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Old-Forest Species: the Importance of Specific Substrata vs. Stand Continuity in the Case of Calicioid Fungi

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Appropriate conservation management of old-forest species depends on the causes of their old-forest affinity, which, however, are insufficiently known. Calicioid fungi are often considered old-forest dependent because of their special requirements for microhabitat, microclimate, and stand continuity for at least two tree generations. We demonstrate that, for several methodological or interpretational problems, published studies do not provide unequivocal evidence for such mechanisms and even for old-forest dependency of calicioids in general. We then analyse a large Estonian dataset (ca. 2300 records of 32 species) representing various management types and site types to answer whether old forests have more calicioid species, and any specific species, than could be expected for the substratum availability observed. Although old growth had more species and records than mature managed stands or cutover sites, those substratum types that occurred at roughly similar abundances also hosted comparable numbers of species in different management types. The characteristic substrata adding extra species to old growth were snags and root-plates of treefall mounds; wood surfaces in general comprised more than half of all calicioid records. Although substratum abundance did not fully explain the species-richness contrast between old growth and mature stands, additional evidence suggested that the unexplained variance is rather due to small-scale habitat characteristics than stand-scale continuity or microclimate. Finally, we review the evidence for old-forest affinity of calicioid species and distinguish a set of threatened species. We conclude that the availability of specific substrata is the main limiting factor for calicioid fungi in forests, and its quantitative and stochastic nature explains the large random and region-specific variation in the published lists of 'old-forest species'.

Keywords conservation, continuity, forest management, habitat, lichen, limiting factor, structural diversity

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1 Introduction

Worldwide, many forest-dwelling species are confined to stands that have long retained their main structural characteristics, notably canopy cover (Spies and Franklin 1996, Esseen et al. 1997). A high probability of finding such specific species and their communities remains the main context of recognising "(natural) old (growth) forests" even when other types of practical shortcuts are preferred (e.g. Kneeshaw and Gauthier 2003, Rouvinen and Kouki 2008). There are two main ecological causes of why species' association with old forest can emerge: slow development of their habitat (including both abiotic and biotic conditions; for example, microclimate, certain hosts or prey) or populations (via dispersal and establishment; Nordén and Appelqvist 2001). At a particular site, those causes act in concert. For example, high-quality habitats can support more individuals and, thus, promote population persistence even after dispersal from outside has ceased (Rose and Wolseley 1984), while low-quality habitats may become inhabited in case of frequent immigration (e.g. Tittler et al. 2006).

Although difficult to achieve in field studies, an explicit understanding of the causes of old-forest affinity of species is important because of distinct implications for forest management and conservation (Kouki et al. 2001, McCune et al. 2003, Fenton and Bergeron 2008). For the species primarily limited by old-forest resources, structural retention during timber harvesting and using natural mixtures of tree species for regeneration can dramatically improve the quality of managed forests (Hansen et al. 1991, Kouki et al. 2001, Lõhmus and Lõhmus 2008), while species sensitive to microclimatic fluctuations under closed canopy may only tolerate continuous-cover forestry (Hedenås and Ericson 2003, Humphrey 2005, Shields et al. 2007). For dispersal-limited populations, sustaining landscape connectivity is crucial in the long run, but very rare and threatened species may additionally need to be artificially dispersed in the short term (Lidén et al. 2004). Finally, old-forest association of a species may represent non-functional relationships; for example, when the habitat characteristics favouring certain species have, at the same time, discouraged disturbance by logging or fire (Hörnberg et al. 1998, McCune et al. 2003).

Many studies have established microhabitat development as a key factor for the distinct biota of old forests, but the role of the other factors remains uncertain. This is because dispersal limitation and dependency on microclimate are difficult to measure directly for most taxon groups, and because separating the effects of co-varying factors requires large sample sizes and/or direct manipulation of habitat features – the options rarely available for old-forest research. The few analyses explicitly considering habitat and time factors have concluded that the independent effect of time since severe disturbance on species richness is generally non-significant (Ohlson et al. 1997) or at least taxon dependent (Fenton and Bergeron 2008, Fritz et al. 2008). Still, the latter study, reporting significant time-effects on epiphytic lichens, can be criticised for including only one general habitat variable for a diverse taxon group. In such case, unexplained variance (interpreted as a support for the time effect) can arise from ignored habitat qualities (see Section 5.3). To include relevant habitat factors, and to account for taxon-dependency, studies should focus on ecologically distinct taxon groups. Additional insights could be achieved from comparisons of their old-growth affinity across regions differing in habitat distribution, macroclimate and resource use by the species. However, such systematic approaches are only emerging (e.g. Ódor et al. 2006, Carroll and Johnson 2008).

This paper is focused on calicioid fungi, which represent one of the best documented cases of old-forest associated taxa among microlichens and allied fungi (Tibell 1992, Selva 1994, 2003, Holien 1996, 1998, Bradtka et al. 2010, McMullin et al. 2010, Nascimbene et al. 2010). This "functional group" (Rikkinen 1995, Spribille et al. 2008) of morphologically and ecologically distinct, but phylogenetically diverse, ascomycetes comprises >200 species worldwide (Hawksworth et al. 1995). Typically, they have sexual reproduction mode only, tiny (<4 mm) stalked fruitbodies and/or mazaedia (structures of free spore mass). Despite a variety of life forms (lichens and saprobes on woody plants; parasites of other epiphytes), the general strategy of calicioids appears to be stress tolerant for their regular occurrence in extreme microhabitats – very dry or wet, sunlit or shady, or chemically challenging such as on acidic bark, resin or weathered wood (e.g. Hyvärinen et al. 1992, Rikkinen 2003). Accordingly, calicioid fungi form significant parts of a few relatively distinct communities, such as some described under *Calicion hyperelli*-alliance in a British classification (James et al. 1977).

In this study we have three related aims. First, we critically review published evidence of old-forest affinity of calicioid fungi. We demonstrate why this evidence is inconclusive for several methodological or interpretational problems. Secondly, we use a large original dataset from a comparative block design to describe forest management effects on individual calicioid species and on total calicioid species richness in Estonia, hemiboreal Europe. We ask whether old forests have more calicioid species, and any specific species, than expected for the observed availability of substrata. Thirdly, in the light of the original and published studies, we assess the conservation status of the Estonian species (Appendix) and discuss the general evidence of old-forest affinity and threat factors for calicioids.

2 Critical Assessment of Previous Studies

There are three types of published conclusions on old-forest affinity of calicioid fungi, which have repeatedly been cited as prominent examples of the importance of forest 'continuity' (e.g. Esseen et al. 1997, Will-Wolf et al. 2002, Mosseler et al. 2003). We argue below that most such conclusions are in fact questionable.

First, several case studies demonstrate that some *calicioid species* are most abundant in the oldest stands, interpreting this as their old-growth dependency (Holien 1998) and indicator value for stand continuity (Tibell 1992) or age (Kuusinen and Siitonen 1998). One problem with these studies is that they only compare mature and old stands (Tibell 1992, Selva 1994, Kuusinen and Siitonen 1998, Marmor et al. 2011) or only have limited data from earlier successional phases (Holien 1998). Clearly, it is premature to establish old-forest dependency without knowing whether the species could also inhabit structural legacies after stand-replacing disturbances and timber harvesting, or trees in semi-natural communities.

Another problem with simply filtering a few species from extensive species lists (using 'statistically significant' abundance differences or the average positions of species in ordination space) is the increased frequency of Type I errors. Indeed, great discordances can be discovered when exploring the species extracted in different studies (Table 1). To give just a few examples: based on his otherwise clear species-selection procedure, Tibell (1992) proposes *Chaenotheca gracilenta* as a continuity indicator, but rejects *C. brachypoda* and *C. trichialis* for Sweden. In Norway, Holien (1996) classifies both latter species as "the most typical old forest species" among calicioid lichens (both are also listed by Kuusinen and Siitonen 1998 in Finland) and *C. gracilenta* as site-type specific but "showing no correlation with forest stand age". In turn, Selva (2003) lists *C. trichialis* as 'early- to mid-successional' species, *C. gracilenta* as a 'mid-successional' and *C. brachypoda* as a 'late-successional' species. Still other sequence of old-forest affinity emerged from our study (Table 1; see below). A part of such variation may reflect geographical differences in species' ecology, notably microhabitat variation (e.g. Groner 2010), and thus the conclusions may be regionally valid (Will-Wolf et al. 2006). However, the extent of such geographical variation is unknown and it can be explicitly rejected in several cases (examples in Section 5.2). The species, for which contradictions have not become evident, tend to be extremely rare to sample or not studied ever after.

