, are distinguished for the practical planning and monitoring of Estonian forests (Lõhmus 1984, Raudsaar et al. 2018; Additional file 1). Common natural site type groups are meso-eutrophic (27%; usually Norway spruce Picea abies mixtures with deciduous trees), dry boreal (23% of forest land; most dominated by Scots pine, Pinus sylvestris), eutrophic paludifying (16%; mostly birch Betula spp., often in mixtures with P. sylvestris), and eutrophic boreo-nemoral forests (10%; typically Betula spp., Populus tremula, and grey alder Alnus incana). The dominant anthropogenic forests are drained peatland forests (14%; mostly Betula ssp. and P. sylvestris). All the main forest trees are native; 31% of forest area is dominated by P. sylvestris, 30% by Betula ssp., 19% by P. abies, 9% by Alnus incana and 6% by P. tremula (Raudsaar et al. 2018). Stands of exotic trees comprise 0.1% of forest land. Over 25% of the forest land has been drained and over 300,000 ha planted,
but there are few intensive plantations and stands usually consist of more than one (most often three) tree species.

The main secondary habitats for polypores are semi-natural and urban areas with sparse tree cover. Of these, most traditional wooded meadows were lost during the twentieth century due to the re-organization of agriculture; only <10,000 ha remain (Sammul et al. 2008). Compared with Western Europe, the Estonian agricultural landscapes still retain significant areas with natural components such as scattered tree rows and single trees (e.g., Kikas et al. 2018). Biodiversity hotspots in the countryside include rural parks that may have dead wood amounts comparable with those in production forests (e.g., Lõhmus & Liira 2013), and riparian zones that contain specific habitats (such as large Salix trees) rarely found in forests. Finally, ca. 2% of Estonian land cover comprises human settlements, often with a significant proportion of green space and trees. A distinct polypore habitat feature of the green space is a diverse mixture of exotic tree species, planted as ornamental species or sometimes as tree collections. Tallinn alone (excluding its botanical garden) hosts 449 exotic species in addition to the 31 native species of trees (Sander et al. 2003).

**Estonian polypore data**

The Estonian polypore data used includes ca 40,500 basidiome records (Table 1). A ‘record’ refers to collected specimens or archived observations, usually at the level of one distinct substrate unit (e.g., a single fallen trunk). About 10% of records – such as some historical species lists and ecological studies (e.g., Lõhmus 2011) – refer to occurrences at the scale of a forest stand. The specimens we collected are deposited in the fungaria of Tartu University (TU) and the Estonian University of Life Sciences (TAAM); all these records, together with their molecular DNA data and occasional photographs, are archived in the PlutoF database (Abarenkov et al. 2010). At the time of compiling of this study, the molecular data (mostly ITS sequences; in a minority of cases additionally LSU sequences) were available for 3% of all records (Table 1).

The material comprised three methodologically distinct parts.

(I) One-third of the material were all records until 2004, which were originally summarized by Parmasto (2004). These are mostly specimens collected during casual surveys by Parmasto and his colleagues in the period 1950–2004, and a critical revision of all older collections. The material has been sampled throughout the country, although some regions (such as eastern and south-western Estonia) have been more intensively covered (Fig. 1A). Parmasto (2004) admits paying more attention to Phellinus (sensu lato) and old-forest fungi; a re-analysis of the whole dataset by Löhmus (2009) suggested a more general bias (compared with frequencies in nature) toward easily recognizable species with perennial basidiomes. A preference to visit certain biodiversity ‘hotspots’ (such as protected areas, some maritime islands and certain city parks) is also obvious in the location data. For the current study, most original specimens of poorly identifiable rare species (see Löhmus 2009 and under “Difficult species” below) were morphologically re-checked and, by necessity, sequenced (Table 1).

(II) Fifty-seven percent of all records were obtained from systematic surveys of polypore assemblages by

### Table 1 Main sources of the Estonian polypore data

| Data source or sampling design | No. of records (sequences)a | Studied ecosystems | Publications |
|-------------------------------|-----------------------------|--------------------|--------------|
| I. Historical data until 2004 | 13,249 (48)                 | All                | Parmasto 2004 |
| Ila. Systematic sampling in a 4-km² forest landscape in E Estonia, 2008–2009 | 3560 (3) | All forest land; mostly eutrophic and meso-eutrophic mixed sites | Löhmus 2011 |
| Ilb. Standard surveys in 30 2-ha plots and their surroundings in SW Estonia, 2013 | 2393 (122) | Pinus sylvestris dominated drained peatland forests | Runnel et al. 2015 [https://doi.org/10.15156/BIO/786358](https://doi.org/10.15156/BIO/786358) |
| IIC. Standard surveys in 144 2-ha plots, 2005–2016 | 17,012 (334) | Forests and clear-cuts of various types, except of bog and drained wetland types | Runnel & Löhmus 2017 [https://doi.org/10.15156/BIO/786363](https://doi.org/10.15156/BIO/786363) [https://doi.org/10.15156/BIO/786357](https://doi.org/10.15156/BIO/786357) |
| IId. Fallen retention trees in 48 clear-cuts in mainland, 2010–2011 | 259 (19) | Sites on mineral soils | Runnel et al. 2013 |
| Illa. Casual collections after 2004 | 3020 (631) | All                | PlutoF database |
| Illb. Surveys of 27 species in protected areas, 2015–2016 | 922 (89) | All                | PlutoF database (partly) |
| Total | 40,415 (1246) | | | |

* no. of sequences deposited in the PlutoF database (Abarenkov et al. 2010)
K.R and A.L in 2005–16. These surveys have been planned and (mostly) published to address questions of forest ecology and conservation (Table 1). Accordingly, this material represents most Estonian forest ecosystems, although it is geographically biased toward mainland Estonia, especially southern, eastern, and north-eastern parts of the country (Fig. 1B). The surveys were...
performed in the top basidiome production season (September–October), with efforts to record all species either at the habitat patch or substrate scale (to analyse also species absences) along with detailed descriptions of the habitats and substrates. The substrate descriptions have routinely included tree species, condition, diameter, and decay stage (five classes, I–V, according to Renvall 1995). About 15% of the field observations are supported by collections, focusing on basidiomes that could not be reliably identified in the field, represented poorly studied taxa, or atypical substrates (Runnel et al. 2014, Lõhmus et al. 2018a). The collected basidiomes have all been inspected microscopically and ca. 20% of the specimens have been sequenced (Table 1).

Three field protocols were followed in the systematic surveys. The main set of surveys (Table 1: IIb–IIc; 48% of all records) followed a fixed-area-fixed-effort survey protocol, as presented and analysed for bias by Lõhmus et al. (2018a). Each survey was carried out during 4 h in a precisely delineated 2-ha plot by a single observer (the plots listed in Additional file 2). For each species in each plot, substrates of the first ten records were described in detail. Up to 150 such records per plot could be obtained within the 4 h. A less thorough method was used in an East Estonian forest landscape study (Table 1: IIa) where all forest stands in a 4-km² area were sampled by adjusting survey time with stand area (range 0.1–7 ha; see Lõhmus 2011 for details). For most species, one substrate type in one stand comprised one record, but rare and threatened species were recorded at the scale of individual substrate items. Finally, a small study on retention trees in four Estonian regions recorded all species at the scale of individual tree trunks (Runnel et al. 2013; Table 1: IID).

III Post-2004 casual records comprise 10% of all records, from two sources (Table 1: III). The majority are specimen and observation data as extracted on 8 November 2018 from the PlutoF database (Abarenkov et al. 2010). These data originate from casual surveys similar to Parmasto’s (2004) material from professional and, increasingly, amateur mycologists all over Estonia (Fig. 1b). All the observations obtained from the database were quality-scanned, and doubtful identifications were discarded. We additionally included 922 observations of 27 easily identifiable protected, rare or old-forest indicator species (full list is available upon request) during publicly funded fungal surveys by Indrek Sell in two protected areas in mainland Estonia: the Soomaa National Park in 2015 and the Muraka Nature Reserve in 2016.

Data processing

Updating species list and documenting taxonomic uncertainties For ecological analyses, the set of casual records included in this paper are as of 8 November 2018. However, Table 2 has been updated based on casual collection data (Table 1: IIa) as of 20 July 2019, with the records of Amylocystis lapponica updated according to Runnel et al. (2020), and Inonotus ulmicola and Spongipellis spumea including the observations by Pau (2018). Phellinus igniarius sensu stricto is defined as all species records from Salix spp.

We use conservative nomenclature for genera whose classification is still in flux, such as Antrodia, Phellinus, Inonotus, and Polyporus.

To update the species list, special attention was paid to specimens that represented taxa with recently updated taxonomy (notably the species concept) and potentially unresolved groups. Such specimens were checked microscopically, and multiple dried basidiomes sequenced for rDNA ITS (in the case of high variability also D1–D2 domains of the more stable LSU region) for comparisons with references in public databases and our personal database. For obtaining the ITS sequences, we used primers ITS1F (Gardes & Bruns 1993) or ITSOF-T (Tedesco et al. 2008) and ITS4 (White et al. 1990); for the D1–D2 domains of the LSU region we used primers CTB6 (Garbelotto et al. 1997) and LR7 (Vilgalys & Hester 1990) or LBW (Tedesco et al. 2008). DNA extraction, polymerase chain reaction (PCR), and sequencing of the target loci followed protocols described by Tamm and Pöldmaa (2013). ITS and LSU sequences were also produced for 82 species that had no previously sequenced voucher specimens from Estonia.

In eight difficult/unresolved species groups, we explicitly illustrate the variation in their Estonian ITS (in some cases also LSU) sequence material and the accompanying ecological data on substrate and habitat type. The sequences were edited and assembled using Sequencher 5.1 (Gene Codes, Michigan, USA), first aligned automatically using Mafft 7 online version (Katoh et al. 2017) and then edited manually in AliView (Larsson 2014). The Estonian dataset of each taxon group was complemented with the most similar basidiome based sequences (> 95% similarity) available at GenBank and UNITE database (Nilsson et al. 2018). In UNITE, a species hypothesis at 1.5% threshold level was calculated for a voucher specimen of each distinct lineage (Köljalg et al. 2013). Outgroups were chosen based on the latest molecular taxonomic works on the target taxa, except in Byssoporia, Coltricia cinnamomea, Physisporinus and Sidera that had difficult to align ITS/
Table 2: Estonian polypore species, their voucher specimens in fungaria, no. of records by sources (I: historical data up to 2004; II: systematic sampling; III: casual collections), habitats, and national Red-List status (Category and Criteria). Habitat data denote presence by: forest successional stage (E, early-successional; M, mid-successional; L, late-successional forests), host tree species (S, *Picea abies*; P, *Pinus sylvestris*; A, *Populus tremula*; B, *Betula* spp.; D, other deciduous species, O, ornamental conifers), woody substrate (C, coarse downed deadwood; F, fine downed or standing deadwood; Sn, snags and stumps; L, live trees), and decay stage (E, early; M, medium; L, late). For species with ≥25 records from systematic sampling, the habitat summary is given as % of species records in the systematic sample.

