

Recovery of the Critically Endangered bracket fungus *Amylocystis lapponica* in the Estonian network of strictly protected forests

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Abstract In regions where primeval forests have vanished it is unclear whether forest protection can sustain specialized old-forest biota, and over what time scale. We report on population expansion of an old-growth specific fungus of European conservation concern, *Amylocystis lapponica*, in the forest reserve network of Estonia. This conspicuous species was known for 40 years from only single records in one old-growth forest and was categorized nationally as Critically Endangered. During the last 10 years *A. lapponica* has expanded over the eastern half of the country, with nine subpopulations, in 12 localities, now known, all in long-protected old-growth forests and several > 50 km apart. In most of the new localities historical absence of the species can be reliably assessed based on earlier surveys. The historical remnant subpopulation has also increased. The population size (c. 100 mature individuals) in Estonia indicates the species should be recategorized nationally as Endangered. This success story suggests that more than 50 years of non-intervention may be needed even in large old-forest reserves for old-growth specialist species to recover.

Keywords *Amylocystis lapponica*, bracket fungus, forest, fungal conservation, old growth, *Picea abies*, refuge population, succession

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In many developed countries a major conservation challenge is to sustain old-forest biota despite historical loss of natural forests. Most European countries retain < 1% of their primary forest (Sabatini et al., 2018) and reserves already cover > 12% of current forest area (Forest Europe, 2015). In degraded forests many old-forest specialist species may not be viable and will be extirpated unless their habitat is restored (Hanski, 2000). The global Aichi Biodiversity

Targets (Convention on Biological Diversity, 2010) provide political support to improve this situation by further expanding reserve networks, restoring degraded ecosystems, and preventing species extinctions. However, the targets do not specify how to combine conservation options in practice (e.g. Jørgensen, 2013; Venter et al., 2014).

A central management problem in historically degraded, but now protected forests is that old-growth qualities develop slowly, and the prospects for old-forest biota depend on unpredictable colonization and extirpation processes. In most countries protected forest networks have existed for only a few decades and thus have limited structural recovery (e.g. Meyer & Schmidt, 2011; Paillet et al., 2015; Bujoczek et al., 2018). There is some evidence of broad-scale recovery of species with moderate old-forest associations within a few decades of the protection of secondary forests (e.g. Vandekerckhove et al., 2012; Deinet et al., 2013; Romero et al., 2013), but such recoveries depend on species' life history traits, location of source populations, and dispersal capabilities (Sverdrup-Thygeson et al., 2014). Non-intervention management has also enabled a disturbance-phase specialist fungus to spread across large naturally disturbed areas (Bässler & Müller, 2010). However, for the most demanding old-forest species broad-scale recoveries attributable to reserve network initiatives have not been described.

Here, we report on population expansion of an old-growth specific fungus *Amylocystis lapponica* (Agaricomycetes, Polyporales, Polyporaceae) in the forest reserve network of Estonia. Although its preliminary global Red List status is Least Concern (IUCN, 2018), in Europe it is one of the 33 threatened fungi recommended for listing in the Bern Convention (Dahlberg & Croneborg, 2003). In the last 30 years this species has been recorded in eight European countries, with the majority of the population in the boreal zone. Outside the boreal zone, this species is only present in a few refugia in the best-preserved Central European primeval forests (Holec & Kučera, 2007). In Estonia (the hemiboreal zone) *A. lapponica* was known for 40 years from a single old-growth patch (Parmasto, 2004), has been categorized as Critically Endangered since 1998, when first assessed (Lilleleht, 1998; Lõhmus et al., 2018b), and is legally protected.

Forests currently cover 51% of Estonia's 45,228 km² land area but old natural stands cover only 1% (< 500 km²), over half of which is in reserves (Raudsaar et al., 2018). Before significant spread of agriculture, c. 3000 BCE, forest cover was

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probably at least 85%; spruce forests are a major ecosystem of the east and south (Laasimer, 1965). At least 21% of land has remained long-term forest (although repeatedly logged), and other forests are either 20th century reforestations (various types of agricultural lands) or new forests on drained wetlands.

In the second half of the 20th century most Estonian forests were managed with a medium-intensity semi-natural approach, which maintained tree species diversity and relatively high volumes of dead wood. As a consequence, many generalist old-forest species could inhabit production forests (e.g. Lõhmus et al., 2016; Runnel & Lõhmus, 2017). Nevertheless, several highly specialized species, including *A. lapponica* and other fungi of spruce-dominated forests, remain highly threatened in protected old-forests or have already become regionally extinct (Runnel & Lõhmus, 2017; Lõhmus et al., 2018b).