Secondly, the *sampling designs* used undermine the conclusions of some major studies. A likely geographical bias in Tibell's (1992) study has been discussed by Nordén and Appelqvist (2001). Also problematic is the study by Selva (1994) who found more calicioid species in a set of stands previously assigned as 'old-growth' than in old stands 'not previously investigated'. Selva used this as an evidence for "increasing number of species ... over time", suggesting "that the total number of Caliciales species collected at a site may, in itself be an indicator of continuity". Later, he elaborated that evidence to numerical targets of calicioid species richness in old growth (Selva

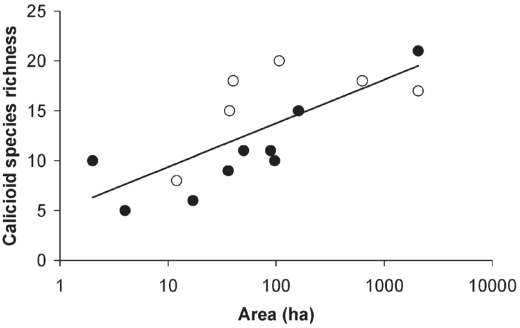

Fig. 1. Calicoid species richness in relation to study plot size in old forests of Maine, U.S.A. (drawn from the data presented for 15 plots by Selva 1994). Filled circles indicate angiosperm-dominated sites and empty circles are gymnosperm-dominated sites; the largest plot included both types and is plotted twice. The pooled relationship presented is $y = 1.9 \log(x) + 5.0$; $R^2 = 0.55$; $p_{\mathrm{slope}} = 0.001$.

2003), which McMullin et al. (2008) failed to use. While McMullin et al. (2008) doubt that their sampling was thorough enough, the actual reason may be that Selva's (1994) data were from plots of highly varying size (2–2000 ha) and that explains most of the variance in calicioid richness reported (Fig. 1). Even though Selva used roughly similar sampling efforts per site, many more specific substrata and their confined species can be found in larger areas. Thus, the contribution of forest age to calicioid species richness remains obscure and, if Selva's (2003) numerical targets can be used at all, they must be adjusted to area.

Thirdly, even where the species occurrence or community characteristics have been explicitly shown, exploration of the *causes and extent of old-growth affinity* remains obscure (see also Nordén and Appelqvist 2001, Rolstad et al. 2002). For example, Tibell (1992) provides no reasoning when he suggests microclimate, notably moisture, to be of primary importance for old-forest lichens. Regarding calicioid fungi, the main counter-argument is that different species have contrasting light and moisture requirements, including many species confined to dry and well-lit conditions of ancient trees (James et al. 1977). For example, while the species inhabiting Norway spruce prefer shade, those inhabiting Scots pine do not (Hyvärinen et al. 1992). Hence, although two studies demonstrate some negative, probably microclimate-driven, edge effects on calicioid fungi on spruce (Kruys and Jonsson 1997, Kivistö and Kuusinen 2000), this cannot be regarded a general 'microclimatic effect' on this taxon group. At best, microclimatic diversity in a stand might matter, but its role on the community has still to be demonstrated. Similarly, Selva (1994) speculates that dispersal limitation causes the stand-continuity requirements of calicioid fungi, while data rather indicate that they are relatively good dispersers (Tibell 1994, Kruys and Jonsson 1997). Some studies having actually measured environmental parameters cannot separate between intercorrelated factors because of using only univariate analyses (Holien 1996, Kuusinen and Siitonen 1998). Finally, Holien's (1996, 1998) concept of "old-growth species" should be taken with caution, because his studies in Norway spruce stands were performed in an area where the spruce had been established for < 700 years, i.e. for only 3–4 generations since the last glaciation.

3 Material and Methods

3.1 Study Area and Study Design

Our field study was carried out in mainland Estonia (Fig. 2). Block design of study plots was used to take into account the location (landscape), edaphic conditions (site type), and dominant tree species. Each of the 29 blocks represented a cluster of four plots (four management types of one site-type group) on a particular landscape, and each plot represented a different stand. For each of the five site-type groups, there were six clusters (five in swamp forests) for a grand total of 116 plots.

Four site-type groups represented the natural variation of Estonian forests along soil richness and moisture gradients (Lõhmus 1984): 1) dry boreal forests (mostly *Vaccinium* type) on higher fluvioglacial landforms and till mounds with Podzols (pH 3.5–5.0) where water rises to the soil surface only sporadically and the top layer is periodically dry; 2) meso-eutrophic forests (mostly *Oxalis* type) on till mounds or rolling plains with

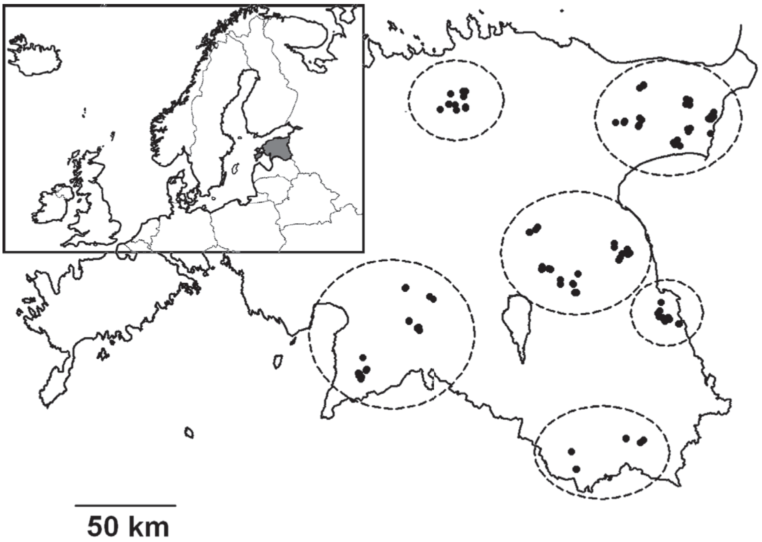

Fig. 2. Locations of the study plots (filled circles) in six regions (dashed ovals) in Estonia.

Podzols or Stagnic Luvisols (pH 3.2–4.2) where ground water is deeper than 2 m; 3) eutrophic boreo-nemoral forests (mostly *Aegopodium* type) predominantly on undulating sandy till plains with favourably moist (in springtime anaerobic) Gleyic Gambisols or Luvisols (pH 4.7–6.5) and almost no organic horizon; 4) mobile-water swamp forests on thin flooded Eutric Histosols and Fluvisols (pH 5.0–6.5) in lowlands and valleys along rivers or around bogs. Additionally, we included 5) artificially drained swamp forests (*Oxalis* type), which represent long-term drainage effects and are considered transitional from site-type group 4 to 2 (Lõhmus 1981). The stands of *Vaccinium* type were dominated by Scots pine (*Pinus sylvestris* L.), while the other types represented conifer/deciduous mixtures with Norway spruce (*Picea abies* (L.) Karst.) or (in some *Oxalis*-type stands) with Scots pine. All the main tree species in the forests have been present in mainland Estonia for more than 8000 years (Niinemets and Saarse 2009).

The four management types were: i) old growth (OG; dominant trees 100–180 years, coniferous >125 years old, stand ages up to at least 300 years, i.e. stand continuity for at least two tree generations); ii) mature (65–95 years) semi-natural commercial forests (both recently thinned and unthinned; most documented to be secondary stands of clear-cut origin); and clear-cuts (usually 3–7 years post-harvesting), iii) with, and iv) without, retention trees. Soil scarification had only been practised in some cutover plots of the *Vaccinium* type. The retention cuts (management type iii) had on average 20 m^3 ha^{-1} of live retention trees (range 2–69 m^3 ha^{-1}), which, however, produced only 3% average canopy cover (maximum 11%).

Survey stands were pre-selected from the database of the State Forest Management Centre; condition of the preselected stands was then confirmed in the field (particularly the lack of harvesting in OG stands and the abundance of retention trees in cutovers; also site type). The OG stands were those the least affected by human activity that could be found; they differed from mature stands structurally by more abundant deadwood, large live trees and regeneration, but not in terms of tree species diversity (Lõhmus and Kraut 2010). In addition to that, we attempted to control the variation potentially important for old-forest biota in various ways (see Lõhmus and Kraut 2010 for other details on the plot delineation). Terrain effects in Estonia are generally minor because of the country's flat topography but, additionally, landform differences within plot-clusters were kept at minimum and altogether only two clusters sampled were situated above 50 m a.s.l. To reduce landscape effects, the mature and cutover plots of each cluster were established as close as possible to the OG plots and each other (usually within 20 km); different site types were also studied within the same landscapes if present. Immediate edge effects were addressed by planning the plots for central parts of the stands (at least 5–10 m from adjacent stands). Rectangular areas were preferred, but in some cases landscape features led to more complex shapes. Some OG stands only covered 2 ha and were considered in full; however, no such stand had abrupt man-made edges. Also, there was no systematic difference (relevant for microclimatic effects) in the mean canopy cover of the mature stands (57%; range 39–82%) and OG (54%; range 35–74%).