| Species1 | Voucher No. of records | Succ. stage | Tree species | Subst. type | Decay stage | Cat. Crit. |
|----------|------------------------|-------------|--------------|------------|-------------|------------|
| Abortiporus biennis | (Bull.) Singer | TU104564 2 0 4 | D | L | VU | D1 |
| Albatrellus citrinus | Ryman | TU106597 16 16 10 | ML | G | LC |
| Albatrellus confluentus | (Alb. & Schwein.) Kotl. & Pouzar | TU106802 24 1 1 | L | G | DD |
| Albatrellus ovinus | (Schaeff.) Kotl. & Pouzar | TU118663 69 51 11 | 51M49L | G | LC |
| Albatrellus subrubescens | (Murrill) Pouzar | TU106803 14 0 2 | G | DD |
| Amylocystis lapponica | (Romell) Bondartsev & Singer ex Singer | TAAM185465 1 1 59 | L | S | C | EML | CR | D1 |
| Anomoloma albolutescens | (Romell) Niemelä & K.H. Larss. | TAAM174473 1 0 0 | | | | |
| Anomoloma mycelium | (Peck) Niemelä & K.H. Larss. | TU101934 5 26 1 | 65M35L | 27S73P | 27C73F | 42E38M19L | VU | D1 |
| Anomoporia borrbycina | (Fr.) Pouzar | TU111116 6 0 3 | C | NT | D1 |
| Antrodia cretacea | K. Runnel, V. Spirin & A. Löhmus | TU121005 6 6 7 | EL | S | CSn | EML | EN | B2ab(iii); C2a(i) |
| Antrodia heteromorpha | (Fr.) Donk | TAM001039 4 0 0 | | | | |
| Antrodia leucaena | Y.C. Dai & Niemelä | TU129577 1 7 7 | EML | A | CF | EM | VU | C1 |
| Antrodia maca | (Sommerf) Niemelä | TU129573 9 4 3 | EM | DA | F | EM | DD |
| Antrodia mellita | Niemelä & Penttilä | TU114649 7 0 7 | A | C | EN | D1 |
| Antrodia piceata | K. Runnel, V. Spirin & J. Vlasák | TU129574 4 13 19 | L | S | C | EML | EN | B1ab(kv); 2ab(kv); C2a(i) |
| Antrodia pulvinascens | (Pilát) Niemelä | TU117272 12 2 42 | E | A | CF5n | M | VU | D1 |
| Antrodia ramentacea | (Berk. & Broome) Donk | TU122933 3 3 3 | M | P | F | EM | DD |
| Antrodia serialis | (Fr.) Donk | TU20464 >100 >100 25 | 24E33M44L | 95S5P1D | 72C115n17F | 32E59M9L | LC |
| Antrodia sinuosa | (Fr.) P. Karst. | TU117300 >100 >100 29 | 17E49M34L | 38S61P180A | 72C25n26F | 22E56M21L | LC |
| Antrodia xantha | (Fr.) Ryvarden | TU127274 >100 >100 17 | 13E37M50L | 10S5P1D | 73C65n21F | 27E56M18L | LC |
| Antrodia bellinella | Niemelä & Ryvarden | TU117326 2 30 13 | 10E17M73L | 83S3P7B7A | 90C35n7F | 10E30M60L | LC |
| Antrodia faginea | Vampola & Pouzar | TU212940 3 20 4 | EML | PD5A | CSnF | EML | LC |
| Antrodia niemelaei | Vampola & Vlasák | TU30078 2 1 3 | E | D | F | L | VU | D1 |
| Antrodia pallascens | (Pilát) Niemelä & Miettinen | TU117329 74 >100 9 | 12E72M16L | 11D86B3A | 54C155n31F | 7E53M40L | LC |
| Antrodia parasitica | Vampola | TAM0164505 1 0 0 | | | | |
| Antrodia ramentellii | (Donk) Niemelä | TU129193 19 47 6 | 20E73M7L | 60D33B7A | 9C25n88F | 48E40M12L | LC |
| Antrodia serpula | (P. Karst) Spirin & Niemelä | TU115334 72 78 19 | 5E65M20L | 87D10B3A | 23C375n40F | 23E54M23L | LC |
Table 2: Estonian polypore species, their voucher specimens in fungaria, no. of records by sources (I: historical data up to 2004; II: systematic sampling; III: casual collections), habitats, and national Red-List status (Category and Criteria). Habitat data denote presence by: forest successional stage (E, early-successional; M, mid-successional; L, late-successional forests), host tree species (S, *Picea abies*; P, *Pinus sylvestris*; A, *Populus tremula*; B, *Betula* spp.; D, other deciduous species, O, ornamental conifers), woody substrate (C, coarse downed deadwood; F, fine downed or standing deadwood; Sn, snags and stumps; L, live trees), and decay stage (E, early; M, medium; L, late). For species with ≥25 records from systematic sampling, the habitat summary is given as % of species records in the systematic sample.

| Species1 | Voucher | No. of records | Succ. stage | Tree species | Subst. type | Decay stage | Cat. Crit. |
|-----------|---------|--------------|-------------|--------------|-------------|-------------|------------|
|           |         | I  II  III   |             |              |             |             |            |
| Aporpium canescens (P. Karst.) Bondartsev & Singer ex Singer | TU129596 | 23 39 13 | 5E 3SM 57L | 3SD4185TA | 73C195n8F | 24E383M38L | LC         |
| Aporpium macroporum T. Niemelä, V. Spirin & O. Miettinen | TU129583 | 2 6 17 | EML | A | CSn | EM | VU | C1         |
| Aurantiporus croceus (Pers.) Murrill | TU11103 | 2 0 6 | D | L | CR | D1 |   |            |
| Aurantiporus fissilis (Berk. & M.A. Curtis) H. Jahn ex Ryvarden | TU117130 | 14 7 2 | ML | DA | CF | EML | NT | D1         |
| Aurantiporus priscus Niemelä, Miettinen & Manninen | TAAM199806 | 3 0 0 |   |   |   |   |   | CR | C2a(l); D1 |
| Bjerkandera adusta (Willd.) P. Karst. | TU18559 | >100 >100 35 | 34E42M24L | 4S34D35B35A | 44C32Sn22F1L | 52E40M8L | LC         |
| Bjerkandera fumosa (Pers.) P. Karst. | TAAM123459 | 40 4 4 | M | DB | CSnF | EM | LC         |
| Boletopsis grisea (Peck) Bondartsev & Singer | TU17299 | 15 0 13 | G | VU | D1 |   |            |
| Boletopsis leucomelaena (Pers.) Fayod | TU210100 | 4 1 3 | L | C | DBA | CF | EML | VU | D1         |
| Bsatodontia millavensis (Bourdot & Galzin) Duhem & H. Michel | TAAM201266 | 18 0 22 | O | FL | VU | D1 |   |            |
| Byssoporia terrestris (DC.) M.J. Larsen & Zak | TU30449 | 1 7 0 | EML | SPA | CF | EML | VU | D1         |
| Ceriporia aurantiocarnescens (Henn.) M. Pieri & B. Rivoire | TU22039 | 0 2 3 | M | DA | C | M | DD         |
| Ceriporia bresadolea (Bourdot & Galzin) Donk | TU22499 | 3 0 1 | P |   |   | M | BN | D1         |
| Ceriporia excelsa (S. Lundell) Parmasto | TU17253 | 18 32 8 | 53E31M16L | 13D6622A | 75C35n22F | 3665M2L | LC         |
| Ceriporia purpurea (Fr.) Donk | TU15545 | 20 11 9 | EML | DBA | CSnF | EML | LC         |
| Ceriporia reticulata (Hoffm.) Domanski | TU21840 | 21 51 5 | 40E36M24L | 2P48D30B20A | 24C25n74F | 22E58M20L | LC         |
| Ceriporia tarda (Berk) Ginns | TAAM196177 | 1 0 8 | S |   |   |   |   | CR | D1         |
| Ceriporia torpida (Spirin & Miettinen | 0 0 1 | A |   |   |   |   |   | DD         |
| Ceriporia viridans (Berk. & Broome) Donk | TU22216 | 34 41 9 | 48E28M25L | 3P18D53B28A | 45C38n48F | 37E70M27L | LC         |
| Ceriporiopsis aneirina (Sommerf) Domanski | TU17256 | 37 70 28 | 36E93M36L | 100A | 69C15n30F | 61E37M2L | LC         |
| Ceriporiopsis pseudogilvescens (Pilát) Niemelä & Kinnunen | TU129597 | 2 14 11 | ML | DA | CSnF | EML | LC         |
| Ceriporiopsis resinsascens (Romelli) Domanski | TU15564 | 19 2 1 | EL | DA | CF | M | LC |   |            |
| Cerrena unicalar (Bull) Murrill | TU10682 | >100 >100 17 | 55E32M13L | 4D92B4A | 28C41Sn30F | 28E51M21L | LC         |
| Cinereomyces lindbladii (Berk) Jülich | TU17259 | 28 >100 22 | 35E25M22L | 44S32P6D18B | 63C15n36F | 7E32M11L | LC         |
| Cistocystis borealis (Fr.) Kotl. & Pouzar | TU18900 | >100 42 29 | 26E17M57L | 100S | 31C69n48 | 54E36M10L | LC         |
| Coltricia cinnamomea (Jacq.) Murrill | TU06861 | 0 0 6 | G |   |   | VU | D1 |            |
### Table 2
Estonian polypore species, their voucher specimens in fungaria, no. of records by sources (I: historical data up to 2004; II: systematic sampling; III: casual collections), habitats, and national Red-List status (Category and Criteria). Habitat data denote presence by: forest successional stage (E, early-successional; M, mid-successional; L, late-successional forests), host tree species (S, *Picea abies*; P, *Pinus sylvestris*; A, *Populus tremula*; B, *Betula* spp.; D, other deciduous species, O, ornamental conifers), woody substrate (C, coarse downed deadwood; F, fine downed or standing deadwood; Sn, snags and stumps; L, live trees), and decay stage (E, early; M, medium; L, late). For species with ≥25 records from systematic sampling, the habitat summary is given as % of species records in the systematic sample (Continued).

