

Research Article

Community dynamics of lignicolous lichens on standing deadwood in a 275-year chronosequence

Aleksi Nirhamo¹✉, Pemelyn Santos¹, Mariina Günther¹, Jari Kouki¹ and Tuomas Aakala¹

School of Forest Sciences, University of Eastern Finland, Joensuu, Finland

Correspondence: Aleksi Nirhamo (aleksi.nirhamo@uef.fi)

Oikos

2026: e11835

doi: [10.1002/oik.11835](https://doi.org/10.1002/oik.11835)

Subject Editor: Sa Xiao

Editor-in-Chief:

Paulo R. Guimaraes

Accepted 20 January 2026



Dead trees provide discrete habitat patches in which patch quality changes gradually due to wood decomposition. Although in most cases these patches persist for not more than a few decades, in some ecosystems deadwood decomposition and the consequent change in habitat patch quality can be a centuries-long process, potentially leading to dynamics of deadwood-associated communities taking place over a similar time scale. We studied the dynamics of lignicolous lichen communities on snags in near-natural European boreal forests. We surveyed lichens on 331 *Pinus sylvestris* snags and obtained their year of death with dendrochronological methods. The snags comprised a chronosequence of 275 years in time since tree death. Most lichen species (86%) displayed an association with either fresh, intermediate or long-standing snags, with only few species occurring at a similar rate throughout the chronosequence. Thus, the habitat patches provided by snags were indicated to be characterized by a sequence of colonizations by and extinctions of lichen species with differing niches. Accordingly, community composition was closely connected to time since tree death. Associations with long-standing snags were most frequent (46% of species), and consequently, species richness increased with time since tree death – approximately a 2.5-fold increase from 20 to 90 years from death – but increased no further beyond 90 years since death. Several obligate lignicoles occurred only on long-standing snags indicating their dependence on this specific type of deadwood. Our findings show that time since tree death is a primary determinant of the species composition and richness of lignicolous lichens on snags. Thus, lignicolous lichen communities are intrinsically linked with snag dynamics that occur over centennial time scales in boreal forests. Lignicolous lichen diversity is dependent on long-persisting standing deadwood that typically occurs only in natural forests.

Keywords: boreal forests, epiphytic lichens, epixylic lichens, kelo trees, snag dynamics, snag longevity, succession

Introduction

Many species communities occur in habitat patches that are spatiotemporally dynamic, such that their formation and disappearance can be distinguished, and the species

in these communities must succeed in tracking these habitat patches (Thomas 1994, Snäll et al. 2003). From the perspective of a given species, habitat patches may also become unsuitable due to changes in patch quality (Amarasekare and Possingham 2001). This ‘patch-tracking metapopulation’ model, in which habitat patches are spatiotemporally dynamic and extinctions are (almost) exclusively deterministic, has been used to describe epiphytes (Snäll et al. 2003, 2005, Johansson et al. 2012) and deadwood-associated taxa (Jönsson et al. 2008, Caruso et al. 2010). Deadwood provides habitat patches that emerge from tree mortality and eventually disappear due to wood decomposition. Moreover, decomposition causes constant change in patch quality, leading to compositional change along the decomposition gradient in communities associated with deadwood (Kushnevskaya et al. 2007, Ulyshen and Hanula 2010, Fukasawa 2018, Lepinay et al. 2022, Lettenmaier et al. 2025).

There is considerable variation in the decomposition rate of deadwood (Harmon et al. 2020) and, thus, the longevity of the habitat patches they provide. In particular, decomposition rate is significantly lower in standing dead trees (i.e. snags) than fallen dead trees (Yatskov et al. 2022). Tree species and macroclimate are major factors affecting snag longevity (Oberle et al. 2018, Oettel et al. 2023, Aakala et al. 2024). Consequently, there is much variance among forest biomes in snag dynamics (Everett et al. 1999, Vanderwel et al. 2006, Aakala et al. 2008, Onodera and Tokuda 2015). In some cases, snags may remain standing for several decades or even centuries after death (Daniels et al. 1997, Everett et al. 1999, Rouvinen et al. 2002). Understanding of the dynamics of deadwood-associated communities over such long time scales has been hindered because, like many other long ecological processes, they are challenging to assess empirically.

Lignicolous epiphytes on the wood surface, consisting mostly of lichens on snags, are a distinct part of deadwood-associated biotic communities. Lignicolous communities potentially have many similarities with corticolous epiphyte communities on the bark of living trees. Chronosequence studies suggest that corticolous communities remain dynamic over the tree life span, which may be up to several centuries (Johansson et al. 2007, Fritz et al. 2008). In corticolous communities, the occurrence of a given species is often concentrated in trees of a certain age range. A common pattern is that relatively few species are associated with young trees, and a much larger number of species with old trees, leading to species replacement combined with increasing species richness as trees age (Johansson et al. 2007, Fritz et al. 2008, Nascimbene et al. 2009, Marmor et al. 2011). Such patterns of species replacement in corticolous communities have been linked to changes in bark properties as trees age, i.e. changing patch quality, which renders the tree unsuitable for species associated with young trees but produces crucial microhabitats for other species on older trees (Löbel et al. 2006, Ranius et al. 2008, Fritz et al. 2009).