3.2 Lichen Survey

We used a fixed-area fixed-effort method designed for standardised field assessment of the status of large taxon groups, notably of species distributed sparsely across large forest areas (Lõhmus and Lõhmus 2009). In each 2-ha plot a 4-h inventory of lichen-forming and lichenicolous fungi from all substrata was carried out by the same observer (P. L.). The abundance and substratum types inhabited by each species were listed, and the number of species added to the list was noted at 30 min intervals. For rare species each individual record (occurrence on one substratum entity, such as a tree trunk, a root-plate, ca 1 m^2 of ground, or a stump) was listed separately. For general purposes, a five-point frequency scale of species abundance was used based on the number of records: one record (1), 2–5 records (2), 6–15 records (3), 16–100 records (4) or more than 100 records (5). When the same tree hosted a species both on distinct bark and wood microhabitats (for example, in the case of dead trees or wounded live trees with wood exposed), 0.5 records were assigned to each microhabitat.

The 4-h time expenditure was a compromise between the reliability of the results for between-plot comparisons and logistic constraints; the inclusion of all lichens was reasonable for using the expertise and effort for wider purposes (Lõhmus and Lõhmus 2009). In most lichen-rich plots, up to 120 lichen species and 400 records could be listed during that time. Preliminary field tests indicate that at least 70% of calicioid species were discovered, while the numbers of records range from about 10% of true numbers in generalist species up to 50% in species inhabiting distinct, rare and well detectable microhabitats (Lõhmus et al., in prep.). Such estimates have independent support in case of a common specialist species, *Chaenotheca furfuracea*, whose populations were thoroughly mapped on treefall mounds after the 4-h surveys in 24 forests (Lõhmus et al. 2010b). It appeared that 87% of the 23 inhabited plots were detected and, on average, 38% of the records were made in the 4 hours.

Specimens not identifiable in the field were collected for laboratory examination. Reference materials are deposited in the lichenological herbarium of the Natural History Museum of the University of Tartu (TU). The taxonomy follows the Estonian checklist (Randlane et al. 2009), which currently includes 58 calicioid species. Considering the management-type effects and substratum-use data collected and all other data available for the rarest species, we distinguished the main threat factors and assessed the population status of the Estonian species according to the IUCN guidelines (Appendix).

3.3 Describing the Habitat

The procedure of measuring stand structure has been described in detail by Lõhmus and Kraut (2010). In brief, along four straight 50-m transect lines in each plot, we used a combination of area-based methods for estimating the densities of standing trees and treefall mounds, line-intersect methods for volumes of downed woody material, and visual point estimates (at 10% accuracy) of canopy cover at 10-m intervals. In the structurally poor dry boreal forests and cutover plots, we added 1–2 transect lines in order to increase sample sizes. All the lines were established using a standard GIS-based procedure prior to fieldwork and, for the purpose of this study, one (average) estimate for each plot is used.

In addition to site type and management type, which were parts of the study design, we selected a total of 10 variables, which, according to previous knowledge and hypotheses, might constitute crucial habitat characteristics for calicioid fungi. Five such characteristics reflected the abundance of the main substrata (no. ha^{-1} of all live trees – Kruys and Jonsson 1997; live coniferous trees – Tibell 1992, Kuusinen and Siitonen 1998; standing dead trees – Lõhmus and Lõhmus 2001; all large standing trunks – Holien 1996, Selva 2003; treefall mounds – Lõhmus et al. 2010b). For inclusion, minimum diameters at breast height were 10 cm for any trees and 40 cm for 'large' trunks; the minimum height was 30 cm for tip-up mounds of uprooted trees and 1 m for standing dead trees (hereafter: snags). Additionally, species diversity of live trees (Shannon index based on the number of trees) was included to express the availability of microhabitats, because epiphytic calicioids tend to prefer particular tree taxa depending on bark structure, acidity, shade etc. (James et al. 1977, Hyvärinen et al. 1992). *Betula* spp. and *Salix* spp. were treated at the generic level. Three variables were proxies describing microclimatic conditions, notably shade: the average canopy cover of live trees and its coefficient of variation, and the density of undergrowth (woody plants < 10 cm diameter at breast height and ≥ 0.4 m tall). Finally, we calculated the diversity of deadwood decay stages (Shannon index based on the relative volumes of items ≥ 10 cm in diameter among five decay stages; see Lõhmus and Kraut 2010 for the stages and volume calculation) to indicate habitat continuity in each plot (Stokland 2001).

3.4 Analysing Community Characteristics at the 2-ha Scale

With the main focus on management-type effects, we analysed the plot-scale species richness and community composition of calicioid fungi using four procedures: two including all four management types and two describing in detail the contrast between OG and mature stands.

Determinants of plot-scale species richness were explored with two general linear modelling approaches in STATISTICA 9.1 software. First, we used a robust approach to check for general effects of management type (a repeated measure within the 29 plot-clusters), site type (a factor variable), and their interaction. Secondly, we restricted the analysis to forests only – to explain the species richness via relevant stand-structure variables, and to check whether management type retains significance when added to such a model. Site type was omitted based on the results of the previous approach (Section 4.2); spatial autocorrelation was addressed by including 'region' as a random factor (6 regions; Fig. 2). This analysis included four steps:

1) pre-selection of potentially important habitat variables – we explored the substratum distribution of records to detect most frequently inhabited substrata and, in particular, the substrata that could contribute to the species richness of some management types where they occur most frequently. The latter was distinguished based on the knowledge on differences in substratum abundance in the same and other Estonian sites (Lõhmus et al. 2005, Lõhmus and Kraut 2010);
2) testing the relationship between habitat availability (the pre-selected substrata) and the species richness. In addition to the significance of a linear relationship, we also tested for non-linearity of the relationship by including square term of the habitat availability. Based on the results we selected the most appropriate form of the habitat availability term for the next steps;
3) exploring whether any of the remaining habitat characteristics improves the significant model of step 2;
4) testing whether management type (OG vs. mature) retains significance when sequentially (Type I sums of squares) added to the model incorporating all significant habitat variables.

We used PC-ORD 5 software (McCune and Mefford 2006) for two analyses of the distinctness of OG in terms of calicioid community composition. First, we compared the communities of OG and of mature stands within each of the five site-type groups. We used multi-response permutation procedures (MRPP) with Sørensen distance (McCune and Grace 2002) and only included the 22 species that occurred in at least 3 plots. Secondly, we calculated indicator values (Dufrêne and Legendre 1997) for individual species based on their abundance and frequency. To reduce the number of tests, the significance was established for the maximum observed value only, as compared with the mean and SD based on 1000 Monte Carlo permutations (Dufrêne and Legendre 1997). We defined ‘old-forest specific species’ as those having a significant ($p<0.05$) maximum indicator value for OG and, at the same time, indicator values for each other management type significantly smaller than the mean.

4 Results

4.1 Species Pool and General Pattern of Habitat Use

In the 116 plots, a total of 32 species of calicioid fungi were recorded: 31 species in OG, 23 spe-

Table 1. The number of records of calicioid fungi (total number of inhabited plots in parentheses) by site-type groups and management types in mainland Estonia. n – number of plots studied; for each site type×management type combination, six or (in swamp forests) five 2-ha plots were studied. Old-growth specific species (derived from an indicator species analysis) are **in bold**.