| Species | Voucher | No. of records | Succ. stage | Tree species | Subst. type | Decay stage | Cat. Crit. |
|---------|---------|----------------|-------------|--------------|-------------|-------------|------------|
|         |         | I | II | III | | | |
| *Coltricia confluens* | TAAM181460 | 0 | 0 | 2 | G | | NE |
| *Cortinarius perennis* | TU120468 | >100 | 13 | 9 | EML | G | | LC |
| *Daedalea quercina* | TU06561 | >100 | 0 | 18 | D | | LC |
| *Daedaleopsis controversa* | TU118931 | 87 | 49 | 42 | 14E71M14L | 90D10B | 16C39Sn43F2L | 47E46M7L | LC |
| *Datronia mollis* | TU09290 | >100 | >100 | 21 | 21E49M29L | 26D34B40A | 39C3Sn58F | 51E42M7L | LC |
| *Dickinsonia campestris* | TU117217 | 12 | 8 | 26 | M | D | SnF | EM | NT | D1 |
| *Dickinsonia squamosa* | TU121329 | 6 | 4 | 0 | EML | SP | CF | EM | EN | C2a(i) |
| *Diplomitoporus crustulinus* | TAAM134247 | 1 | 0 | 0 | | | RE |
| *Diplomitoporus flavescens* | TU01542 | 52 | >100 | 48 | 8E90M3L | 1599P | 11C66Sn23F | 83E17M | LC |
| *Fiboporia gossypium* | TU117250 | 8 | 8 | 14 | EML | SP | CF | EML | VU | D1 |
| *Fibroporia norlandica* | TU12622 | 0 | 12 | 0 | EM | SPB | CF | EM | LC |
| *Fibroporia vaillantii* | TAAM184863 | 12 | 1 | 1 | E | PO | F | L | VU | D1 |
| *Fistulina hepatica* | TU118753 | 86 | 0 | 11 | D | | L | NT | D1 |
| *Fomes fomentarius* | TU117322 | >100 | >100 | 55 | 17E58M25L | 5D93B2A | 45C37Sn18F | 38E48M14L | LC |
| *Fomitopsis pinicola* | TU117240 | >100 | >100 | >100 | 16E55M28L | 49S15P8B24B4A | 52C37Sn10F | 41E50M9L | LC |
| *Fomitopsis rosea* | TU117293 | >100 | >100 | >100 | 16E55M28L | 49S15P8B24B4A | 52C37Sn10F | 41E50M9L | LC |
| *Funalia trogii* | TAAM202749 | 20 | 73 | 8 | 83E10M6L | 2D4893A | 50C317F2L | 41E57M4L | LC |
| *Ganoderma applanatum* | TU118898 | 60 | >100 | >100 | >100 | 1E16M84L | 99S3P1B6A | 38E48M14L | LC |
| *Ganoderma lucidum* | TU126966 | 1 | 0 | 0 | Pat. | | | NA |
| *Ganoderma lucidum* | TU125603 | 40 | 25 | 0 | 44E52M41L | 20S20D56B4A | 28C68Sn4F | 9M91L | LC |
| *Gelatoporia subvermispora* | TU112080 | 1 | 6 | 6 | EML | SDBA | | CF | ML | NT | D1 |
| *Gloeophyllum abietinum* | TU111350 | 48 | 12 | 10 | EML | S | CF | EM | NT | C1 |
| *Gloeophyllum odoratum* | TU118351 | >100 | >100 | >100 | 74E13M14L | 93S4P1D | 16C68Sn5 | 5E52M43L | LC |
| *Gloeophyllum septarium* | TU066410 | >100 | >100 | >100 | >100 | 76E14M86L | 83S9P1B7A | 38C14Sn48F | 48E46M5L | LC |
| *Gloeophyllum trabeum* | TU120451 | 13 | 10 | 4 | E | DBA | | CF | ML | NT | D1 |
| *Gloeopus dichrous* | TU114774 | 42 | 51 | 4 | 16E70M14L | 25S29D64B4A | 43C20Sn4F | 7E49M24L | LC |
| *Gloeopus pannonicus* | TU117298 | 46 | 51 | 12 | 4E53M43L | 25S3D55B8A | 84C10Sn4F2L | 30E38M32L | LC |
| Species         | Voucher | No. of records | Succ. stage | Tree species | Subst. type | Decay stage | Cat. Crit. |
|-----------------|---------|---------------|-------------|--------------|-------------|-------------|------------|
| *Grifola frondosa* (Dicks.) Gray | TU120007 | 8 | 0 | 10 | DO | L | CR | D1 |
| *Hapalopilus aurantiacus* (Rostk.) Bondartsev | TU129768 | 5 | 3 | 3 | E | SP | CSn | EM | BN | D1 |
| *Hapalopilus ochraceolentius* (Bondartsev) Bondartsev & Singer | TU121752 | 4 | 2 | 3 | E | SP | CSn | M | EN | D1 |
| *Hapalopilus rutians* (Pers.) Murrill | TU118885 | 78 | 51 | 23 | 6E68M8L 2S18D80B | 14C14Sn73F | 22E62M16L | LC |
| *Haploporus tuberculatus* (Fr.) Niemelä & Y.C. Dai | TAAM201365 | 1 | 0 | 1 | D | | | CR | D1 |
| *Heterobasidion annosum* (Fr.) Bref. | TAAM201141 | 20 | 2 | 19 | EM | PB | CSn | EL | LC |
| *Heterobasidion parviporum* Niemelä & Korhonen | TU118616 | >100 | >100 | 27 | 12E34M55L 98S2P1B | 77C20Sn3F1L | 34E50M16L | LC |
| *Hyphodontia flavipora* (Berk. & M.A. Curtis ex Cooke) Sheng H. Wu | TU129751 | 2 | 7 | 2 | ML | DBA | CF | EM | NT | D1 |
| *Hyphodontia lastians* (Bourdot & Galzin) E. Langer | TU129697 | 1 | 7 | 4 | ML | DBA | CF | EML | EN | B1ab(iv,v)+2ab(iv,v)+ C2a(i); D1 |
| *Hyphodontia radula* (Schnader) E. Langer & Vesterholt | TU129685 | 8 | >100 | 6 | 7E68M25L 151P40D55B3A | 34C45Sn62F1L | 25E57M16L | LC |
| *Hyphodontia paradoxa* (Fr.) Langer & Vesterh. | TU112988 | 33 | 26 | 4 | 15E50M35L 54D3888A | 4C12Sn85F | 15E66M16L | LC |
| *Inonotopsis subiculosa* (Peck) Parmasto | TAAM058545 | 1 | 0 | 0 | | | | |
| *Inonotus dryadeus* (Pers.) Murrill | | | | | | | |
| *Inonotus dryophilus* (Berkm.) Berkm. | TAAM196870 | 2 | 0 | 2 | D | L | | CR | D1 |
| *Inonotus obliquus* (Ach. ex Pers.) Pilát | TU120209 | >100 | >100 | 24 | 2E71M27L 6D93B1A | 6C19Sn2F73L | 7E52M6L | LC |
| *Inonotus radiatus* (Sowertb) P. Karst. | TU118763 | >100 | >100 | 35 | 14E62M24L 84D1681A | 27C52Sn18F2L | 51E42M7L | LC |
| *Inonotus rheades* (Pers.) P. Karst. | TAAM171200 | 39 | 1 | 12 | M | A | F | E | NT | D1, C1 |
| *Inonotus ulmicola* Cortl. | TAAM178664 | 5 | 0 | 45 | D | L | | NT | D1 |
| *Irpex lacteus* (Fr.) Fr. | TU121351 | 14 | 11 | 4 | E | DB | | F | EML | LC |
| *Irpex lacteus* (Wahlenb.) P. Karst. | TU201112 | >100 | >100 | 36 | 11E35M54L 78S22P | 72C21Sn7F | 32E50M18L | LC |
| *Junghuhnia autumnale* Spirin, Zmitr. & Malysheva | TU12604 | 0 | 6 | 1 | ML | DA | CF | E | VU | D1 |
| *Junghuhnia collabens* (Fr.) Ryvarden | TU117284 | 10 | 40 | 43 | 8M93L 98S3P | 95C3Sn3F | 8E38M55L | NT | C1 |
| *Junghuhnia fimbriatella* (Peck) Ryvarden | TU117288 | 2 | 1 | 8 | L | SDA | C | L | BN | D1 |
| *Junghuhnia lacera* (P. Karst) Niemelä & Kinnunen | TU113260 | 1 | 6 | 2 | EML | DBA | CF | EML | DD |
| *Junghuhnia luteolba* (P. Karst) Ryvarden | TU122833 | 14 | >100 | 9 | 26E67M7L 6594P | 59C5Sn36F | 16E70M14L | LC |
| *Junghuhnia nitida* (Pers.: Fr.) Ryvarden | TU117246 | 81 | >100 | 14 | 26E58M17L 1542D32B26A | 13C2Sn85F | 22E62M17L | LC |
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| Species1 | Voucher | No. of records | Succ. stage | Tree species | Subst. type | Decay stage | Cat. Crit. |
|----------|---------|----------------|-------------|--------------|-------------|-------------|------------|
| **P** | | | | | | | |
| *Junghuhnia pseudozilingiana* (Parmasto) Ryvarden | TU111359 | 27 24 >100 ML | BA | CSnFL | EM | VU CI |
| *Laetiporus sulphureus* (Buill.) Murrill | TU18392 | >100 5 40 L | DA | CF | EM LC |
| *Lenzites betulina* (L.: Fr.) Fr. | TU20080 | 99 >100 19 59E36M6L | 16D81B12A | 23C15Sn61F | 46E47M7L | LC |
| *Leptoporus erubescens* (Fr.) Bourdot & Galzin | TU17236 | 6 9 19 EML | 100P | CSn | EM NE |
| *Leptoporus mollis* (Pers.) Quél. | TU129005 | 47 35 56 9E45M46L | 100S | 66C12Sn21F1L | 56E44M | LC |
| *Lindtneria trachyspora* (Bourdot & Galzin) Pilát | | 5 1 0 9E45M46L | 100S | 66C12Sn21F1L | 56E44M | LC |
| *Meruliopsis taxicola* (Pers.) Bondartsev | TU120635 | 42 26 14 12E69M19L | 4596 | 65C15Sn19F | 85E15M | LC |
| *Obba rivulosa* (Berk. & M.A. Curtis) Miettinen & Rajchenb. | TU121738 | 0 1 0 1M | 6S | F | M EN D1 |
| *Onnia leporina* (Fr.) H. Jahn | TU29416 | 34 4 6 L | S | CSn | E EN A2(a); 4(a,b); C1 |
| *Onnia tomentosa* (Fr.; Fr.) P. Karst. | TU06685 | 47 5 26 EML | SA | F | M LC |
| *Oxyporus corticola* (Fr.) Ryvarden | TU17341 | >100 88 40 17E23M60L | 85D6B81A | 78C9Sn12F1L | 48E45M7L | LC |
| *Oxyporus latermarginaris* (E.J. Durand & Mont) Donk | TU121210 | 2 2 1 E | B | Sn | ML EN D1 |
| *Oxyporus obducens* (Pers.) Donk | TAAM20244 | 1 0 1 D | F | DD |
| *Oxyporus populinus* (Schumach.) Donk | TU18657 | >100 64 27 2E47M52L | 59D34B6A | 14C25Sn3F58L | 56E33M11L | LC |
| *Oxyporus ravidus* (Fr.) Bondartsev & Singer | Niemelä 7215 | 2 0 0 | | | |
| **P** | | | | | | | |
| *Perenniporia medullapantis* (Jacq.) Donk | TAAM189567 | 9 0 3 D | C | EN D1 |
| *Perenniporia narymica* (Pilát) Pouzar | TU82808 | 1 1 0 B | C | L NA |
| *Perenniporia subacida* (Peck) Donk | TU17317 | 28 20 27 EML | SPDBA | CSnF | EML NT D1 |
| *Perenniporia tenuis* (Schwein.) Ryvarden | TAAM189637 | 1 0 0 | | | |
| **P** | | | | | | | |
| *Phaeolus schweinitzii* (Fr.) Pat. | TU18304 | 45 3 14 L | SP | CSnE | M NT D1 |
| *Phellinus alni* (Bondartsev) Parmasto | TAAM191398 | >100 >100 51 10E52M44L | 100D | 18C19Sn3F60L | 71E27M2L | LC |
| *Phellinus chrysoloma* (Fr.) Donk | TU18916 | >100 71 75 30M70L | 100S | 26C27Sn3F42L | 60E38M3L | LC |
| *Phellinus conchatus* (Pers.) Quél. | TU20539 | >100 50 23 14E46M22L | 100D | 32C30Sn14F24L | 46E46M8L | LC |
| *Phellinus ferrugineofuscus* (P. Karst) Bourdot | TU17283 | 35 28 >100 29M71L | 100S | 93C7F | 23E85M19L NT CI |
| *Phellinus ferruginosus* (Schrad.) Pat. | TU11127 | 18 2 29 M | D | CSnF | E LC |
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| Species                                      | Voucher  | No. of records | Succ. stage | Tree species | Subst. type | Decay stage | Cat. Crit. |
|----------------------------------------------|----------|----------------|-------------|--------------|-------------|-------------|------------|
| Phellinus hippophaeicola                     | H. Jahn  | TU128014       | 0 0 1       |              |             |             | NE         |
| Phellinus igniarius                          | (L) Quél.| TAAM191408     | >100 21 27  | EML D        | CSnFLEM     |             | LC         |
| Phellinus laevigatus                         | Bourdot & Galzin | TU17262 | >100 >100 14 | 6E38M56L 1008 | 60C85n32F1L | 32E57M11L | LC         |
| Phellinus undellii                           | Niemelä  | TU11270        | 22 17 5     | EML DB       | CSnFEML     |             | LC         |
| Phellinus nigricans                          | (Fr.) P. Karst. | TU122789 | >100 >100 17 | 10E65M25L 1008 | 20C41Sn9F31L | 51E40M9L | LC         |
| Phellinus nigroliminitatus                   | Bourdot & Galzin | TU17268 | 45 49 45    | 4E12M84L 1005 | 98C2F       | 6E81M13L | LC         |
| Phellinus pini                               | (Brot.) A. Ames | TU109982 | >100 >100 >100 | 32M68L 100P | 2C13Sn85L | 86E14M | LC         |
| Phellinus populicola                         | Niemelä  | TU111223       | >100 34 84  | 9E59M32L 100A | 9C21Sn71L | 70E30M | LC         |
| Phellinus punctatus                          | (P. Karst) Pilát | TU20544 | >100 93 27  | 11E68M22L 96D3B1A | 14C44Sn30F12L | 49E42M9L | LC         |
| Phellinus robustus                           | (P. Karst) Bourdot & Galzin | TU18766 | 54 0 7      | D L          |             |             | LC         |
| Phellinus tremulae                           | Bondartsev Bondartsev & P.N. Borisov | TAAM191400 | >100 >100 44 | 12E56M32L 100A | 12C35n2F83L | 73E26M2L | NT A2      |
| Phellinus tuberculatus                       | (Baumg.) Niemelä | TAAM196106 | 60 0 2     | O L          |             |             | LC         |
| Phellinus viticola                           | (Schwein.) Donk |             | 1 0 0      |             |             |             | RE         |
| Phylloporia ribis                            | (Schumach.) Ryarden | TAAM196444 | 29 0 21    | O L          |             |             | LC         |
| Physporinus sanguinolentus                   | (Alb. & Schwein.) Pilát | TU117267 | 9 >100 9    | 46E24M30L 36S15P26D188SA | 45C20n35F | 20E47M33L | LC         |
| Physporinus vitreus                          | (Pers.) P. Karst. | TU122877 | 51 99 5    | 42E36M22L 7S1P69D19B3A | 37C65n57F | 25E59M16L | VU D1      |
| Physporinus undatus                          | (Pers.) Donk | TU17254 | 3 1 2      | EML DS       | C L         | NE         |
| Piptoporus betulinus                         | (Buill) P. Karst. | TU189004 | >100 >100 56 | 3E78M19L 1008 | 17C23n59F1L | 55E42M3L | LC         |
| Polyporus badius                             | (Pers.) Schwein. | TU120199 | 19 51 46   | 6E33M61L 25S6D108B2A | 76C10Sn14F | 15E70M15L | NT A2      |
| Polyporus brunonis                           | (Pers.) Fr. | TU129816 | 79 79 10   | 81E16M3L 30D68B1A | 11C9Sn80F | 15E55M33L | LC         |
| Polyporus ciliatus                           | Fr.       | TU118306 | 81 91 8    | 97E2M1L 18D8B1A | 7C19Sn74F1L | 10E65M34L | LC         |
| Polyporus leptocephalus                      | (Jacq.) Fr. | TU106392 | >100 40 31 | 23E45M33L 9D41B50A | 44C3Sn53F | 55E39M6L | LC         |
| Polyporus melanopus                          | (Pers.) Fr. | TU118072 | 3 0 16     | DP GC        |             | VU D1      |
| Polyporus pseudobetulinus                    | (Murashk. ex Pilát) Thorn, Kotir. & Niemelä | 1 0 0 |          |             |             | RE         |
| Polyporus (Cerioporus) rangiferinus           | (Bolton) Zmitr, Volobuev, I. Parmasto & Bondartseva | TU17400 | 2 1 7     | L D          | GC          | DD         |
| Polyporus squamosus                          | (Huds.) Fr. | TAAM205984 | >100 0 27    | L D          | CL M        | LC         |
| Polyporus submelanopus                       | H.J. Xue & L.W. Zhou | TAAM185810 | 1 0 0     |             | NA         |            |
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| Species1 | Voucher | No. of records | Succ. stage | Tree species | Subst. type | Decay stage | Cat. Crit. |
|----------|---------|----------------|-------------|--------------|-------------|-------------|------------|
|          |         | I | II | III | | |
| Polyporus tubaeformis | (P. Karst.) Ryvarden & Gilb. | TU114240 | 8 | 0 | 0 | VU | D1 |
| Polyporus ulleungus | H. Lee, N.K. Kim & Y.W. Lim | TU129852 | 0 | 1 | 0 | M | B | F | M | NE |
| Polyporus umbellatus | (Pers.) Fr. | TU113128 | 7 | 0 | 12 | G | EN | D1 |
| Porothamnium fimbiatum | (Pers.) Fr. | TU172313 | 45 | 24 | 9 | EML | SPDBA | CSnF | EML | LC |
| Porphyrellus mucidus | (Pers.) Jülich | TU111192 | 42 | 37 | 0 | 16E47M37L | 86S7P2D2B12A | 73C15Sn14F27 | 46E4M13L | LC |
| Postia auricoma | Spiran & Niemelä | TU129235 | 0 | 3 | 1 | ML | P | C | EL | VU | D1 |
| Postia balsamea | (Peck) Jülich | TU128005 | 1 | 0 | 1 | O | L | DD |
| Postia caesia | Niemelä & Vampola | TU130387 |
| - Postia alni | Schrad. | P. Karst. | TU127228 |
| - Postia cyanescens | Miettinen | TU130591 |
| - Postia populi | Miettinen | OM21796 |
| - Postia simulans | (P. Karst) Spiran & B. Rivoire | TU129873 |
| Postia ceriflua | (Berk. & M.A. Curtis) Jülich | TU122511 | 1 | 2 | 1 | L | DSP | CF | EM | EN | D1 |
| Postia floriformis | (Quél.) Jülich | TU12617 | 21 | 39 | 5 | 18E28M54L | 95S5P | 72C15Sn13F | 46E4M13L | LC |
| Postia fragilis | (Fr.) Jülich | TU117295 | 73 | >100 | 14 | 2E55M43L | 59S41P | 62C9Sn29F | 31E6M8L | LC |
| Postia guttulata | (Peck) Jülich | TU111192 | 42 | 37 | 12 | 3E84M14L | 49S5P1 | 65C16Sn14F5L | 37E6M37L | LC |
| Postia hibernica | (Berk. & Broome) Jülich | TU122822 | 14 | 5 | 0 | M | SP | CF | EM | VU | D1 |
| Postia lichenella | (Murrill) Jülich | TU129611 | >100 | >100 | 8 | 4F07M20L | 125S8P | 51CnM8F | 26E6M8L | LC |
| Postia psathyrocarpa | (F. Ludw.) Vesterh. | TU118995 | 8 | 16 | 27 | 27E24M49L | 75S2P3A | 76C8Sn16F | 30E6M8L | LC |
| Postia rennyi | (Berk. & Broome) Rajchenb. | TU121994 | 12 | 9 | 0 | EML | SP | CSnF | M | LC |
| Postia ronelli | M. Pieni & B. Rivoire | TU128819 | 29 | 20 | 0 | EML | SP | CSnF | EML | DD |
| Postia siptica | (Pers.) Jülich | TU122881 | 48 | 83 | 6 | 16E47M37L | 86S7P1D2B2A | 48C26Sn24F2L | 56E3M8L | LC |
| Postia tephroleuca | (Fr.) Jülich | TU129599 | 72 | >100 | 9 | 1E52M37L | 67S15P1D2B5A | 63C12Sn24F | 24E6M8L | LC |
| Postia undosa | (Peck) Jülich | TU115562 | 14 | 61 | 4 | 8E61M31L | 65S17P2D2B15A | 73C3Sn23F | 25E6M8L | LC |
| Pycnoporellus alboluteus | (Ellis & Everh.) Kotl. & Pouzar | TAAM197000 | 0 | 0 | 11 | S | C | CR | D1 |
| Pycnoporellus fulgens | (Fr.) Donk | TU210127 | >100 | >100 | >100 | 7E37M56L | 85S3P1D10B2A | 85C10Sn5F | 26E6M8L | LC |
| Pycnoporus cinnabarinus | (Jacq; Fr) P. Karst. | TU118399 | 73 | >100 | 19 | 96E4M | 23D77B | 20C25Sn78F | 22E6M8L | LC |
Table 2: Estonian polypore species, their voucher specimens in fungaria, no. of records by sources (I: historical data up to 2004; II: systematic sampling; III: casual collections), habitats, and national Red-List status (Category and Criteria). Habitat data denote presence by: forest successional stage (E, early-successional; M, mid-successional; L, late-successional forests), host tree species (S, Picea abies; P, Pinus sylvestris; A, Populus tremula; B, Betula spp.; D, other deciduous species, O, ornamental conifers), woody substrate (C, coarse downed deadwood; F, fine downed or standing deadwood; Sn, snags and stumps; L, live trees), and decay stage (E, early; M, medium; L, late). For species with ≥25 records from systematic sampling, the habitat summary is given as % of species records in the systematic sample.