The Estonian network of strictly protected forests developed slowly from 1924 until the 1990s, without central planning (Tuvi et al., 2011). Later focused developments include designation of Natura 2000 sites of European importance and, nationally, targeting minimum areas for old-growth forest species in each forest type (Lõhmus et al., 2004). The area of strictly protected forests increased from c. 3% of forest land in the early 1990s to 6% in 2001 and 13% by 2018 (Lõhmus et al., 2004; Raudsaar et al., 2018). However, reflecting general forest history, few of the strictly protected sites include any primeval forest and > 50% of their total area will still be < 100 years old by 2030 (Lõhmus, 2016). Recently intensified timber harvesting has fragmented the landscapes and isolated the strictly protected sites (Forest Europe, 2015; Lõhmus, 2016).

The *A. lapponica* material we analysed is based on fruit-body records from three main sources, and survey histories in these localities to evaluate historical absences (Supplementary Material 1). (1) All casual collections of Estonian polypores are documented in public database Plutof (Abarenkov et al., 2010). Polypores have been well surveyed since the 1950s in Estonian forests, with emphasis on old forests and rare species. Parmasto (2004) published all material up to 2004 (> 13,000 records), mostly collected by professional mycologists. Later data include increasing contributions from amateur mycologists, national monitoring activities, and results of fungal surveys in several protected forest areas. (2) Over 20,000 polypore records originate from c. 180 systematic stand-scale surveys during 2005–2018, representing the main forest types and stages of forest age and naturalness. The survey method detects local species pools and also documents species absences (Lõhmus et al., 2018a). This dataset has been instrumental in assessing the national conservation status of polypores (Runnel & Lõhmus, 2017; Lõhmus et al., 2018b). (3) *A. lapponica* is the most strictly protected (Category I) species under the national Nature Conservation Act, and its confirmed and

potential localities have been monitored by IS during 2008–2018. The fruit bodies of *A. lapponica* are easily detectable when mature and fresh (Lõhmus, 2009), but parts of juvenile or old fruit bodies that could not be reliably identified have been collected for microscopy. Substrate descriptions of the records were made on-site, but stand characteristics are reported according to the National Forest Registry (based on geographical coordinates of the records).

The synthesis of these datasets reveals a recent expansion of *A. lapponica* from a single forest reserve to other long-protected parts of the national network of protected forests. Its fruit bodies were first discovered in eastern Estonia in 1969, in a 19-ha old-growth patch, protected since 1924 (the first Estonian forest reserve) and surveyed by mycologists since the 1930s. Despite frequent visits to this reserve, the species was re-recorded on a single trunk only in 1991, 2001, 2006 and 2008. The findings became annual from 2010 (three records), and with 10 records in 2018, the species had spread over most of the reserve.

During 2011–2018 there were a total of 53 additional records. The number of known subpopulations (here defined as localities separated by > 5 km) expanded to nine (Fig. 1); these include 12 separate localities (contiguous forest areas with records typically < 1 km and no more than 3 km apart). In 2011 two records were made in Muraka nature reserve (north-eastern Estonia), which is probably the largest surviving primeval spruce forest in the country (officially protected since 1959; surveyed by mycologists since the 1960s). In 2016 another locality 2.8 km away and another subpopulation 7 km away were discovered. In 2017, two new subpopulations were found elsewhere in Estonia: in Alam-Pedja Nature Reserve in east-central Estonia (de facto protected since 1948 when it became a Soviet military area) and in old-growth stands in Karula National Park, southern Estonia (officially protected since 1979). There were a total of 22 records in 2018, all in long-protected forests and most in previously surveyed areas (Supplementary Material 1). These records included four additional subpopulations, all to the west of previously known records, and thus the species' known western range in Estonia has shifted from 27°E in 2011 to 25°E in 2018.

All fruit bodies were found on medium to well-decayed downed Norway spruce *Picea abies* trunks (diameter at breast height 28–61 cm). The 34 forest stands inhabited were either mesic to eutrophic highly productive stands on mineral soil (25 stands; site types ranging from *Oxalis-Rhodococcum* to *Aegopodium*) or old drained peatland forests (9 stands). Their common feature was a developed old-growth structure, with variable coverage of spruce in the overstorey (5–86%). Six stands had a dominant tree layer < 100 years old; this was a result of natural succession after historical disturbance or natural replacement of old-growth spruce forest with nemoral broad-leaved trees.