Species [a]	No. of individuals (no. of occupied plots)									
	Site-type group [b]					Management type [c]				Total
	DB n=24	ME n=24	EU n=24	SW n=20	DS n=24	Old n=29	Mature n=29	GTR n=29	Clear-cut n=29	n=116
Calicium abietinum	1(1)	2(1)		6(1)	1(1)	1(1)		1(1)	8(2)	10(4)
C. glaucellum [3,4]	69(19)	9(5)	7(5)	3(3)	23(7)	50(15)	12(7)	8(5)	41(12)	111(39)
C. parvum [2,6]	2(2)	4(4)				1(1)	4(4)	1(1)		6(6)
C. pinastri	1(1)	1(1)				1(1)	1(1)			2(2)
C. salicinum	2(2)	1(1)	1(1)	2(2)	3(2)	6(6)		2(1)	1(1)	9(8)
C. trabinellum	5(3)			1(1)	2(2)	2(2)	2(1)	2(2)	2(1)	8(6)
C. viride [4]		1(1)	1(1)			1(1)		1(1)		2(2)
Chaenotheca brachypoda [3,5]	3(3)	16(10)	22(12)	28(12)	53(8)	92(24)	25(16)	4(4)	1(1)	122(45)
C. brunneola [3,6]	13(5)	5(3)	3(3)	3(3)	2(2)	15(9)	4(3)	1(1)	6(3)	26(16)
C. chlorella [3,4,5]	2(1)	5(4)	5(4)	14(4)	10(4)	31(13)	4(3)	1(1)		36(17)
C. chrysocephala [4,6]	42(11)	90(17)	51(13)	54(12)	42(9)	168(27)	89(24)	19(8)	3(3)	279(62)
C. ferruginea [3]	127(16)	126(16)	37(10)	76(12)	42(10)	221(25)	149(25)	35(11)	3(3)	408(64)
C. furfuracea [4]	4(3)	51(12)	72(18)	83(18)	204(19)	229(24)	113(21)	51(15)	21(10)	414(70)
C. gracilenta [1,3]			1(1)	5(3)	4(2)	9(5)	1(1)			10(6)
C. gracillima				1(1)	3(3)	2(2)	1(1)		1(1)	4(4)
C. laevigata [1, 5]	1(1)					1(1)				1(1)
C. phaeocephala	4(2)					4(2)				4(2)
C. stemonea [3]	4(2)	14(9)	20(7)	7(3)	20(8)	50(20)	15(9)			65(29)
C. subroscida [2,3]	1(1)					1(1)				1(1)
C. trichialis [3,4,6]	6(3)	18(9)	15(6)	14(8)	22(9)	37(19)	35(13)	2(2)	1(1)	75(35)
C. xyloxena [6]	23(10)	27(12)	25(13)	39(13)	59(18)	59(23)	72(24)	31(12)	11(7)	173(66)
Chaenothecopsis consociata [4]			1(1)		1(1)	2(2)				2(2)
C. haematopus [1]		2(2)	3(2)	1(1)	4(3)	4(3)	6(5)			10(8)
C. nigra	1(1)					1(1)				1(1)
C. pusilla	6(4)	5(5)	6(4)	5(5)	5(5)	13(11)	8(6)	3(3)	3(3)	27(23)
C. pusiola [6]	12(8)	9(5)	5(4)	4(4)	2(2)	9(6)	15(10)	6(5)	2(2)	32(23)
C. savonica	3(2)	1(1)	12(8)	5(4)	17(9)	11(7)	17(9)	9(7)	1(1)	38(24)
C. viridireagens					1(1)		1(1)			1(1)
Microcalicium disseminatum [5,6,7]		3(2)	4(3)	5(4)	1(1)	11(8)	2(2)			13(10)
Mycocalicium subtile	96(22)	69(19)	45(16)	85(14)	90(19)	71(22)	55(20)	115(24)	144(24)	385(90)
Sclerophora peronella [2,5,6]					1(1)	1(1)				1(1)
Stenocybe pullatula	2(1)	3(3)	2(2)	2(2)	7(2)	4(4)	1(1)	5(3)	6(2)	16(10)
Total no. of records	430	462	338	443	619	1108	632	297	255	2292
Total no. of species	24	22	21	22	25	31	23	19	17	32
No. of records per plot [d]	18±16	19±13	14±11	22±11	26±21	38±15	22±8	10±7	9±8	20±15
No. of species per plot [d]	5.2±3.7	5.9±3.5	5.6±3.4	6.5±3.6	6.2±3.6	9.9±2.5	7.1±2.4	3.7±1.8	2.7±1.6	5.8±3.6

[a] Old-forest specificity of species: [1] indicator of forest continuity (Tibell 1992); [2] species probably related to forest continuity (Tibell 1992); [3] old-growth species (Holien 1998); [4] intolerant of anthropogenic disturbance (Trass et al. 1999); [5] late-successional species (Selva 2003); [6] indicator of ecological continuity in the Scottish pinewoods (Coppins and Coppins 2002); [7] indicator of old near-natural forest (Bradtka et al. 2010)

[b] Site-type groups: DB, dry boreal (mostly *Vaccinium* type); ME, meso-eutrophic (mostly *Oxalis* type); EU, eutrophic boreo-nemoral (mostly *Aegopodium* type); SW, swamp (mostly mobile-water swamp); DS, drained swamp forest

[c] Management types: old, old growth; mature, mature managed forest; GTR, cut area with solitary green trees retained; clear-cut, cut area with no trees retained

[d] Mean ± SD

Table 2. Substratum distribution of records and species of calicioid fungi among the management types. See the Appendix for species accounts.

Substratum	% of records (no. of species)				
	Old growth	Mature	Retention	Clear-cut	Total
Structure					
Live tree	36 (15)	41 (14)	16 (6)	3 (3)	31 (21)
Standing dead tree	48 (26)	41 (17)	40 (13)	26 (10)	43 (28)
Root plate	12 (9)	10 (5)	17 (5)	9 (4)	12 (12)
Fallen/felled trunk	1 (6)	3 (8)	4 (2)	5 (3)	2 (12)
Fine woody debris	<1 (3)	1 (3)	<1 (1)	<1 (1)	1 (6)
Stump	2 (10)	5 (14)	23 (12)	57 (13)	12 (19)
Surface [a)]					
Bark	48 (16)	46 (17)	26 (7)	6 (6)	40 (21)
Wood	45 (25)	47 (18)	67 (17)	89 (15)	54 (27)
No. of records	1108	632	297	255	2292

[a)] Additionally, 6% of records (7 species) on other surfaces (resin, soil, litter, thin roots etc.)

cies in mature stands, 19 species in retention-cuts and 17 species in clear-cuts (Table 1). Twelve species were confined to forests; there were no unique species in cut areas. Of the forest species, five were found in both management types, although *Calicium pinastri* and *Chaenotheca gracilenta* occurred in mature stands just once. The single record of *Chaenothecopsis viridireagens* was from a mature drained stand. Six species (*Chaenotheca laevigata*, *C. phaeocephala*, *C. subroscida*, *Chaenothecopsis consociata*, *C. nigra, Sclerophora peronella*) were only observed in OG, 1–2 times each.

Those substrata, which occurred at roughly similar abundances in different management types, also hosted comparable numbers of species, while characteristic substrata added new species (Table 2). In forests, such similar substrata comprised live trees, fine woody debris and bark surfaces in general, but OG hosted clearly more species than mature stands on snags, on root-plates of treefall mounds, and on wood surfaces in general. In cutovers, the retention of live trees and snags was reflected in slightly elevated species richness in retention cuts, while stumps and fine woody debris were similarly used in the two cutover types (Table 2). Among all records, those from snags were most abundant, and more than half of calicioid records were from wood surfaces (Table 2).

The total number of species found was surprisingly uniform among site types (Table 1; but note that the swamp type was slightly under-represented). Drained swamp sites had the largest total numbers of species and records; however, the latter was largely due to the high abundance of *Chaenotheca furfuracea*. Yet, the greatest plot-scale abundance (86 records in 4 hours, 14 species altogether) was also observed in a drained OG stand.

4.2 Species Richness at the 2-ha Scale

Up to 15 species of calicioid fungi were found in a 2-ha plot; the means varied from 3 in clear-cuts to 10 in OG (Table 1). According to repeated-measures ANOVA, the mean plot-scale species richness depended on management type ($F_{3,72}=66.5$, $p<0.001$), but not on site-type group (main effect: $F_{4,24}=1.4$, $p=0.25$; interaction with the management type: $F_{12,72}=0.7$, $p=0.78$). Among the management types, only the contrast between retention cuts and clear-cuts was non-significant (Tukey's test: $p=0.28$). Compared with OG levels within each plot-cluster ($n=29$), mature stands retained, on average, 76 ± 11% (95% CI) species, while retention cuts had 40 ± 9% and clear-cuts 30 ± 9% of the species richness of OG plots (Fig. 3; note that *Vaccinium* and *Oxalis* types as

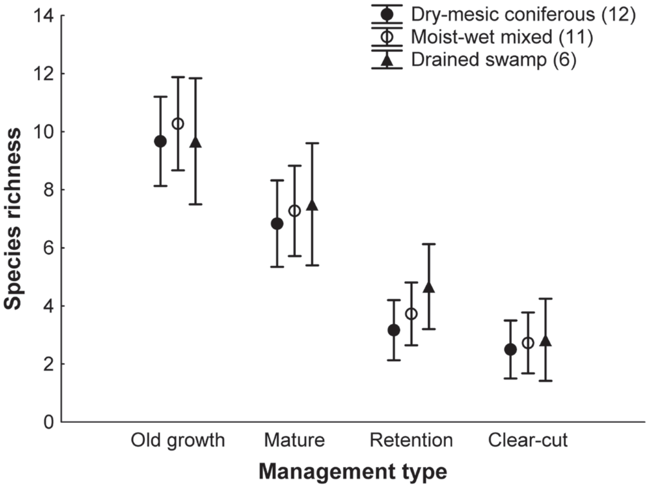

Fig. 3. Plot-scale (2-ha) mean no. of species of calicioid fungi in four management types and three broad groups of site types (total n = 116 plots). Whiskers are 95% confidence intervals; sample sizes for each management type (the number of stand clusters) are given in parentheses.

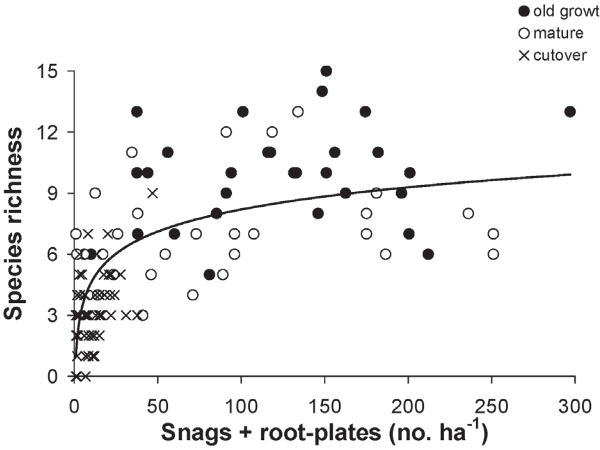

Fig. 4. Plot scale (2-ha) mean no. of species of calicioid fungi in relation to the density of their specific substrata (snags and root-plates of treefall mounds; n = 116 plots). The logarithmic relationship (line) including cutover sites is shown for illustrative purposes only (see Table 3 for detailed analyses based on forest plots).