Habitat patches utilized by lignicolous communities emerge with bark loss after tree death. Over time, the wood surface of snags undergoes a gradual transformation due to

abiotic weathering and biotic decomposition changing its physicochemical properties (Fukasawa 2018, Arpaci et al. 2021). Since epiphytes have differentiated niches regarding physicochemical substrate properties (Fritz et al. 2009, Zarate-García et al. 2020, Tatsumi et al. 2023), the transformation of the wood surface can be expected to induce species replacement in lignicolous communities during the persistence of the habitat patch. This would be caused by sequential colonizations and extinctions by species with differing niches. Similarly as in relation to tree age in corticolous communities, lignicolous lichen species richness has been shown to be higher on snags that have been dead for longer, but so far this has been shown only using broad categories of time since death (Santaniello et al. 2017, Nirhamo et al. 2024), providing limited information on community dynamics and the time scales over which they occur.

In this study, we examined the community dynamics of lignicolous lichens on snags using a chronosequence of 275 years in time since tree death. Our general study question was: how do lignicolous lichen communities on snags develop with increasing time since tree death? We examined patterns in taxonomic species composition and species richness. By doing this, we aimed at understanding links between deadwood dynamics and lignicolous lichen communities and their diversity by addressing the significance of snag longevity. We hypothesized that the chronosequence will be characterized by species replacement, which would be caused by changing patch quality due to the wood surface transformation and the consequent colonization–extinction dynamics among species. In addition, similarly as in corticolous communities on living trees, we expected that the species replacement sequence is combined with increasing species richness because of a larger number of species being associated with long-standing snags than fresh or intermediate ones. We were also interested in investigating whether these dynamics continue for the entire duration that snags may remain standing after death.

For these purposes, we collected presence–absence data of lignicolous lichens on 331 *Pinus sylvestris* snags in near-natural boreal forests in three regions in Finland, with individual snags representing discrete habitat patches. The habitat patches of lignicolous communities emerge at bark loss, but dating bark loss in retrospect is not possible. Instead, we used tree rings to obtain the death year of the trees and used time since death as the basis of the analyses.

Material and methods

Study sites

The data used in this study was collected from nature reserves in three landscapes in Finland: Lieksa, Kuusamo and Salamanperä (map in the Supporting information). In Lieksa, the data was collected from two reserves that were 50 km apart. In the other two landscapes, the data was collected from single reserves. The reserves range approximately 7.5–30 km² in area. The landscapes vary 0.5–4°C in mean annual temperature, 620–770 mm in annual precipitation,

and 130–280 m a.s.l. They consist of mosaics of mineral soils, peatlands and small lakes. The forests in these landscapes include spruce-dominated *Picea abies* forests or spruce-pine mixtures on mesic site types (sensu Cajander 1926) and, more commonly, pine-dominated *Pinus sylvestris* forests on sub-xeric and xeric site types. In addition, a small but varied proportion of trees consists of broadleaved species.

The study landscapes were selected for their near-natural condition. Scattered old cut stumps indicated historical selective logging that had targeted the largest tree size classes. The density of cut stumps varied within the study landscapes and were absent in some localities. Selective logging had not been performed at least since the mid-1900s. Clearcutting for commercial forestry has never been conducted in these landscapes, but parts of them have likely been historically used for slash-and-burn agriculture. Data from Salamanperä reveals a fire history typical for Fennoscandia: elevated fire frequency in the 18th and 19th centuries due to human activity, and an absence of fire since then (Tariyal et al. 2025). Fire scars in old trees indicated similar fire histories in the other study landscapes.

Study tree selection

We selected study trees in a three-step procedure. In the first step, we laid a 250 × 250 m grid over the study landscapes. Grid nodes were used as candidate plot locations. Using site type information in the forest compartment data of Metsähallitus (a national institution that governs the reserves), we aimed to cover xeric, sub-xeric and mesic sites at a similar rate, and prioritized ease of access, i.e. vicinity to roads or trails. The minimum distance between plots was 500 m. Beyond this, study plot locations were chosen randomly. In 2022, we established circular plots with a radius of 30 m (0.28 ha) in the chosen locations and mapped all dead *P. sylvestris* snags with a dbh ≥ 10 cm from the plots. We aimed at a roughly equal number of plots in each of the landscapes with 38, 41 and 37 plots eventually sampled in Salamanperä, Lieksa and Kuusamo, respectively.

After having mapped a total of 2293 standing dead *P. sylvestris* on these plots in 2022, in the second step in 2023, we selected 935 of these for determining their year of death with a stratified random selection. We aimed at sampling thirty trees in each combination of tree size class (10–19.9, 20–29.9, 30–39.9, >40 cm dbh), site type (xeric, sub-xeric, mesic) and study landscape. However, we fell short of this number in some of the combinations, particularly since there were only a few xeric plots in Salamanperä. In addition, we sampled all snags on the plots that appeared to have been dead for very long based on a hard and rough surface. This was done to make the chronosequence more comprehensive for high values of time since death, since randomized tree selection was expected to yield a small number of such snags given their relative scarcity (Rouvinen et al. 2002).