Continued

| Species | Voucher | No. of records | Succ. stage | Tree species | Subst. type | Decay stage | Cat. Crit. |
|---------|---------|----------------|-------------|--------------|-------------|-------------|------------|
|         |         | I   II    III |             |              |             |             |            |
| Rhodonia placenta (Fr.) Niemelä, K.H. Larss. & Schigel | TU117299 | 17 | 31 | 42 | 19M81L | 5S339P3D3A | 9C35n6F | 13E55M32L | LC |
| Rigidoporus crocatus (Pat.) Ryvarden | TU117325 | 30 | >100 | 34 | 4ES8M39L | 12S2P51D3B3A | 93C7F | 10E67M23L | LC |
| Sarcoporia polyspora P. Karst. | TU117066 | 4 | 5 | 1 | ML | SP | C | EML | EN | D1 |
| Sidera lenis (P. Karst.) Miettinen | TU010553 | 31 | 6 | 4 | ML | SP | C5nF | ML | VU | D1 |
| Sidera vulgaris (Fr.) Miettinen | TU122882 | 69 | 79 | 20 | 3ES1M47L | 48S39P5D3B5A | 60C38F | 6E48M66L | LC |
| Sistotrema alboluteum (Bourdot & Galzin) Bondartsev & Singer | TU117100 | 9 | 12 | 1 | ML | SP | CF | EML | NT | D1 |
| Sistotrema confinens Pers. | TU118544 | 31 | 0 | 20 | G | | | | |
| Sistotrema denissi Malençon | TAAM6601 | 1 | 0 | 0 | | | | |
| Sistotrema muscicola (Pers.) S. Lundell | TAAM18078 | 2 | 6 | 1 | ML | PD | CF | ML | NT | D1 |
| Skeletocutis armpophora (Fr.) Kotl. & Pouzar | TU020616 | >100 | >100 | 16 | 18E64M18L | 32568P | 60C245n16F | 6E535M | LC |
| Skeletocutis biguttulata (Romell) Niemelä | TU122884 | 60 | >100 | 3 | 12E73M15L | 7589P2D2B1A | 27C355n70F | 26E55M91L | LC |
| Skeletocutis brevispora Niemelä | TU117344 | 1 | 3 | 5 | L | S | C | EML | CR | C2a(i) |
| Skeletocutis carneogrisea A. David | TU122445 | 65 | >100 | 7 | 765M38L | 69531P | 64C55n31F | 23E74M32L | LC |
| Skeletocutis cummata A. Korhonen & Miettinen | TU128007 | 4 | 1 | 0 | M | S | SnF | M | EN | D1 |
| Skeletocutis delicata Niemelä & Miettinen | TU129588 | 0 | 2 | 2 | ML | SP | C | ML | NE |
| Skeletocutis exilis Miettinen & Niemelä | TU129591 | 0 | 1 | 0 | L | S | C | L | NE |
| Skeletocutis jellici Toretic & A. David | TU111188 | 0 | 1 | 3 | M | S | C | L | EN | D1 |
| Skeletocutis kuehneri A. David | TU129264 | 6 | 18 | 9 | ML | SP | CF | EML | LC |
| Skeletocutis nivea sl | | | | | | | | |
| - Skeletocutis funis (Fr.) Miettinen & A. Korhonen | TU129978 | | | | | | | |
| - Skeletocutis nemoralis A. Korhonen & Miettinen | TU130512 | | | | | | | |
| - Skeletocutis semipileata (Peck) Miettinen & A. Korhonen | TU122998 | | | | | | | |
| Skeletocutis odora (Peck ex Sacc.) Ginns | TU117273 | 26 | 14 | 59 | EML | SPA | CSn | EML | VU | A3c; C1 |
| Skeletocutis papryacea A. David | TU122787 | 17 | >100 | 6 | 2E79M19L | 14S86P | 54C15n45F | 26E67M7L | LC |
| Skeletocutis stellae (Pilát) Jean Keller | TU120605 | 43 | 16 | 33 | EML | SP | CF | ML | NT | D1 |
| Spongipellis spumea (Sowerby) Pat. | TAAM18991 | 11 | 0 | 11 | D | L | | VU | D1 |
| Steccherinum oreophilum Lindsey & Gilb. | TAAM158353 | 1 | 2 | 3 | M | BA | F | M | DD |
| Trametes gibbosa (Pers.) Fr. | TU117579 | 1 | 0 | 13 | D | | | VU | D1 |
Table 2: Estonian polypore species, their voucher specimens in fungaria, no. of records by sources (I: historical data up to 2004; II: systematic sampling; III: casual collections), habitats, and national Red-List status (Category and Criteria). Habitat data denote presence by: forest successional stage (E, early-successional; M, mid-successional; L, late-successional forests), host tree species (S, *Picea abies*; P, *Pinus sylvestris*; A, *Populus tremula*; B, *Betula* spp.; D, other deciduous species, O, ornamental conifers), woody substrate (C, coarse downed deadwood; F, fine downed or standing deadwood; Sn, snags and stumps; L, live trees), and decay stage (E, early; M, medium; L, late). For species with ≥25 records from systematic sampling, the habitat summary is given as % of species records in the systematic sample.