Table 3. General linear models explaining plot-scale species richness of calicioid fungi in forests (n = 58 plots).

Model and factor [a)]	Statistics Coefficient	 *F*	 df	 *p*
(a) *Substratum model* (Type III)				
Intercept	7.158	53.1	1, 50	<0.001
Region		0.7	5, 50	0.615
‘Snags + root-plates ha^{-1}’	0.044	7.3	1, 50	0.010
(‘Snags + root-plates ha^{-1}’)^2	–0.0001	4.6	1, 50	0.037
(b) *Substratum model* (Type III)				
Intercept	0.840	108.9	1, 51	<0.001
Region		0.6	5, 51	0.682
Log$_{10}$ (‘Snags + root-plates ha^{-1}’)	0.109	7.6	1, 51	0.008
(c) *Subtratum + management type* (Type I)				
Intercept	0.844	5441.6	1, 50	<0.001
Region		0.8	5, 50	0.557
Log$_{10}$ (‘Snags + root-plates ha^{-1}’)	0.063	9.3	1, 50	0.004
Management type	0.114	12.6	1, 50	0.001

[a)] Region is a random factor (6 regions). The analysis (a) used unmodified values of species richness; analyses (b) and (c) are based on log-transformed values. ‘Management type’ consists of two categories (old growth vs. mature).

well as *Aegopodium* and swamp types have been combined for illustrative purposes).

Explanatory modelling of the calicioid species richness in forests revealed a significant relationship with the abundance of the specific OG substrata (snags, root-plates; Section 4.1). When that relationship was analysed using non-transformed values of species richness (marginally meeting the normal-distribution assumption; Kolmogorov-Smirnov test $p = 0.15$, Lilliefors test $p = 0.01$), both the linear and squared term of substratum availability appeared significant (Table 3a). This indicated that the relationship was non-linear. After exploring the distribution of the values, log-transformation was selected for the substratum variable, and we also log-transformed species richness for a better fit with normal distribution (Kolmogorov-Smirnov test $p > 0.2$, Lilliefors test $p = 0.1$; Table 3b). We found that no other habitat characteristic measured significantly improved such a model, but the OG-mature forest contrast still contributed to it (Table 3c).

Presenting a logarithmic relationship between the species richness and OG substrata for the whole set of 116 plots indicated that cutover sites generally correspond to that as well (Fig. 4). At the levels of 100 substratum items ha^{-1} (common in mature forests, but not in cutovers) roughly 80% of maximum species richness of calicioid fungi was reached, while 10 substratum items ha^{-1} (often present in cutover plots as well) still supported about 50% of the species richness (Fig. 4).

4.3 Distinctness of Communities and Species in Old Growth

The difference between the calicioid communities of OG and mature stands depended on site-type group. According to MRPP tests, that contrast was significant in dry boreal ($p = 0.027$), mesotrophic ($p = 0.008$) and drained swamp forests ($p = 0.032$), while it was not significant in eutrophic boreo-nemoral ($p = 0.25$) and swamp forests ($p = 0.15$). Based on the indicator species analysis, almost half of calicioid species differed in their abundance and frequency among management types: 13 species had significant maximum observed indicator values for OG, one (*Chaenotheca xyloxena*) for mature stands and one (*Mycocalicium subtile*) for clear-cuts. Comparisons of the maximum values with those for the other management types restricted the list of old-growth specific species to five (Table 1), of which only *Chaenotheca chlorella* had an indicator value >20 (35).

5 Discussion

5.1 Importance of Old Forests, Snags and Treefall Mounds

Our field study confirmed that old forests host more calicioid species than mature managed stands or cutover sites both at the stand scale and in total. The magnitude of the forest-management effects clearly exceeded the ca. 9% mean reduction reported for lichens in Europe (Paillet et al. 2010), while the OG-mature stand contrast was near the milder end of such contrasts for saproxylic species richness in Fennoscandia (18–75% more species in old-growth; Siitonen 2001). Because the only species present in mature stands and absent from OG (*C. viridireagens*) was represented by a single record, it is likely that old growth can host the full set of forest calicioid species.

The results also demonstrated a general significance of woody substrata for calicioid fungi, and – importantly for explaining their diversity in OG – the contributions of snags and root-plates of treefall mounds. In Estonian OG stands, those two substratum types have more than three and approximately two times higher densities than in mature managed stands, respectively, and very large snags of >50 cm diameter at breast height only occur in OG (Lõhmus and Kraut 2010). The importance of decorticate snags for lichen diversity in general (e.g. Humphrey et al. 2002, McMullin et al. 2010) and for calicioid species in particular is well known (Holien 1996, Lõhmus and Lõhmus 2001), but root-plates have been recognised as valuable lichen habitat only recently (Lõhmus et al. 2010b). Although root-plates hosted fewer calicioid species than some other substrata (Table 2), they contributed distinct taxa. Two rare species, *Chaenothecopsis nigra* and *Microcalicium arenarium*, appear to fully depend on root-plates in Estonia; these are also important for the Vulnerable *Chaenotheca gracilenta* (Appendix).

The remarkably high frequency of obligate wood-dwellers among calicioid fungi (Spribille et al. 2008) inspires to use them as a focal group for conservation management of other epixylic species (Lõhmus et al. 2010a). We elaborated this idea by extracting a non-linear relationship between the abundance of the two key substrata and calicioid richness. The 'threshold' values observed may seem relatively low (Fig. 4); however we remind that the stand descriptions only included large snags (≥10 cm diameter at breast height), which form ca. 20% of all snags in mature and OG forests in Estonia (Lõhmus and Kraut 2010). Therefore, although habitat thresholds estimated for species richness tend to be more obscure than those for specialist species (Guénette and Villard 2004), our results are actually comparable with those estimated for dead-wood dependent woodpeckers (Lõhmus et al. 2010a). Although, for lichens, large snags are probably quality structures due to their longevity and diversity of microhabitats (Lõhmus and Lõhmus 2001), the importance of smaller snags should be explicitly studied in the future.

5.2 Controversial Evidence of Old-Forest Dependent Species

While old forests obviously provide abundant substrata for calicioid fungi and are thus species rich, it does not confirm old-forest dependency of species or the whole group. Even if crucial substrata are less abundant in forests managed for timber production, the vast area of such forests nowadays might still host the majority of calicioid populations. Remarkably, all the species exclusively found from OG in our study only inhabited 1–2 stands. That can easily result from substratum distribution among our balanced sample of management types, or from a sampling bias – as in case of *C. phaeocephala*, which mostly inhabits semi-natural habitats and even wooded buildings (Appendix, Svensson et al. 2005).

One prediction in case of strict functional dependencies of species on old forests is that such species should possess distinct habitat requirements and adaptations, for which they appear as confined to old forests consistently among studies. However, our literature review revealed much controversy (Section 2), and the case study deepened the doubts. For example, *Chaenothecopsis haematopus*, a saprobic species on Tibell's (1992) list of continuity indicators, was most frequently found in mature stands. Pykälä (2004) suggested that this taxon may include two species, of which only the one inhabiting deciduous snags is old-forest dependent (the other can rapidly colonize shaded spruce deadwood). Yet, all the records in our study were from soft deciduous wood. In our opinion, this taxon belongs to a deadwood-dependent community thriving at ages from ca. 60 to 100 years since stand initiation in naturally regenerated mixed forests, when pioneer deciduous trees extensively die giving way to shade-tolerant spruce. Since Tibell (1992) explored long-developed conifer forests only, *C. haematopus* was understandably rare. Such species are threatened by uniform planting of conifers followed by intensive thinning and clear-cutting at short rotations (e.g. Martikainen et al. 1998) rather than by the lack of true old growth. An open question is whether they could also inhabit young naturally regenerating deciduous stands at the stage of stem exclusion.

The case of *Calicium salicinum*, one of our five "old-growth specific species", demonstrates how important it is to critically interpret technical results. The six records from OG vs. none from mature stands seem at least tentative evidence of old-forest dependency, particularly as two other studies based on similar comparisons agree (Rose and Wolseley 1984, Holien 1998). Its indicator value for OG stayed significant even when cutover sites (3 records; Table 1) were included, but the picture changed when all Estonian records were listed – almost half of them came from semi-open habitats (Appendix). Using similar ordination techniques to analyse such habitats (wooded meadows) in closely located areas, Leppik and Jüriado (2008) placed *C. salicinum* among shade-loving species (typical of overgrown sites) in Estonia, while Jönsson et al. (2011) extracted it as an indicator of traditional management in Gotland. In turn, Arup et al. (2003) found it less frequently in the grazed 'outland' areas in Öland compared to woods near villages. Selva (2003) even considers it early-successional in North America. To summarize, no stand-scale preferences of *C. salicinum* can be distinguished, even where 'significant' results are based on generally appropriate statistics in individual studies.