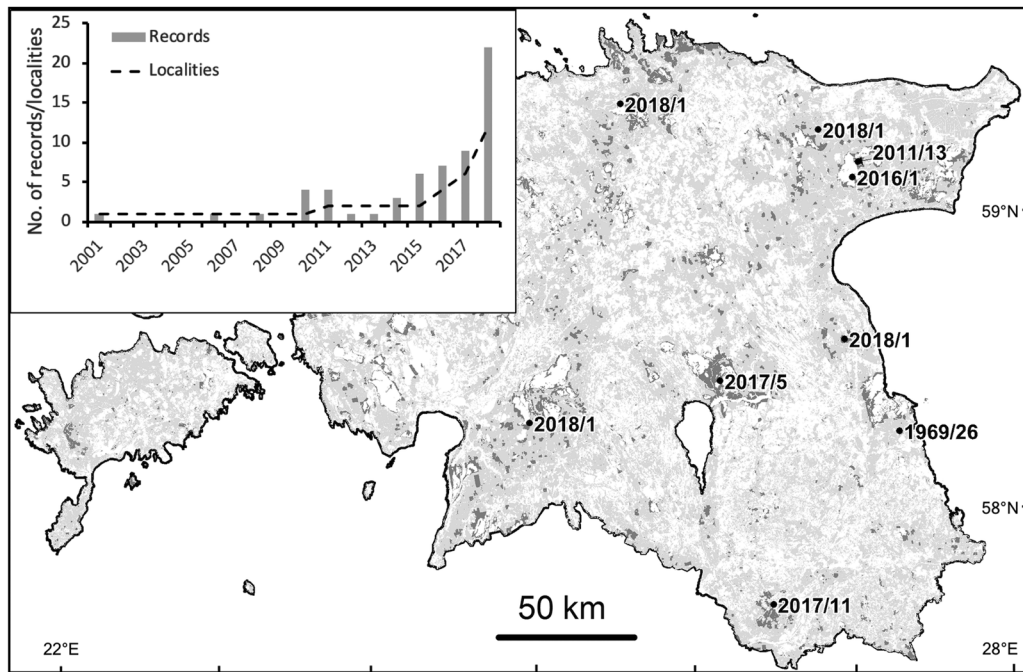


FIG. 1 Distribution of *Amylocystis lapponica* subpopulations in Estonia (discovery year/total no. of records). Light grey indicates forests, dark grey indicates strictly protected forests. The graph shows the annual number of records and cumulative no. of known localities, 2001–2018.

Based on annual maximum numbers of recent records, we estimate that *A. lapponica* currently inhabits > 50 spruce trunks in the 12 known Estonian localities, with c. 100 mature individuals (Dahlberg & Mueller, 2011). It should thus be categorized nationally as Endangered under criterion D, based on population size (IUCN, 2001). Given the adequate protection of existing localities and the population increase observed, the species has potential to improve nationally to Vulnerable (in terms of population size). However, the records also confirm the species' strict requirements for long-developed natural forest (Dahlberg & Croneborg, 2003; Holec & Kučera, 2007; Nordén et al., 2018). Such habitats have almost vanished outside strictly protected forests and the improving status of *A. lapponica* depends on a network of such forests. Given the long history of spruce-dominated old-growth ecosystems in Estonia (Reitalu et al., 2013), it is thus plausible that *A. lapponica* passed a population bottleneck in Estonia during the unprecedented forest loss of the first half of the 20th century (e.g. Meikar & Etverk, 2000). However, there are no mycological records available to attest to its status in preceding centuries.

We highlight the data quality of our assessment, which includes long-term monitoring in key locations, systematic surveys, and the availability of all historical data. Specifically, we used the significance of the species to assess absences based on site visits: iconic species are likely to be reported whenever specialists visit the sites (see also Halme et al., 2012), and documentation of all records of this species is legally required in Estonia. Frequent visits are, however, more

likely to attractive habitats (in this case old-growth forests); to confirm that such visiting bias (cf. Lõhmus & Lõhmus, 2009) did not undermine documentation of the actual distribution of *A. lapponica*, we used a separate sampling scheme representing less attractive habitats (e.g. younger forests; Runnel & Lõhmus, 2017). Despite careful synthesis of multiple data sources, only one location was known for the first 50 years of the survey history and the expansion of records was not related to parallel expansion of site visits.

The qualities of the Estonian strictly protected forest network that have supported *A. lapponica* require study. The network's extent facilitated the species' range expansion (Fig. 1) and the presence of old-growth forest was needed for formation of local populations that could act as future sources, but we cannot yet explain the historical absences of *A. lapponica* in those patches and the species' relatively rapid spread. We suggest, however, that the explanation lies in the dramatic socio-economic changes in forest management in the 1940s, which reversed forest loss (increasing landscape connectivity; cf. Penttilä et al., 2006), and reduced timber harvesting and local forest use (e.g. Tomson et al., 2015). Several localities appear to have become de facto protected during this time, even if forest reserves and the networks for strictly protected forests were only established later. Thus, habitat development for *A. lapponica* may require > 50 years of non-intervention even in old stands. The exact reasons for such long time delay, opportunities for active habitat restoration, and the role of dispersal sources are unknown. At least in north-east Estonia,

there may have been eastern cross-border colonization, but the recent accelerated spread of the species (Fig. 1) indicates an increasing role of local dispersal. Our findings indicate that, for fungi, the merits of non-intervention management regimes and large strictly protected forest networks may become evident only in the long term, and therefore research on such species requires a combination of species indicators, monitoring schemes and historical data.

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Author contributions Study design and fieldwork: KR, IS, AL; data analysis and writing: KR, AL.

Conflicts of interest None.

Ethical standards The research complies with the *Oryx* guidelines on ethical standards and was carried out following Estonian laws for handling protected species.

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