| Species | Voucher | No. of records | Succ. stage | Tree species | Subst. type | Decay stage | Cat. Crit. |
|---------|---------|---------------|-------------|--------------|-------------|-------------|------------|
| **Trametes hirsuta** (Wulfen) Pilát | TU120101 | >100 | 24 | 78E15M8L 1S37D48B13A | 20C95m71F 49E44M7L | LC |
| **Trametes ochracea** (Pers.) Gilb. & Ryvarden | TU120126 | >100 | 17 | 44E37M19L 1S85D0B42A | 27C16Sn56F1L 56E40M4L | LC |
| **Trametes pubescens** (Schumach.) Pilát | TU101930 | 58 69 3 | | 55E38M7L 13D75B12A | 36C35m3F2L 28E62M10L | LC |
| **Trametes suaveolens** (L.) Fr. | TU128010 | 13 0 16 | D | SnL | CR CR C2a; D1 |
| **Trametes versicolor** (L.) Lloyd | TU118802 | >100 | 17 | 82E16M2L 254D53B2A | 19C44Sn37F 28E47M25L | LC |
| **Trametopsis cervina** (Schwein.) Tomsovský | TU109320 | 0 0 2 | | | NE |
| **Trechispora candidissima** (Schwein.) Bondartsev & Singer | TU123416 | 4 8 1 | EML | SPD8 | C5nF | EML | LC |
| **Trechispora hymenocystis** (Berk. & Broome) K.H. Larss. | TU129229 | 56 82 3 | | 22E52M26L 25526P10D98B | 36C105n53F 5E38M67L | LC |
| **Trechispora mollusca** (Pers.) Libert | TU129726 | 45 83 3 | | 30E30M40L 4459P9D36B3A | 33C5Sn62F 11E51M38L | LC |
| **Trichaptum abietinum** (Pers. ex J.F. Gmel.) Ryvarden | TU118911 | >100 | 30 | 1S57M28L 7053P0 | 50C19Sn32F 66E35M1L | LC |
| **Trichaptum biforme** (Fr.) Ryvarden | TU120047 | 24 58 7 | 3E79M17L 3D97B | 43C2Sn48F7L 30E58M15L | LC |
| **Trichaptum fuscoviolaceum** (Ehrenb.) Ryvarden | TU118960 | 42 | >100 | 26E69M5L 259P8 | 31C21Sn48F 68E32M | LC |
| **Tyromyces chioneus** (Fr.) P. Karst. | TU120543 | 83 | 4 | 6E531M4L 1P10D81B8A | 28C16Sn53F 14E58M28L | LC |
| **Tyromyces fumidiceps** G.F. Atk. | TAAM18968 | 4 0 0 | | | | | |
| **Xanthoporus syringae** (Parmasto) Audet | TAAM15946 | 4 0 0 | | | | | |

1 life history strategy: p parasite; m mycorrhizal; m* partly mycorrhizal; ? uncertain
LSU regions. To avoid rooting with distant taxa and producing arbitrary branching orders, their phylogenetic trees were centrally rooted. We organized the sequences as Maximum Likelihood (ML) phylogenies based on IQ-TREE (version 1.2.2; Nguyen et al. 2015), 1000 bootstrap replicates and the ‘best-fitted model’. Collection data for the examined Estonian specimens in difficult/unresolved species groups and the GenBank or UNITE accession numbers of their ITS and LSU sequences are presented in Additional file 3, data for public reference sequences from elsewhere are in Additional file 4. The final alignments for all data sets were stored in TreeBASE (http://www.treebase.org; accession number 25415).

Analysing polypore assemblages along habitat gradients Primary data for assessing correspondence between polypore assemblages and habitat gradients were the systematic surveys in stands > 20 years old (datasets IIa-IIc in Table 1). We categorized the stands into ‘habitat types’ according to: (1) site-type group – proxy of soil nutrient and humidity combinations (Lõhmus 1984, Additional file 1); (2) tree canopy composition class – Picea abies forests and Picea-deciduous mixedwood; Pinus sylvestris forests and Pinus-deciduous mixedwood; deciduous forests (≥80% deciduous species); and (3) old stands (dominant tree layer > 100 years) vs. other stands. We then compiled species lists for each habitat type by pooling species data from all stands belonging to this type. Such approach allowed us to address relative importance of permanent (soil) and temporary variation (tree composition and successional stage) for polypore assemblages. We did not analyse the distinct post clear-cut assemblages of permanent (soil) and temporary variation (tree composition and successional stage) for polypore assemblages. We re-coded the decay stages I–III as early-decayer (most records originate from the systematic surveys (datasets IIa-d). We initially developed woody substrates, excluding building timber for which we only report the state of the knowledge.

The records are from the datasets I-IIIa (Table 1) and, for Juniperus communis, as summarized by Sell & Kotiranta (2011). Host tree species have been indicated in all these datasets. We additionally distinguished the main woody fractions and decay stages – those data mostly originate from the systematic surveys (datasets IIa-d). We re-coded the decay stages I–II sensu Renvall (1995) as ‘early’, III as ‘medium’, and IV–V as ‘late’; in the latter we also included casual records describing the wood as “extremely decayed”. Fine woody debris (FWD) includes species with 23,362 original records and 54 habitat types. We then recoded species’ record numbers for a three-class scale (0, no records; 1, one record; 2, > 1 records) as a compromise between observation bias in raw record numbers (resulting from varying habitat coverage and species detectability) and the presence-absence scale’s emphasis on rare species.

To illustrate how assemblage composition varies among habitat types, we used non-metric multidimensional scaling (NMDS; vegan package in R, Oksanen et al. 2016). The environmental matrix comprised three categorical variables: site-type group (ten groups; Additional file 1), soil fertility (two classes: fertile vs poor/thin), and tree species composition (three classes, see above). The analyses were run using the Bray-Curtis dissimilarity index with random starting configurations; searching for two-dimensional solutions, and rotating the final solution to depict the largest variance of site scores on the first axis. Assemblage differences were tested separately for each environmental variable using Multi-Response Permutation Procedures (MRPP) with Bray-Curtis dissimilarity index, and Bonferroni corrected p-values.

Substrate analyses
We followed the concept of functional traits as presented by Dawson et al. (2019) and categorized species mostly according to Niemelä (2016). We first divided the species between strictly or facultatively ectomycorrhizal and wood-inhabiting life-strategy groups. The wood-inhabiting group was further divided by: (a) typical colonization time – parasites of live trees (‘necrotrophs’ sensu Dawson et al. 2019), early-decayer (most records on trees of decay stage I–II) and late-decayer saprotrophs (stage III–V); and (b) physical decay strategy – white-rot and brown-rot producing species. The saprotrophs include some polypores that are frequent on very fine debris, and some ‘follower’ species that require wood decayed by other parasitic or saprophytic basidiomycetes (Holmer et al. 1997, Niemelä 2016).

We pooled all the available polypore records on naturally developed woody substrates, excluding building timber for which we only report the state of the knowledge.

The records are from the datasets I-IIIa (Table 1) and, for Juniperus communis, as summarized by Sell & Kotiranta (2011). Host tree species have been indicated in all these datasets. We additionally distinguished the main woody fractions and decay stages – those data mostly originate from the systematic surveys (datasets IIa-d). We re-coded the decay stages I–II sensu Renvall (1995) as ‘early’, III as ‘medium’, and IV–V as ‘late’; in the latter we also included casual records describing the wood as “extremely decayed”. Fine woody debris (FWD) includes...
both fallen and standing dead wood items < 10 cm in diameter at the basidiome location.

Based on the distribution of records among all substrate categories, we distinguished regularly occurring and specialist polypores for a substrate category as follows. ‘Regular’ species, either: had ≥5% records on that substrate category of the species’ total of ≥40 records in Estonia, or had >1 records there of its total of <40 records, or accounted for ≥5% of all polypore records in that substrate category. ‘Specialists’ were a subset of regular species, which had >2 records from a particular substrate category and this formed either ≥90% of all Estonian records of that species, or all records if the total number of records was 3–9.

Similarity of polypore species composition of native host tree species was further explored with hierarchical cluster analysis based on presence-absence data, Bray-Curtis dissimilarity measure and the average linkage method (r package vegan; Oksanen et al. 2016). Because presence-absence data would over-emphasize atypical substrates, only polypores occurring regularly on each tree species (≥5% of total records in the tree or polypore species) were included in this analysis.

RESULTS
Estonian polypore diversity
Parmasto (2004) reported 212 polypore species in Estonia, of which 198 can be currently considered accepted, although several have been subdivided on a larger geographical scale (e.g. Antrodia crassa, Antrodia sitchensis, Polyporus tuberaster, Postia sericeomollis and Skeletocutis nivea s. str. are not known in Estonia). Six of those species are now listed as Regionally Extinct based on the lack of records for > 50 years: Antrodia heteromorpha, Diplomitoporus crustulinus, Inonotopsis subiculosa, Inonotus dryadeus, Phellinus viticola, and Polyoporus pseudobetulinus (Table 2). Probably, they were already extinct in 2004. Excluded species include seven formerly recognized taxa (Antrodia albida, Ceriporia subretticulata, Phellinus cinereus, Postia lactea, Sistotrema albopallascens, Skeletocutis subincarnata, and Trametes velutina) that are now merged with other species known in Estonia. We also excluded two putative new Phellinus species on Parmasto’s list (status as independent species not supported). Five species were excluded because the historical material had been misidentified: Antrodia canadensis, Ganoderma adspersum, and Skeletocutis alutacea (all specimens checked), and Postia lateritia and Trichaptum laricinum (most specimens checked, none confirmed). Two species, Aurantiporus priscus (a part of “Hapalopilus salmonicolor” records in Parmasto 2004) and Ganoderma carnosum, remain on our list based on Parmasto’s original identifications; the collections have survived but we failed to obtain sequences from this old material.

As of July 2019, the list comprises 221 verified extant species (Table 2), including 11 with no post-2004 records (Anomoloma albotuctes, Antrodia parasitica, Aurantiporus priscus, Ganoderma carnosum, Oxyporus ravidus, Perenniporia tenuis, Polyporus submelanopus, P. tubaeformis, Sistotrema dennisi, Tyromyces fumidiceps, and Xanthoporus syringae). Seventeen extant species have been only recorded once, and six only twice (Table 2); 11 of these extremely rare species were recorded in 2005–18. Based on the numbers of accepted species, singletons and doubletons, the Chao (1987) estimate for expected species richness is 245 extant species. Additionally, there are records of at least 20 lineages that may deserve species status (see under Difficult species below; Table 3). Three species are, according to current records, restricted to the West-Estonian, and nine to the East-Estonian geobotanic regions (only species with >1 records considered).

Species were added to the 2004 list for three reasons (only from casual collections) and include two species newly reported for Europe (Polyoporus submelanopus, P. ulleungensis):

(1) Ten established species were found in nature for the first time after 2004: Coltricia cinnamomea, C. confluens, Fibroporia norrlandica, Obba rivulosa, Perenniporia narymica, Phellinus hippophaeicola*, Postia auricomata, Pycnoporellus albotuctes*, Skeletocutis jelicii, and Trametopsis cervina*. Eight of these (excluding F. norrlandica and O. rivulosa) are easy to find and identify, and may thus constitute true recent additions to the Estonian mycota.

(2) Nine species have been distinguished from other species present in the area and confirmed or likely to be present in the pre-2004 material of the collective species: Ceriporia bresadolae (from C. purpurea), Hapalolipus aurantiacus and H. ochracolateritius (from “H. salmonicolor” sensu Parmasto 2004), Postia cyanescens, P. simulans and P. populi (from P. alni and P. caesia), and Skeletocutis futilis, S. membralis and S. semipileata (from S. nivea s. str. that is not known in North Europe).

(3) Ten species, now confirmed in Estonia, have been described or reinstated only after 2004. Of these, Antrodia leucaena has been confirmed by us also in the Estonian pre-2004 material, and Polyoporus submelanopus* only in that material. The other species are: Aporpium macroporum, Ceriporia aurantiocarmescens, C. torpida, Junghuhnia
autumnale, Leptoporus erubescens, Polyporus ulleungus, Skeletocutis delicata, and S. exilis.

Difficult species
We distinguished 13 species groups of Estonian polypores, for which the assessment of population status and ecology was complicated (details in Additional file 5). In most cases, the problem was unresolved taxonomy: molecular data revealed that the prevailing species concept included cryptic lineages (Table 3, Additional file 3), some with documented ecological differences.