The pervasive nature of Type I errors in multi-species studies can be further illustrated for *Calicium glaucellum* in Estonia where the country's small area makes geographical variation of species' ecology extremely unlikely. This "hemerophobic" species (Trass et al. 1999) frequently occurred in mid-aged stands in a landscape-scale case study where it, however, was the only such species consistently absent from first-generation forests (Lõhmus and Lõhmus 2008). Yet, characteristics of the species suggested its good dispersal abilities, so that "evidence for continuity" was suspected to be a random error. Indeed, almost half of the records in our study were from cutovers and one-third were from cut stumps, i.e. this wood-dwelling lichen clearly can survive in conventional clear-cutting systems (no stump harvesting).

Chaenotheca chlorella was the only species confined to old forests both according to our study and several others (Table 1). However, given all the controversies described above, we recommend explicit habitat modelling to distinguish the particular habitat qualities involved. Protecting old forests is a promising tool for this species, but it may be neither sufficient nor the only option available. For example, it is not known why *C. chlorella* appears strictly snag-inhabiting in Estonia (Appendix) and northern Fennoscandia, while South-Fennoscandian populations predominantly grow on the bark of broad-leaved trees (Tibell 1999). Species-level modelling would be also useful to clarify the requirements of parasitic calicioids, which were much rarer than their hosts (*Chaenothecopsis pusiola* and particularly *C. consociata* associated with *Chaenotheca xyloxena* and *C. chrysocephala*, respectively; see Table 1). Note that the whole parasitic genus *Sphinctrina* was absent.

5.3 Minor roles of Habitat Continuity and Microclimate

A key result of our study was that an independent enriching effect of OG on calicioid communities persisted after accounting for the abundance of two main substratum types, while other habitat variables (including indicators of stand-scale microclimate and continuity) did not contribute. A similar 'old-growth effect' has been previously found for *Chaenotheca furfuracea* on root-plates (Lõhmus et al. 2010b). Using several lines of reasoning (see also Section 5.2), we argue below that it cannot be attributed to continuity or microclimate at the stand scale, although those factors may be involved at a smaller scale. This conclusion generally concurs with several studies on cryptogams that inhabit distinct woody substrata in other well-forested areas (Ohlson et al. 1997, Groven et al. 2002, Rolstad et al. 2004, Fenton and Bergeron 2008). However, particularly the role of stand continuity may be more pronounced in regions having fragmented forest cover (e.g. Motiejunaite and Fautynowicz 2005), and the opposite also occurs – forest-age effects on bryophyte and lichen richness disappear altogether in some boreal conifer forests where paludification reduces substratum diversity during succession (Boudreault et al. 2002).

Calicioid species richness on live trees was almost similar in OG and mature stands, despite a higher number of records in OG (Table 2), and none of the five 'old-growth specific species' was a specialist on the bark of old trees (Appendix). This was unexpected because, despite slightly lower tree densities, OG contained many more old and large trees (Lõhmus and Kraut 2010). Furthermore, the importance of such trees for lichens emerges from studies separating the effects of tree age from stand age (Boudreault et al. 2000, Fritz et al. 2009, Marmor et al. 2011). The dry rough bark of old trees specifically provides habitat for many calicioids (notably the *Calicion hyperelli* association; James et al. 1977). There is some evidence that the lichens colonising older trees have larger spores (Johansson et al. 2007), which suggests a role for dispersal limitation in such 'specialisation' (assuming spore size–dispersal ability relationship; Tibell 1994). Indeed, when comparing the two main calicioid genera with green-algal symbionts, it is striking that *Calicium* species (having larger spores than *Chaenotheca* spp.) do not inhabit ephemeral substrata such as deciduous snags and upturned root-plates in Estonia (Appendix). On the other hand, bark-confined calicioids frequently inhabit open forests and semi-open habitats (Appendix), which indicates their microclimatic tolerance (Rose and Wolseley 1984, Johansson et al. 2009). Given also that natural longevity of the old-bark stage may compensate for smaller dispersal ability of its specific species, source populations for re-colonising secondary forests can probably survive on scattered trees in even heavily managed landscapes (Rose and Wolseley 1984). Hence, our "unexpected result" indicates that, while calicioid abundance on live trees indeed increases with time, the species preferring old trees are able (at least in Estonia) to colonize mature stands relatively rapidly from the surroundings (see also Lommi et al. 2010 for *Calicium parvum*). For the threatened species that inhabit the bark of hard-wooded deciduous trees and were not found, forests most obviously lack suitable host trees. For (re-)expanding their populations to forest landscapes, retention of their host tree species may be a powerful long-term tool (Rosenvald et al. 2008).

Instead of live trees, key substrata promoting calicioid species richness in OG were snags and root-plates of treefall mounds. Thus, calicioids apparently have an ability to rapidly establish on such ephemeral substrata, which may partly depend on spore dispersal by wood-inhabiting invertebrates and woodpeckers (Rikkinen 1995). Thus, dispersal limitation in such species is probably weak. Although a role of spatial connectivity has been documented in *C. furfuracea* (Lõhmus et al. 2010b), such effect was partly included in the measure of substratum abundance in our analysis (probably contributing to the non-linearity of its relationship with calicioid species richness; Fig. 4). Importantly, we found no effect of temporal deadwood continuity. Hence, dispersal limitation cannot explain the obscure 'old-growth effect' in the species-richness model (Table 3c). This is further supported by the site-type dependency of the OG-mature forest contrast in calicioid community composition – it is unlikely that dispersal limitation generally depends on site type. Although spatial connectivity may contribute again, the likely explanation is that sufficient substratum abundance develops most quickly in the nutrient-rich site types that also lacked a clear management effect on calicioids (*Aegopodium* and swamp). Indeed, the abundance and diversity of snags and root-plates is highest in mature stands of those site types (but OG-mature stand contrasts remain pronounced; Lõhmus and Kraut 2010). Further accumulation of substrata may have progressively smaller effects, given the relatively abrupt and low threshold in the effect of those substrata on species richness (Fig. 4). Note also that Holien (1996) reports the importance of fertile site types, with no obvious forest-age effects, on several calicioid species, including *C. gracilenta* and *Sclerophora coniophaea* regarded as continuity indicators by Tibell (1992).

Obviously, microclimate affects fungi and anthropogenic transformation of landscapes has modified that effect (e.g., the drying effect of agriculture on adjacent woodlands; Rose and Wolseley 1984). We doubt, however, that such changes are generally detrimental in well forested landscapes on calicioid fungi. For example, we found high species richness and abundance of calicioid fungi in artificially drained forests, which does not support the importance of long-term microclimatic stability. More generally, in areas of deciduous and mixed forests, seasonal fluctuations in light and moisture are probably more extreme than those caused by late succession. However, actual measurements are needed to solve such questions, and the possibility that conifer-forest species (notably spruce specialists) have special requirements should be studied as well. Yet, the three most shade-tolerant calicioids (*Chaenotheca furfuracea, C. gracilenta*, *C. stemonea*; Holien 1996) were not confined to spruce-dominated forests in our study (*Oxalis* and drained swamp type; Table 1). Instead, they are distinct morphologically (leprose thallus; *Stichococcus* as the algal partner) and in using a variety of substratum types in shade. *C. gracilenta* and *C. stemonea* also disappeared from cutover sites (Table 1). Hence, microclimate is an important factor for them but in closed-canopy stands it appears influential mainly in the vicinity of the substratum item (see also Rikkinen 1995). Such small-scale diversity of microclimate and microsites is likely to increase in time, as trees age (Vuidot et al. 2011) and the effects of small-scale disturbances accumulate. We suggest that this is a major process behind the unexplained ’old-growth effect’ on calicioid fungi in our study, and its quantitative and stochastic nature explains why there is so much random and region-specific variation in the lists of ’old-forest species’.

To conclude, the arena of calicioid fungus conservation does not have to (and should not) be restricted to a few old-forest reserves. Much more attention should be paid on relevant modifications of silvicultural techniques in managed forests – notably on natural regeneration, retention of live and dead trees, and windthrow management. Outside forests, the declining communities comprising *Cyphelium* spp. are very distinct for growing on man-made wooden structures (James et al. 1977, Svensson et al. 2005, Appendix) and require conservation strategies of their own.

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Total of 84 references

Appendix

Habitat use and conservation status of forest calicioid lichens and fungi in Estonia

1 Methods

Considering the management-type effects and substratum use data collected, we distinguished the main threat factors and assessed the population status of calicioid species in Estonia according to the IUCN guidelines (Standards and Petitions Working Group 2006). The framework of the assessment followed Randlane et al. (2008), including a standard interpretation of key concepts (individual; generation time) according to Hallingbäck (2007). Specific population viability analyses were unavailable; thus the assessments were based on range size, population size, and their reduction and fragmentation (criteria A–D). The taxa, which did not meet the criteria but were close to that, were included in the category Near Threatened (NT).

The set of calicioid species assessed included all forest taxa in Estonia (sensu Lõhmus 2003). All the data accumulated during the process of assessment were saved in the Information System of Estonian Lichens eSEIS (available upon request from T. Randlane). Of those data, we explicitly list all the information on the habitat-use of the species, which were represented with less than 15 records in our study. Those ca. 900 additional records (Table S1) were extracted from the lichen herbarium database of the Natural History Museum of the University of Tartu (TU), literature and unpublished data of lichen experts.

2 Results

Basic data on habitat and substratum use of 57 forest calicioid species is given in Table S1. Almost half of them (27 species) inhabit various substrata both in forests and in semi-open habitats. The other half use more specific habitats and substrata: bark of live trees or wood of snags in forests (20 species), and the coarse bark of old deciduous trees or artificial woody substrata in semiopen habitats (10 species).

According to the IUCN Red-List criteria, 19 species were classified as of Least Concern, 16 species as threatened, 14 as Near Threatened and 8 as Data Deficient (Table S1). The latter category included several rarely found parasitic or saprobic species, which may have been overlooked and do not reveal clear threats to them. This procedure revealed that the main threats are disproportionately represented among ecological groups. Despite their species richness, only four strict forest species appeared threatened (Vulnerable) and only one of them is confined to a specific old-forest substratum type (*Calicium pinastri* to old live coniferous trees). The three other forest species (*Chaenotheca gracilenta*, *C. hispidula*, *C. laevigata*) are currently rare and restricted to forest reserves, suggesting significant population reductions in the past. However, these species use a diverse array of substrata that have not been restricted to reserves to a similar extent as the species; thus, causes of their population reductions remain unknown. Most substratum-specific forest species of conservation concern were listed as Near Threatened for expected reductions in their substratum abundance in the future.

A distinct group of six threatened species (including the Endangered *Chaenotheca cinerea*, and Vulnerable *Calicium adspersum*, *Chaenothecopsis rubescens*, *C. vainioana*, *Sclerophora farinacea*, *S. peronella*) consists of bark-dwellers of hard-wooded deciduous trees (notably *Quercus robur* and *Fraxinus excelsior*). These species inhabit both forests and semi-open areas, and they have experienced significant substratum reduction in forests (Lõhmus et al. 2005, Lõhmus and Kraut 2010). The third group of threatened species (including the Critically Endangered *Cyphelium notarisii*, and Vulnerable *C. lucidum, C. sessile, Microcalicium arenarium, Sphinctrina turbinata, Thelomma ocellatum*) are known from only a few records in restricted areas, while their habitats are not clearly threatened.

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Table S1. Habitats, substrata, and conservation status of forest calicioid lichens and fungi in Estonia (sensu Lõhmus 2003).

Species		Sources[a)]	N	Habitat		Tree species[b)]	No. records according to substratum type[c)]						Red List Category (criteria)[e)]
	Bark/ **W**ood/ **O**ther			Forest	Semi-open[d)]		Live	Snag	Stump	Log	FWD	Windthrow	
Calicium abietinum	B	2,4	**27**	26		1*Bet*3*Pabi* 3*Qrob* 17*Psyl* 2con	20	6					LC
	W	1,2,4,7	**81**	38	30	3*Aglu* 3*Bet* 10*Pabi* 1*Qrob* 35*Psyl* 2con	1	46	16*	10*			
C. adspersum	B	2,8	**12**	5	6	8*Qrob* 1*Pabi* 1*Ugla* 2con	12						VU (A2c; B2ab(iii))
	W	2	**1**	1									
C. glaucellum	B	1	**2**	2		1*Aglu* 1*Psyl*	2						LC
	W	1	**109**	60	49	1*Aglu* 1*Bet* 23*Pabi* 84*Psyl*		62	35*	8	3	1	
C. parvum	B	1,2,4,12,13	**35**	34	1	2*Pabi*28 *Psyl*	31	4					NT
C. pinastri	B	1,2,13	**8**	7	1	7 *Psyl* 1con	8						VU (B2ab(iii))
C. quercinum	B	2	**7**	4	2	1*Fexc* 1*Qrob* 1*Tcor* 1*Ugla* 3dec	5	1					NT
	W	2	**16**	7	9	4*Qrob* 1*Ptre*	1	5	3	5*			
C. salicinum	B	1,2,8,13	**31**	12	19	1 *Aglu* 4*Fexc* 1*Jcom* 1*Psyl* 19*Qrob* 1*Salix* 2*Tcor* 1*Ugla*	29	1					LC
	W	1,2,7,13,11	**46**	32	13	4*Aglu* 5*Bet* 3*Fexc* 1*Malus* 7*Qrob* 7*Pabi* 7*Psyl* 2 *Ptre* 1*Salix* 1*Sauc* 1*Ulae* 1dec	2	37	1**	5*			
C. trabinellum	B	2,13	**2**	2		1*Pabi* 1*Psyl*	2						LC
	W	1,2,4,7,13	**48**	35	13	4*Aglu* 2*Bet* 6*Pabi* 17*Psyl* 3con 1dec		24	16*	3			
C. viride	B	1,2,8,11,13	**196**	81	114	2*Apla* 11*Aglu* 23*Bet* 2*Fexc* 15*Larix* 1*Malus* 36*Qrob* 64*Pabi* 13*Psyl* 1*Sauc* 3*Tcor* 2*Ugla* 17con 4dec	185	6	2	3			LC
	W	1,2	**12**	5	7	1 *Ptre* 2*Pabi* 1*Psyl*	1	3		4**			
Chaenotheca brachypoda	B	1	**18**	17	1	3*Aglu* 5*Bet* 1*Fexc* 3*Pabi* 6*Ptre*	3	14				2	LC
	W	1	**103**	99	4	3*Aglu* 44*Bet* 2*Fexc* 45*Pabi* 4*Psyl* 5*Ptre*		93	8	1*		2	
	O	1	**1**	1		1 *Pabi*						1	
C. brunneola	W	1	**26**	19	7	4*Pabi* 22*Psyl*		23	3**				NT

Species		Sources[a)]	N	Habitat		Tree species[b)]	No. records according to substratum type[c)]						Red List Category
	Bark/ **W**ood/ **O**ther			Forest	Semi-open[d)]		Live	Snag	Stump	Log	FWD	Windthrow	(criteria)[e)]
C. chlorella	B	1	**2**	2		1*Aglu* 1*Pabi*	1	1					NT
	W	1	**35**	34	1	15*Aglu* 3*Bet* 13*Pabi* 2*Psyl* 1*Ptre*	1	33		1			
C. chrysocephala	B	1	**248**	228	20	14*Aglu* 14*Bet* 188*Pabi* 27*Psyl* 5*Tcor*	211	28	4**	1	4		LC
	W	1	**32**	30	2	17*Pabi* 14*Psyl*	15	14	2*			1	
C. cinerea	B	2,12	**4**	2	2	3*Fecx* 1*Ugla*	4						EN (A2c; B2ab(iii))
C. ferruginea	B	1	**351**	318	33	2*Aglu* 58*Bet* 181*Pabi* 109*Psyl*	320	29	3**				LC
	W	1	**57**	52	5	2*Bet* 13*Pabi*41*Psyl* 1con	11	35	5*	5	2		
C. furfuracea	B	1	**175**	151	24	31*Aglu* 56*Bet* 1*Fexc* 78*Pabi* 6*Ptre* 2*Salix*	38	51	13*	1		73	LC
	W	1	**97**	81	16	20*Aglu* 39*Bet* 1*Fexc* 30*Pabi* 2 *Psyl* 4*Ptre*	4	64	14*			15	
	O	1	**143**	111	32	2*Aglu* 26*Bet* 1*Fexc* 104*Pabi* 3*Ptre*					1	142	
C.gracilenta	B	1,2	**13**	11	2	2*Bet* 7*Pabi* 3*Ptre*	4	2				7	VU (A2c)
	W	1,2	**7**	7		1*Aglu* 4*Bet* 1*Fexc*	1	6		1			
	O	1	**1**	1		1*Pabi*						1	
C. gracillima	W	1,2,10,13	**10**	8	2	2*Bet* 8*Pabi*		7	2**			1	NT
C. hispidula	B	2,13	**3**	2	1	2*Aglu* 1*Qrob*	2	1					VU (A2c; B2ab(iii))
	W	2, 4	**5**	5		1*Aglu* 1*Bet* 1*Pabi* 1*Ugla*		4					
C. laevigata	B	2	**3**	3		1*Fexc* 1*Pabi* 1*Salix*	3						VU (A2c; B2ab(iii))
	W	1,2	**3**	2	1	1*Aglu* 1*Psyl*		2	1**				
C. phaeocephala	B	2,8,12,13	**38**	5	33	2*Fexc* 32*Qrob* 2*Tcor* 1*Ulae* 1con	38						LC
	W	1,2,13	**49**	6	43	6*Psyl*		4		42*			
C. stemonea	B	1	**31**	31		6*Aglu* 3*Bet* 19*Pabi* 2*Psyl* 1*Tcor*	15	14	2				LC
	W	1	**34**	34		2*Aglu* 1*Bet* 26*Pabi* 5*Psyl*	7	26	1**				
C. subroscida	B	1,2,4,9,13	**20**	18	2	2*Fexc* 1*Larix* 17*Pabi*	20						NT