Specifically, Estonian specimens referred to in Table 2 by the accepted names Antrodiaella faginea, Byssoporia terrestris, Ceriporia excelsa, C. viridans, Ceriporiopsis pseudogilvescens, Physisporinus sanguinolentus, Sidera vulgaris, and Sistotrema alboluteum represented two distinct lineages each, and those identified as Coltricia cinnamomea, C. perennis, Physisporinus vitreus and Sistotrema muscicola at least three lineages each. Additionally, we sequenced an undescribed lineage related to Sistotrema alboluteum, and found that the Estonian specimens of Sidera lenis do not match with its
prevailing species concept. In the Ceriporiopsis resinas-cens / C. pseudogrisea lineages, the main morpho-
logical characteristics represented a continuum and
some specimens had ITS copies from multiple lineages.
The abundance of records or their habitat diversity indi-
cated no apparent conservation concern in any lineages
of Antrodiaella faginea and Ceriporia viridans, while at
least one likely threatened lineage was detected in Cer-
poria excelsa, Coltricia cinnamomea, C. perennis, and
Sidera vulgaris.

Another, sometimes combined problem was the lack of
stable morphological character combinations to en-
able species identification in recently revised species
groups; this introduced large uncertainty to interpreting
historical collections and observations. For example, the
species earlier known as Postia caesia, P. alni, P. leuco-
mallella, and Skeletocutis nivea have been considered
easily identifiable in the field and their mostly observa-
tional data cannot be ascribed to the recently segregated
species. Also, sequencing of European fungarium speci-
mens of black-stiped Polyporus collections is recom-
dended due to high likelihood of finding species
traditionally not considered to occur in Europe.

Functional traits
Most Estonian polypore species produce annual basi-
diomes, but in 51 species these survive for at least 2–3
years (usually > 3 years in 33 of these). The prevailing life
strategy is saprotrophy, with at least 12 species being fol-
lower species of other wood-inhabiting (parasitic or
saprotrophic) polypores (Table 2). Based on systematic
surveys (datasets IIa–c; Table 1), basidiomes of the fol-
lower species are found 1–3 orders of magnitude less
frequently than their predecessor species. A wide vari-
ation can occur in the same predecessor species, e.g., the
Estonian records among the followers of Trichaptum abietinum range from one (Antrodiaella parasitica) to
380 (Skeletocutis carneogrisea).

Thirty-four polypore species are parasites of live trees
or shrubs, but usually continue living as saprotrophs
after death of the host-tree. Three parasitic species (Het-
erobasidion annosum, H. parviporum, and Phellinus tre-
mulae) are considered economically important forest
pathogens in Estonia. Thirteen polypore species are con-
sidered strictly or facultatively ectomycorrhizal (Alba-
trellus, Boletopsis, Coltricia, and Sistotrema) (Table 2).
Distinctly among functional groups, mycorrhizal polyp-
ores are most diverse in dry and low-productive forest
types: eight species inhabit alvar forests (on calcareous
soil), eight dry boreal, and seven boreal heath forests (on
sandy soil). In contrast, only three mycorrhizal species
have been found in eutrophic sites, five in meso-
eutrophic, and three in swamp forests.

Habitat types and assemblages
Among the three broad forest successional stages (Table
2), the largest numbers of species have been recorded in
mid-successional forests (146; incl. 16 parasitic and five
wholly or partially mycorrhizal species) and late-
successional forests (146; incl. 19 parasitic and eight
wholly or partially mycorrhizal species). The largest
numbers of threatened species were found in late-
successional (38 species) and mid-successional forests
(34). Based on systematic surveys (Table 1; datasets IIa–c), the most abundant species in mid- and late-
successional forests are Fomitopsis pinicola (10.5% of
18,026 records), Trichaptum abietinum (8.5%), and
Fomes fomentarius (7.4%). In post clear-cut (early-suc-
cessional) stands, most abundant are Gloeophyllum
sepiarium (9.0% of 4939 records), F. pinicola (7.5%),
and Trametes hirsuta (6.4%). However, these propor-
tions are underestimates compared with rarer species,
since our sampling included up to ten records of each
species per plot (see Methods).

Estonian polypore assemblages in > 20 year-old forests
are primarily organized along the soil (site type) and tree
species composition gradients (Fig. 2; Additional file 6).
The first ordination axis broadly distinguished assem-
bles on fertile soils from those on poor soils (sandy,
thin calcareous, or peat soils) (MRPP test: A = 0.08, p <
0.001). The second axis ranged from deciduous-
to Pinus-dominated stands, with Picea-dominated forests
in the middle (MRPP tests: A = 0.07–0.09, p < 0.001, for the
contrasts with Pinus-dominated sites; A = 0.03, p = 0.02,
for Picea- vs deciduous-dominated sites). These two gra-
dients overshadowed soil moisture effects; e.g., Pinus-
dominated sites with contrasting moisture conditions
(dry alvar forests, wet drained peatland, and bog forests)
were positioned close to each other, but clearly apart
from moist sites dominated by either Picea or deciduous
(trees (Fig. 2).

Across natural forest types, polypore assemblages formed a continuum in the ordination space (Fig. 2), i.e.,
only distant types differed significantly from each other.
For example, the assemblages in eutrophic sites ap-
peared close to those in meso-eutrophic or swamp sites
(MRPP: A ≤ 0.01, Bonferroni corrected p > 0.1), but dif-
f ered from all other forest site-type groups (A = 0.09–
0.14, p < 0.033 in all comparisons). Such a pattern is also
revealed on the Euler diagrams: increasing proportions
of species common to more similar site types, but a rela-
tively small number of generalists across all habitat types
(Fig. 3A,B middle section). The most distinct assem-
bles in natural forests were in alvar forests that dif-
fered from all others (A = 0.08–0.17, p < 0.034 in all
comparisons), except perhaps heath forests (A = 0.13,
p = 0.067). Specific species in our sample of alvar forests
were the ectomycorrhizal Albatrellus citrus and
Boletopsis leucomelaena, and saprotrophic Anomoloma myceliosum and Skeletocutis jelicii. The largest number of habitat-specific species inhabit natural forests on nutrient-rich soils: 21 such species in eutrophic and swamp sites combined, including 18 extremely rare or threatened species (e.g. Picea-inhabiting Amylocystis laponica, Antrodia piceata, and Skeletocutis brevispora; Populus-inhabiting Aporpium macroporum, Junghuhnia fimbriatella, and Inonotus rheades).

All anthropogenic woodland types (drained peatland forests, parks, and wooded meadows) hosted distinct polypore assemblages (Fig. 2). Drained peatland forests revealed two specific species (Postia auricoma; Antrodia macra) and their full assemblages resembled most those in dry boreal (MRPP test: $A = 0.04$, $p = 0.060$) or meso-eutrophic forests ($A = 0.04$, $p = 0.069$), while all other forest site-type groups were dissimilar ($A = 0.09-0.11$, $p < 0.035$). Parks and wooded meadows were each represented with one pooled species list in our data; thus we could not formally test their assemblage differences. However, as illustrated by the Euler diagrams (Fig. 3), parks had the largest number of specific species (13) and seven polypores are largely confined to large oaks (Quercus robur) and elms (Ulmus glabra) typical of parks and wooded meadows (Daedalea quercina, Fistulina hepatica, Grifola frondosa, Inonotus ulmicola, Phellinus robustus, Perenniporia medulla-panis, and Polyporus umbellatus). Some of the latter species also inhabit the rare natural oak stands in Estonia, which have not been systematically surveyed; casual data show that such stands additionally host some highly threatened species (Aurantiporus croceus and Haploporus tuberculatus).

Woody substrates and substrate specificity
Host tree species data were available for 204 Estonian polypore species that inhabit natural woody substrates (Table 4). Sixty (29%) of these species can be considered tree-species specialists. Picea abies stands out with most
associated species (108) and threatened species (40), and one-third of all specialist species (20, including 11 threatened species). The other polypore-rich trees include *Pinus sylvestris* and *Betula* spp. (the most abundant tree species in Estonia) and *Populus tremula*. *Quercus robur* is the only other tree species with several specialist polypores recorded. In contrast, small-sized woody species – shrubs and trees, which mostly stay in forest understories – generally lack specialist polypores (*Botryodonta milliansens* on *Juniperus communis* being the only exception). *Phellinus tubercolus* and *Phyllopora ribis* are two specialized polypores so far only reliably recorded on fruit trees and shrubs in gardens (Table 4), although both have potential congenerous wild hosts in woodlands (*Prunus padus/spinosa* and *Ribes spp.*, respectively).

Among 152 wood-inhabiting species recorded >10 times in Estonia, 52 (34%) have been found on 1–2 tree species, 50 (33%) on 3–7 tree species, and 49 (32%) on at least 8 tree species. *Bjerkandera adusta* (recorded on 18 host tree species), *Trametes hirsuta* (18), and *T. versicolor* (16) had the widest host range. Host-tree specificity differs among functional groups: parasitic polypores are most often restricted to 1–2 tree species (Fig. 4a), and white-rot producers are more often generalists than brown-rot producers (Fig. 4b).

By their polypore assemblages, native woody hosts form three main clusters that largely follow taxonomic divisions (Fig. 5): (1) the two Estonian conifer trees of *Pinaceae*; (2) common soft-wooded deciduous trees, including all native trees of *Betulaceae* (*Betula* spp. and
Alnus glutinosa being the most similar host pair) and Populus tremula (a distinct host); and (3) the remaining woody species, with the most distinct assemblages on nemoral hardwoods (Acer, Quercus, and Fraxinus); Salix spp. clustering together with Fraxinus; and a similar host pair of the native trees in Rosaceae – Prunus padus and Sorbus aucuparia.

Coarse downed wood (fallen trunks) is by far the most polypore-rich woody fraction, with the largest number of species found in the medium decay stage (Table 4). This is despite a wider range of host species (including shrubs) providing fine woody debris. Betula spp. differs from other main tree species by distribution of species richness among wood fractions: relatively many species

**Table 4** Numbers of polypore species recorded on naturally developed woody substrates in Estonia. The most species rich substrate in each substrate category (column) is indicated with bold script. Species counts by substrate type and decay stage may not correspond to the pooled species count of a tree species since some records lacked detailed substrate data. See Methods for the criteria of ‘regular’ and ‘specialist’ species.

| Substrate types pooled | Native woody species | Exotic woody species |
|------------------------|----------------------|----------------------|
| Substrate type         | Picea abies          | Deciduous            |
|                        | All                  | Fruit trees, bushes |
|                        | 108(40)              | Coniferous           |
|                        | 73(26)               | TOTAL                |
|                        | 20(11)               | 204 (78)*            |
|                        |                      |                      |
|                        | Populus tremula      |                      |
|                        | 102(23)              |                      |
|                        | 58(13)               |                      |
|                        | 11(8)                |                      |
|                        |                      |                      |
|                        | Betula spp.          |                      |
|                        | 97(18)               |                      |
|                        | 67(8)                |                      |
|                        | 8(0)                 |                      |
|                        |                      |                      |
|                        | Pinus sylvestris     |                      |
|                        | 89(25)               |                      |
|                        | 60(16)               |                      |
|                        | 10(1)                |                      |
|                        |                      |                      |
|                        | Alnus glutinosa      |                      |
|                        | 71(7)                |                      |
|                        | 46(4)                |                      |
|                        | 0                    |                      |
|                        |                      |                      |
|                        | Alnus incana         |                      |
|                        | 54(5)                |                      |
|                        | 19(0)                |                      |
|                        | 0                    |                      |
|                        |                      |                      |
|                        | Quercus robur        |                      |
|                        | 54(14)               |                      |
|                        | 16(5)                |                      |
|                        | 6(3)                 |                      |
|                        |                      |                      |
|                        | Salix spp.           |                      |
|                        | 52(7)                |                      |
|                        | 14(1)                |                      |
|                        | 1(0)                 |                      |
|                        |                      |                      |
|                        | Fraxinus excelsior    |                      |
|                        | 50(6)                |                      |
|                        | 18(2)                |                      |
|                        | 0                    |                      |
|                        |                      |                      |
|                        | Corylus avellana     |                      |
|                        | 49(3)                |                      |
|                        | 17(2)                |                      |
|                        | 0                    |                      |
|                        |                      |                      |
|                        | Tilia cordata        |                      |
|                        | 41(1)                |                      |
|                        | 10(1)                |                      |
|                        | 0                    |                      |
|                        |                      |                      |
|                        | Sorbus aucuparia     |                      |
|                        | 40(2)                |                      |
|                        | 7(0)                 |                      |
|                        | 0                    |                      |
|                        |                      |                      |
|                        | Acer platanoides     |                      |
|                        | 33(4)                |                      |
|                        | 10(1)                |                      |
|                        | 0                    |                      |
|                        |                      |                      |
|                        | Ulmus spp.           |                      |
|                        | 30(5)                |                      |
|                        | 7(2)                 |                      |
|                        | 1(1)                 |                      |
|                        |                      |                      |
|                        | Prunus padus         |                      |
|                        | 190(0)               |                      |
|                        | 3(0)                 |                      |
|                        | 0                    |                      |
|                        |                      |                      |
|                        | Juniperus communis   |                      |
|                        | 16(5)                |                      |
|                        | 5(1)                 |                      |
|                        | 1(1)                 |                      |
|                        |                      |                      |
|                        | Frangula alnus       |                      |
|                        | 7(0)                 |                      |
|                        | 1(0)                 |                      |
|                        | 0                    |                      |
|                        |                      |                      |
|                        | TOTAL                |                      |
|                        | 204 (78)*            |                      |

*In addition three species are known from unidentified tree species only

Coarse downed wood (fallen trunks) is by far the most polypore-rich woody fraction, with the largest number of species found in the medium decay stage (Table 4). This is despite a wider range of host species (including shrubs) providing fine woody debris. Betula spp. differs from other main tree species by distribution of species richness among wood fractions: relatively many species

![Fig. 4](image-url) No. of host tree species listed for wood-inhabiting polypore species with > 10 records in Estonia by life strategy (a) and by decay type (b). The categorization for each species given in Additional file 8.
on fine woody debris and in late decay stages. Parasitic polypores are relatively diverse on *Quercus* and exotic (ornamental) deciduous trees, but the scarcity of records among wood decay stages in these trees mainly shows poor substrate documentation.

In addition to natural substrates, there are observations of polypores on building timber. From 2002 to 2008, Pilt et al. (2009) reported four species as regular in wooded buildings: *Antrodia serialis*, *A. sinuosa*, *Fibroporia vaillantii*, and *Fomitopsis pinicola*. Parmasto (2004) additionally mentions rare occurrences of *Fibroporia gossypium* and *Trametes ochracea* as well as “*Cerioporia purpurea*” (probably *C. bresadolae*) on building timber in Estonia.

**DISCUSSION**

Our review demonstrates how integrating multiple data sources and their taxonomic and ecological appraisal can provide new perspectives on fungal species pools and their long-term dynamics. The practical opportunities discussed below included: posing new taxonomic and ecological hypotheses; fixing a state in the fungal biota for biodiversity monitoring purposes and retrospectives; providing a basis for red-listing individual species that considers all available data. The conservation issues can be further elaborated for management, which has been addressed elsewhere (Lõhmus et al. 2018b). Assessing the main factors behind changes in species lists helped us to understand actual changes in the biota and to prioritize research. We conclude that the Estonian polypore biota comprises over 260 species, of which roughly two-thirds were known 15 years ago according to their current species concepts, while the remaining third is divided between newly collected species, species distinguished from formerly known taxa, molecularly documented but yet-undescribed lineages, and species probably present but remaining to be found. Adding environmental DNA-samples to our basidiome data could be a next step to clarify the situation (cf. Kalsoom Khan et al. 2020).

**Estonian polypore biota as a part of the north-European species pool**

The composition of the current Estonian polypore biota can be primarily explained through their woodland habitats and fungal biogeography. Both these patterns refer to post-glacial vegetation development, notably the climate- and land use-driven transformation of Estonian forests during the last millennium (e.g., Reitalu et al. 2013). It remains poorly known how fungal distributions have responded to this history, but some insight can be obtained based on comparisons of current regional biotas.

We documented 221 polypore species and > 20 to be described in Estonia. Comparing ours with the checklists in the neighbouring countries reveals extensive overlap of polypore biota across North-Europe, but clear latitudinal and longitudinal variation in relative abundance of species. Both the Finnish and Norwegian list include 251 species (Niemelä 2016, Tom Hofton, pers. comm.); but at least in Finland fewer species with 1–2 records than in Estonia (calculated from Niemelä 2016). Nevertheless, all the country lists now appear rather complete and the total species pool in Norway, Sweden (excluding its nemoral southern part), Finland and Estonia might be around 300 currently accepted species.

The part of this North-European species pool not found in Estonia comprises: (1) ca. 20 species having northern or north-eastern distributions in boreal forests; (2) several species having southwestern distribution in
the Baltic Sea region, with Fennoscandia records mostly in southern Sweden; and (3) many extremely rare species having poorly explained scattered occurrences in Fennoscandia. Assigning the six species now considered Regionally Extinct in Estonia to the same groups reveals a disproportionate loss of northern species, with only Inonotus dryadeus representing group (2). Latitudinal patterns are further reflected by several southern species found in Estonia, but not in south Finland less than 100 km north. Of such species, Abortiporus biennis, Collinia confluens, Haploporus tuberculatus, and Perenniporia narymica are also present in south Sweden (cf. group 2 above), and only Oxyporus latemarginatus and Trametopsis cervina have no Fennoscandian records at all. Some of these species are thermophilous; e.g., Gloeophyllum trabeum is confined to warm wooden indoor facilities in Finland but has a viable sexually reproducing population in the Estonian nature.

Longitudinal patterns are less apparent and, perhaps, less frequent, but two situations can be distinguished in our data. First, at least Ceriporia tarda, Junghuhnia autumnale and J. fimbriatella have continuous eastern distributions that reach Sweden, but rarely (if at all) Scandinavia. Similar species found in eastern Finland, but not in Estonia, are Antrodia hyalina, A. tanakai, and Postia persicina (Niemelä 2016). Secondly, the DNA-barcoding methods have helped us to record in Estonia Polyporus submelanopus and P. uleungus with so-far known distributions in the Far East (Xue & Zhou 2013, Timpromma et al. 2017). That these species have not been recorded in Europe before may reflect insufficient molecular sampling or, alternatively, natural or human-mediated long-distance dispersal. Natural cross-border immigration from Russia has been hypothesized to have caused recent population increase in Estonia in some eastern species with continuous distributions, such as Amylocystis lapponica (Runnel et al. 2020). In the case of Far-Eastern species there is a possibility of artificial dispersal with long-distance trade in the Soviet period of Estonia (1945–1991).

**Taxonomically unclear and exotic taxa**

Taxonomically difficult situations remain common in European polypores despite much research undertaken. We documented, based on DNA (ITS) barcoding lineages, at least 20 likely undescribed species in Estonia alone. Since ITS differences can be minor among species in some genera, such as Antrodia and Antrodiella (Miettinen et al. 2012, Spirin et al. 2015), this number may increase when multiple genetic markers are used. At genus level, taxonomic revisions of Coltricia, Physistoporus, and Sistotrema (comprising at least 13 undescribed species in Estonia) appear as the priorities to clarify regional polypore biota. For some very rare lineages our data were too scarce to enable any ecological insight, and we encourage field work and international collaboration to add ecologically described records.

Some taxonomically resolved cases remain problematic in field sampling and for red-listing threatened species. For example, the collective taxa Postia alni, P. caesia, and Skeletonitis nivea remain in parallel use, because field identification of their cryptic constituent species is not reliable despite identification keys provided. How to apply those collective species concepts should be decided depending on questions being asked. If the goal is to record all constituent species of the collective taxa, vouchers should be regularly collected for laboratory assessment; e.g., sampling specimens from different substrates (Runnel et al. 2014).

Another uncertain part of the biota comprises exotic species. There is a considerable literature on the spread of wood-inhabiting fungi to exotic host trees, notably in plantations and on ornamental trees. Much less is known on how exotic host trees or anthropogenic substrates have changed the abundance or distribution patterns of the fungi (Burgess et al. 2016). In Estonia, parks, cemeteries, and gardens constitute poorly sampled habitats, and there are six polypore species (3% of the species pool) confined to introduced woody species in such settings. Four species are not applicable (NA) for conservation assessment: Phellinus tuberculatus and Postia balsamea have been only recorded on fruit trees in gardens, Ganoderma carnosum on Abies sp. (an exotic tree), and Ceriporia bresadolea on building timber. Additionally, Phellinus hippophaeicola has been only found once on a Hippophae rhamnoides (naturalized but mostly in plantations), and Phylloporia ribis (a frequent species) only occasionally outside gardens. A well-supported ecological conclusion, however, is that no exotic polypore has so far attained significant functional role in Estonian natural forests.

**Checklist-based detection of changes in fungal biota**

Monitoring fungal diversity remains a challenge (e.g., Halme et al. 2012) and, compared with plants or animals, fungal conservation perspectives have much poorer, often indirect, background knowledge on population dynamics. Unclear background undermines using fungi as indicators, which would be reasonable for different purposes (Lonsdale et al. 2008, Junninen & Komonen 2011, Heilmann-Clausen et al. 2015). A solution has been combining ecological studies on current fungal habitat relationships with habitat changes of the past (e.g., Kouki et al. 2001, Penttilä et al. 2006, Junninen & Komonen 2011). However, this requires key factors to be well known and includes hidden assumptions of stable regional species pools and habitat relationships in
time. It cannot substitute documenting of changes in fungal biota, for which unfortunately no comprehensive and feasible survey methods exist.

Updated and critically revised regional checklists that integrate multiple data sources might thus remain crucial for monitoring full fungal diversity and for red-listing threatened species (Arnolds 2001). Yet, for credible interpretation of records, checklists must incorporate quality assessment, based on intensity and distribution of sampling effort, methodological heterogeneity, and species identification methods used. A set of critical issues assessed for our study (Table 5), implies that: (i) historical changes in the Estonian polypore biota can be summarized only by individual species (total numbers of species recorded are unreliable), (ii) at the current sampling intensity, ‘safe minimum’ temporal resolution of detecting strong trends and extirpation is ca. 30 years (see below), (iii) detectability (conspicuousness; identification; ecological impact) is a key consideration for evaluating the species’ trends.

Case studies illustrate these points. Regarding point (ii), a few iconic species can be perhaps monitored even at < 10 year resolution in Estonia (Runnel et al. 2020). More typically, however, a viable population of *Trametes suaveolens* (last seen in 1984 in the country) was discovered in much-visited Tallinn city in 2018; it would have been premature to consider the species Regionally Extinct (Runnel et al. 2018). Other long record gaps of rare, but apparently viable, populations include *Hapalopilus aurantiacus* and *H. ochraceolateritius* (1962–2006) and *Dichomitus squalens* (1980–2004). Highlighting point (iii), casual collection probability has varied by two orders of magnitude among Estonian polypore species, being smallest in species that produce poorly identifiable annual basidiomes (Lõhmus 2009). Such species are most likely to be missed in the country, especially if naturally rare, recently described, and inhabiting ecosystems not yet targeted by efficient ecological sampling schemes (see Lõhmus et al. 2018a). We can list around a dozen likely additions based on the well-studied Finnish biota (Niemelä 2016), e.g., *Anomoporia kamtschatica*, *Antrodia infirma* and *A. mappa*.