Species	**B**ark/ **W**ood/ **O**ther	Sources[a)]	N	Habitat		Tree species[b)]	No. records according to substratum type[c)]						Red List Category (criteria)[e)]
				Forest	Semi-open[d)]		Live	Snag	Stump	Log	FWD	Windthrow	
C. trichialis	B	1	**35**	34	1	3*Aglu* 4*Bet* 1*Fexc* 1*Jcom* 21*Pabi* 4*Qrob* 1*Tcor*	27	7				2	LC
	W	1	**39**	37	2	3*Aglu* 2*Bet* 26*Pabi* 8*Psyl*	18	15	4*	1		2	
	O		**1**	1		1*Pabi*						1	
C. xyloxena	B	1	**4**	4		4*Aglu*		4					LC
	W	1	**169**	127	42	26*Aglu* 54*Bet* 1*Fexc* 55*Pabi* 29*Psyl* 2*Ptre* 1*Ugla* 1con	2	137	19*	4*		7	
Chaenothecopsis consociata	B	1,2	**19**	18	1	1*Bet* 16*Pabi* 1*Pin*	15	4					NT
	W	2	**1**										
C. debilis	B	2	**1**		1	1*Fexc*	1						DD
	W	1,2	**1**		1	1*Apla*							
C. epithallina	B	2	**7**	2	5	2*Aglu* 1*Larix* 4*Qrob*	6	1					NT
C. haematopus	W	1,2,13	**36**	36		1*Aglu* 13*Bet* 3*Pabi* 1*Psyl* 12*Ptre* 1dec		32	2			2	NT
C. hospitans	B	2	**1**	1		1*Qrob*	1						DD
C. nana	B	5	**2**	2		2 *Pabi*	2						DD
C. nigra	O	1,2,10,13	**6**	6		5 *Pabi* 1*Psyl*						6	NT
C. pusilla	B	1	**5**	4	1	1*Apla* 1*Fexc* 3*Pabi*	3					2	LC
	W	1	**20**	15	5	4*Aglu* 3*Bet* 7*Pabi* 5*Psyl* 1*Ptre*		17	2**	1			
	O	1	**2**	2		2*Pabi*						2	
C. pusiola	B	1	**1**	1		1*Aglu*		1					LC
	W	1	**31**	23	8	4*Aglu* 4*Bet* 6*Pabi* 17 *Psyl*		26	5*				
C. rubescens	B	2	**5**	2	3	2*Fexc* 2*Qrob* 1*dec*	5						VU
	W	2	**3**	3		1*Bet* 1*Fexc* 1*Ptre*		3					
C. savonica	B	1	**2**	2		1*Aglu* 1*Bet*	1	1					LC
	W	1	**36**	26	10	4*Aglu* 15*Bet* 2*Fexc* 9*Pabi*5*Psyl* 1*Tcor*		29	6*			1	

Species	**B**ark/ **W**ood/ **O**ther	Sources[a)]	N	Habitat		Tree species[b)]	No. records according to substratum type[c)]						Red List Category (criteria)[e)]
				Forest	Semi-open[d)]		Live	Snag	Stump	Log	FWD	Windthrow	
C. subparoica	B	3	**1**		1	1 *Psyl* (parasitic on *Chrysothrix* sp.)							DD
C. vainioana	B	2	**8**	2	6	8 *Qrob*	8						VU (A2c; B2ab(iii))
C. viridireagens	W	2	**2**	1	1	1 *Malus* 1*Pabi*		2					DD
Cyphelium inquinans	B	2	**7**	1	6	1*Bet* 1*Larix* 1*Qrob*	7						NT
	W	2	**8**		8					7**			
C. lucidum	B	2	**1**	1		1*Psyl*	1						VU (D2)
C. notarisii	W	6	**1**		1					1**			CR (D1)
C. sessile	B	2	**7**		7	7*Qrob*	7						VU (D2)
C. tigillare	B	2	**2**		2	2*Psyl*	1	1					NT
	W	2	**6**		6	3*Psyl*	1	2		3**			
Microcalicium ahlneri	W	2	**4**	4		3*Psyl*		3	1				DD
M. arenarium	B	2,13	**4**	3		3*Pabi*1dec	1					3	VU (D2)
	O	2	**2**		2	2 sandstone							
M. disseminatum	B	1,2,8,13	**34**	31	3	2*Aglu* 18*Pabi* 2*Psyl* 4*Qrob* 3*Tcor* 2dec	27	6	1				NT
	W	1,2	**9**	9		2*Aglu* 1*Qrob* 3*Pabi* 3*Psyl*	2	6				1	
Mycocalicium subtile	W	1	**384**	126	258	19*Aglu* 46*Bet* 1*Fexc* 177*Pabi* 136 *Psyl* 2*Ptre* 2*Salix* 1*Ugla*	3	214	123*	30*	1	13	LC
	O	1	**1**		1	1*Pabi*						1	
Phaeocalicium populneum	B	2	**1**		1	1*Ptre*				1			DD
P. praecedens	B	2	**1**	1		1dec				1			DD
Sclerophora coniophaea	B	2,13	**19**	4	15	17*Qrob* 2dec	18	1					NT
S. farinacea	B	2	**6**	4	2	1*Apla*3*Fexc* 1*Qrob* 1*Ugla*	6						VU (A2c+3c; B2ab(ii,iii))

Species	**B**ark/ **W**ood/ **O**ther	Sources[a)]	N	Habitat		Tree species[b)]	No. records according to substratum type[c)]						Red List Category (criteria)[e)]
				Forest	Semi-open[d)]		Live	Snag	Stump	Log	FWD	Windthrow	
S. pallida	B	2,12,13,	**59**	14	45	1*Apla* 31*Frax* 1*Pabi* 1Pyrus 2*Ptre* 8*Que* 1*Salix*8*Ugla* 6*Ulae*	59						LC
	W	2	**1**	1		1*Ugla*		1					
S. peronella	B	2,12,13	**8**		8	1Ahip 1*Apla* 1*Fexc* 4*Ugla*1*Ulae*	8						VU (A2c; B2ab(iii))
	W	1,2	**2**	1	1	1*Bet* 1*Fexc*		1					
Sphinctrina turbinata	B	2	**3**	3			3						VU (D2)
Stenocybe pullatula	B	1	**15**	5	10	11*Aglu* 3*Ainc* 1*Tcor*	13	1		1			LC
	W	1	**1**		1	1*Aglu*					1		
Thelomma ocellatum	W	2	**5**		5				2**	3**			VU (D2)

Note: in case of sources 2–13, habitat classifications of a few records are missing; in such cases the subcategories do not sum up N.

[a)] Sources: 1 – this study; 2 – the lichen herbarium database of the Natural History Museum of the University of Tartu (TU), http://erast.ut.ee//temp/plutof2 (Accessed 1 January 2010); 3 – Ekman et al. 1989; 4 – Lõhmus and Lõhmus 2001; 5 – Randlane and Saag 2004; 6 – Areskoug and Thor 2005; 7 – Lõhmus et al. 2007; 8 – Leppik and Jüriado 2008; 9 – Jüriado et al. 2009; 10 – Lõhmus et al. 2010; 11 – Suija et al. 2010; 12 – I. Jüriado and A. Suija: unpublished data of the Estonian Science Fund project no. 5849; 13 – personal communications, October 2010: E. Leppik, P. Lõhmus, L. Marmor, M. Nõmm, A. Suija.

[b)] Tree species: Ahip – *Aesculus hippocastanum*, Aglu – *Alnus glutinosa*, Ainc – *Alnus incana*, Apla – *Acer platanoides*, Bet – *Betula* spp., Fexc – *Fraxinus excelsior*, Larix – *Larix* sp., Malus – *Malus* sp., Qrob – *Quercus robur*, Pabi – *Picea abies*, Psyl – *Pinus sylvestris*, Ptre – *Populus tremula*, Salix – *Salix* spp., Sauc – *Sorbus aucuparia*, Tcor – *Tilia cordata*, Ugla – *Ulmus glabra*, Ulae – *Ulmus laevis*, con – undetermined coniferous tree, dec – undetermined deciduous tree.

[c)] * Including man-made (sawn) substrata; ** Man-made (sawn) substrata only

[d)] In the current study findings from clear-cuts, but if all Estonian data are included, also findings in parks and woodwed meadows are considered.

[e)] According to Standards and Petitions Working Group 2006.