Table 5 A quality assessment scheme (quality criteria) proposed for regional checklists of macrofungi, exemplified by the current study

| Quality criterion | Assessment for the current checklist | Limitations derived |
|-------------------|--------------------------------------|----------------------|
| Completeness      | < 10% unrecorded valid species (estimated from Chao index based on singletons/doubleton ratio [1]; also by analyzing species recorded in neighbouring countries) | Total no. of recorded species poorly comparable |
| Taxonomic stability | Ca. 5% recorded species taxonomically unresolved; up to 10% further additions as currently undescribed lineages | Previous checklists cannot be used for direct comparisons |
| Documentation quality of source data | All collections in public fungaria; 3% with publicly accessible DNA bar-codes (incl. vouchers of most taxa). > 95% observations geo-tagged and in public databases; however, samples from ecological studies largely identified based on observations. | All species can be re-assessed from original material, but not all individuals (especially of common taxa). |
| Presentation quality | References to remarkable specimens and datasets presented. Difficult specimens analyzed for phylogenetic relationships. Taxonomic and ecological data linked. | Undescribed species can be followed in the material. |
| Differences between subsequent checklists | Within 15 yrs., 15% increase in the no. of valid species, mostly due to adding ecological sampling designs. | Different bias in historical [2] and current data (numbers of records cannot be simply corrected for sampling intensity) |
| Geographic coverage | Western part of the country poorly studied using ecological sampling designs. | Frequencies underestimated: taxa with western distributions. |
| Ecological representativeness | Important understudied habitats: naturally disturbed areas, riverine woodlands, oak stands, and wooded grasslands with ancient trees [3–4]; also gardens and buildings | Frequencies underestimated: taxa inhabiting semi-open natural or cultural landscapes. |
| Species detectability bias | Apparent in casual collections [5]; reduced in the main ecological sampling scheme used [6]. | Difficult-to-detect species poorly represented in ecosystems with casual collection data only. |
| e-DNA data | Not included. Extensive sequencing of soil fungi and some studies of wood samples have not revealed new species, but would probably reveal wider ecological niches of many taxa [3, 7]. | Frequencies and ecological niches underestimated, specifically in mycorrhizal species. |

References: [1] Chao 1987; [2] Parmasto 2004; [3] Runnel & Lõhmus 2017, [4] Lõhmus et al. 2018b, [5] Lõhmus 2009; [6] Lõhmus et al. 2018a; [7] Ovaskainen et al. 2013
(i.e., up to 10 losses and a comparable number of gains). The losses comprise six species officially listed as Regionally Extinct (see above) and probably a few others not encountered for decades (Aurantiporus priscus – since 1980, Xanthoporus syringae – since 1998) or unknown to have formed actual population in Estonia (Ganoderma carnosum – a record in 1975, Antrodiaella parasitica – in 1995, Perenniporia tenuis – in 2004). All extirpated species were very rare by the twentieth century. Most reliable gains are among well-established conspicuous species with habitats or locations frequently visited. Such recent novelties include at least three southern species (Coltricia cinnamomea and Inonotus ulmicolà first discovered in 2002, and Trametopsis cervina – 2015), three species with eastern distributions (Ceriporia tarda – 2004, Pycnoporellus alboluteus and Junghuhnia autumnale – 2010) and Postia auricoma (2013). Less conspicuous newcomer candidates include Skeletocutis jelicii (4 locations since 2015), Hyphodontia latitans (a single record in 1992, then 11 records since 2012) and Gelatoporia subvermispora (a single record in 1991, then 12 records since 2006). Trametes gibbosa (a southern species) may also have recently formed a true population (three locations since 2005) after a single, possibly occasional record in 1954.

Secondly, while species turnover refers to expansions and contractions of biogeographic ranges (perhaps related to climate change; cf. Musters & van Bodegom 2018), other strong trends of extant Estonian polypores suggest ecological mechanisms. Thus, no clear declines are apparent in species inhabiting common deciduous trees, including no support to Parmasto’s (2004) notes of decline in Pycnoporus cinnabarinus and Trichaptum biforme. There are some obvious increases instead, such as possibly climate-supported trends in southern species Hyphodontia flavipora (see also Heilmann-Clausen & Boddy 2008), H. radula and Dichomitus campestris – all formerly been considered very rare (Parmasto 2004). Increases in record numbers of less conspicuous species in similar habitats (e.g., Antrodiaella romellii and Ceriporia reticulata) are rather caused by better sampling. Assuming that increased records of most inconspicuous annual polypores on strongly decayed wood follow survey effort as well, the 1–2 similar species with reductions in records may indicate actual population declines – Poromyces mucidus and, perhaps, Anomoporia bombycina.

In conifer-inhabiting polypores, three ecological tendencies can be distinguished. Some management-sensitive species that inhabit fallen Picea abies trunks have increased, probably due to efforts to protect old forests. The case of Amylocystis lapponica is well documented (Runnel et al. 2020); other rare species with similar record patterns are Antrodia piceata and Antrodiaella citrinella; and among more frequent species – Fomitopsis rosea, Junghuhnia collabens, and Postia undosa. Contrasting patterns, probably revealing population declines, are apparent in Onnia leporina, Climacotrys borealis and Skeletocutis stellae. Our data also support the decline of Gloeophyllum abietinum already noted by Parmasto (2004). We hypothesize that these species may be suffering from reduction of certain wood qualities, perhaps slowly grown trees (note that O. leporina and C. borealis often inhabit Picea abies snags). Finally, we notice increases in two formerly uncommon Pinus-inhabiting species that are now widespread in various forests, including extensive drained forests on former wooded mires – Junghuhnia luteoalba and Skeletocutis papyraceae.

**Broad-scale ecological patterns**

Ecological case studies have been crucial for quantifying local variation in populations and assemblages, e.g. revealing their impoverishment by intensive forest management and the loss of natural forest (e.g., Penttilä et al. 2006, Junninen & Komonen 2011; for Estonia, see Lõhmus 2011, Runnel & Lõhmus 2017). Our review places those findings in the context of species pools, showing eventual extirpation of some species, but also some partial recoveries in protected forests and parallel, possibly climate-driven, shifts in distribution ranges (see above). Simultaneously, the taxonomic revisions clarify confusing reports of some putative old-forest indicator species inhabiting wider forest environments in Estonia. We now know that these represent distinct taxa (such as Antrodia crotacea instead of A. crassa, and Postia roemelli instead of P. sericeomollis; cf. Runnel et al. 2014 and Runnel & Lõhmus 2017), multiple species/lineages (such as among “Hapalopus salmonicolor”, Sidera vulgaris coll., and Physisporinus vitreus coll.) or misidentification (Postia lateritia). Based on our review, ca. half of the species listed 20 years ago as old-forest (‘hemerophbic’) polypores in Estonia (Trass et al., 1999) should probably be replaced or removed from that list to keep its focus.

Our analyses of species pools indicated that, under natural conditions, polypore assemblages would mostly vary along soil conditions and dominant forest trees. This parallels with findings on soil fungi (Tedersoo et al. 2020) and implies that forestry practices that change those factors, such as draining and artificial regeneration, are likely to be highly influential to all fungi. Distinct polypore biota on calcareous soils (alvar forests) was not known before; this finding is significant because alvar forests have been heavily degraded due to historical logging and agricultural use, and they regenerate slowly after being disturbed (Laasimer 1965). Even protected alvar forests have sometimes been mismanaged by removing dead wood, which is also essential for rare bryophytes (Meier & Paal 2009).
A pattern that soil fertility can create more assemblage variation than soil moisture is not directly applicable because our analysis separated their indirect effects via tree species composition. Both effects together explain why our ordination result (Fig. 2) resembles a Cajanderian organization of forest types solely based on soil characteristics (Lõhmus 1984). At a closer look, the pattern that polypore assemblages in drained peatland forests are more similar to meso-eutrophic forests on mineral soils than to other peatland forests has not been supported for several other organism groups – draining instead appears to produce novel assemblages (Remm et al. 2013). We also acknowledge that our approach to tree species effects was simplified (three categories analysed), and future studies should better address tree-species mixtures that are typical of hemiboreal forests (see also Tedersoo et al. 2016).

The importance of soil conditions highlights a necessity to better survey soil-inhabiting polypores. Our basidiome-based datasets suggested their higher diversity in poorer site conditions that might indicate stricter resource limitation and ecological advantages for mycorrhizal life-style in poor ecosystems. In general, however, polypores are rare and unlikely at key functional positions in mycorrhizal assemblages in Estonia (e.g., Tedersoo et al. 2006, 2020; Bahram et al. 2011); a possible exception is *Coltricia perennis* – a dominant colonizer of early-successional *Pinus* sites (Visser 1995, Kwaśna et al. 2019). Summarizing the work done on DNA-based soil sampling could also improve our understanding of the ecology and conservation status of several species.

Regarding substrates, we found that the species having parasitic or brown-rot decay life strategies tend to be restricted to fewer host-tree species. This is probably linked with trade-offs of these life strategies, of which better understood are the highly demanding growth conditions inside live trees that require specific stress-tolerant traits in parasites (Schwarze et al. 2013). Brown-rot fungi may have distinct physiological limitations, indicated also by their typical disability to degrade pure cellulose (Nilsson & Ginns 1979) or possibly lower wood pH optima (Highley 1976). However, these differences are in need of revision since the dichotomy of white- and brown-rot fungi has been challenged based on genetic data (Riley et al. 2014). Physiological limitations set by wood chemistry and structure and tree defence mechanisms probably explain also our finding that phylogenetically closer tree species tend to host more similar pools of polypore species. Some ecological confounding effects are possible (i.e., related tree species may also grow in similar sites) but not very likely, given our result of the similarity of polypore assemblages in the hydrologically contrasting dry boreal and bog sites (both dominated by *Pinus sylvestris*).

Comparison of species pools on different woody substrates reveals an unexpected issue with natural stand regeneration – a sustainability indicator in forestry (Forest Europe, 2015). In the Estonian clear-cutting based forestry, natural regeneration on fertile sites mostly comprises *Betula, Alnus*, and *Populus* species, which cluster together by polypore assemblages (Fig. 5). Planting *Picea abies* may diversify this situation if the stands are allowed to develop into mixed stands with coarse woody debris present (Lõhmus 2011), while the third cluster of broad-leaved trees would still be absent. Given also that *Picea abies* hosts the most diverse polypore assemblages overall (Table 4), of which large part inhabits old stands (Runnel & Lõhmus 2017), there is clear conservation motivation to use silvicultural alternatives that better account for substrate diversity (see also Lõhmus et al. 2018b). We also noticed that *Fraxinus* and *Ulmus*, both currently suffering from dieback due to introduced pathogens in Europe (Brasier 1991, Pautasso et al. 2013), have only moderately distinct assemblages when the remaining native tree diversity is present (Fig. 5). Thus, these specific dieback episodes are not likely to have strong negative impact on polypore biota in Estonia.

**A perspective**

Our broad question was whether, in the case of fungi, critically appraised checklists might provide standard input to global biodiversity indicators, and whether polypores could constitute a fungal group to be included. Looking at the insights obtained in Estonia, we consider this a promising direction, which depends on standardizing checklist quality, attaining a representative sample of checklists from different parts of the world, and including ecological data. Among potential values of such a scheme would be inclusion of many rare species and utilizing historical information. The possibility for a retrospective might even be a criterion for including fungal groups (e.g., epiphytic lichens; Ellis et al. 2011). However, it is unlikely that current monitoring and retrospectives can use similar methods, which again points at checklists as a common platform. We thus encourage new regional syntheses on polypores and other long-studied fungal groups.

**CONCLUSION**

Our review demonstrates how integrating multiple data sources and their taxonomic and ecological appraisal can provide new perspectives on fungal species pools, rare and undescribed species, and their long-term dynamics. The test case, the Estonian polypore biota, comprises over 260 species, of which 221 are verified extant species, and the remaining are molecularly documented but yet-undescribed lineages or species probably present but remaining to be found. During the last 100 years, the biota experienced ca. 3–5% species turnover, including
Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s43008-020-00050-y.

Additional file 1. Estonian forest types, their main characteristics, and treatment in the polypore habitat analyses.

Additional file 2. The 2-ha plots of systematic polypore surveys in Estonia, their woodland type classifications and references to publications that used the survey results.

Additional file 3. Collection details, UNITE or GenBank accession numbers for ITS and LSU sequences of Estonian specimens analyzed in this study.

Additional file 4. Specimen vouchers, geographic location, and UNITE or GenBank accession numbers for public reference sequences (ITS and LSU) used in phylogenetic trees.

Additional file 5. Taxonomic notes and phylogenetic trees of difficult species.

Additional file 6. Non-metric multidimensional scaling (NMDS) ordination diagrams of polypore assemblages: (A) in forests on fertile and poor (excl. calcareous) soils and thin calcareous soils; (B) in woodlands with Picea and Pinus (including their mixedwood) or dominated by deciduous trees.

Additional file 7. Numbers of common and unique species for habitat combinations not shown on Euler diagrams (Fig. 3).

Additional file 8. Nutritional-mode categorization of wood-inhabiting polypore species with >10 records in Estonia (input data for Fig. 4).

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Adherence to national and international regulations

Not applicable.

Authors’ contributions

KR and AL planned the study, collected and interpreted the data, and drafted the manuscript. KR identified the collected fungal specimens and analysed the data. OM provided additional data on the “Difficult species” section, participated in writing of this section and reviewed the whole manuscript draft. All authors read and approved the final manuscript.

Abbreviations

DNA: Deoxyribonucleic acid; rDNA: Ribosomal ribonucleic acid; ITS: Internal transcribed spacer; LSU: Large subunit; MRPP: Multi-response permutation procedures; NMDS: Non-metric multidimensional scaling

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Availability of data and materials

The datasets generated and/or analysed during the current study are available in the PlutoF repository: https://plutof.ut.ee/#/doi/10.15156/BIO/786358 https://plutof.ut.ee/#/doi/10.15156/BIO/786363

Ethics approval and consent to participate

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Competing interests

The authors declare that they have no competing interests.

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