Finally, from the snags selected for determining year of death, we selected all those that had <20% bark cover on the whole tree and <50% bark cover on the lowest two meters and were at least 1.5 m in height for lichen inventories. This

included 378 snags. The final set of trees used in this study consisted of those where lichen inventory was conducted and an estimate on year of death was successfully obtained.

Obtaining the time since death of snags

We collected increment cores from the 935 trees selected with a stratified random selection using a standard 5.15 mm increment borer. In the lab, the cores were mounted and sanded with progressively finer sandpaper until tree rings were visible. Each core was photographed using the Skippy imaging system (Gärtner et al. 2024), which integrates a Sony Alpha 7R IV (α7R IV) camera body with a Sony FE 90mm F2.8 Macro G OSS (SEL90M28G) lens mounted on a motorized rail system. Multiple overlapping images were captured per core and stitched into high-resolution panoramic composites using PTGui 12.24 (New House Internet Services B.V.).

To obtain tree death dates, the tree ring series were crossdated. For this, ring widths were measured using CooRecorder ver. 9.8.1 (Larsson 2005) and crossdated statistically, using CDendro ver. 9.8.1 (Larsson 2005). We used master chronologies from the International Tree-Ring Data Bank (ITRDB) (Eronen 2002, Schweingruber 2002, Meriläinen et al. 2004). Following the successful dating of at least 20 samples per landscape, we refined the ITRDB chronologies into landscape-specific master chronologies. Statistical crossdating was further guided by the identification of marker rings (Yamaguchi 1991).

Samples were considered successfully dated when ring-width series correlated well (multiple 50-year segments with $r > 0.32$; Holmes 1983) against the master chronology. We used marker rings as additional evidence both for controlling for the statistical dating results (Yamaguchi 1991), but also as the main method for dating challenging samples, particularly when statistical alignment alone was insufficient, but marker rings were clearly visible. When the outer ring was missing or ambiguous, typically due to decay or mechanical damage, the death year was estimated using a sapwood–heartwood model to estimate the number of sapwood rings based on the heartwood ring counts (Haneca 2024, details in the Supporting information).

Year of death was successfully obtained for 331 out of the 378 snags for which a lichen inventory was conducted. From these, the last annual ring was present in 210 snags, and the death year was estimated using the sapwood–heartwood model for 121 snags. The sapwood–heartwood model was used predominantly for snags with high time since death (i.e. approximately > 100 years), in which the sapwood had partially worn out. Among the 331 successfully crossdated snags, 187 had no fire scars and seemingly had not been affected by fire, 144 had a fire scar, 51 had minor charring (meaning that the tree was impacted by at least two fires in its life span, with the first exposing the fire scar, and the second causing charring that was restricted to the previously exposed fire scar), and 14 were extensively charred (meaning that the tree had faced a fire after bark loss, causing extensive charring of the basal stem).

Lichen inventories

We recorded the occurrence (presence–absence) of all lichens (including non-lichenized calicioid fungi) on the lowest two meters of the selected trees. The inventories covered only the lowest parts of the trunk because of difficulties in accessing the upper parts. Lichens on any remnant bark were ignored. We ignored lichens on fire scars when the snag had a smooth surface, indicating a low time since death, but the surface of the wood in the fire scar was rugged, indicating long exposure. In these cases, lichen composition in the fire scar corresponded to the formation of the scar rather than time since the death of the tree. Therefore, a confounding effect caused by old fire scars was removed. Lichen specimens were collected for identification with microscopy and chemical spot tests when needed. Lichen nomenclature followed Pykälä et al. (2024). The classification of obligate lignicoles was based on Spribille et al. (2008), except for *Xylopsora friessii* and *Cladonia bacilliformis* that were not included as obligate lignicoles because they have been frequently observed on bark (Nirhamo et al. 2024).

Statistical analyses

Statistical analyses were performed in R. We assigned snag type associations for species using binomial GAM's with the presence/absence (0/1) of a given species as the response variable and a smooth of time since death as a fixed effect, and landscape as a random effect. Species were assigned as associated with fresh snags if occurrence probability decreased with time since death, with intermediate snags if occurrence probability was unimodal and the mode was at time since death < 100 years, and with long-standing snags if occurrence probability increased with time since death or was unimodal with the mode at time since death > 100 years. Lastly, species were assigned as generalists if the smooth term for time since death was statistically insignificant ($p > 0.05$), or the regression curve indicated occurrence probability to be over 25% throughout the chronosequence (Supporting information). Snag type associations were assigned for all species with 33 or more observations (i.e. recorded on minimum 10% of surveyed trees), and for species with 15–32 observations when the smooth term for time since death was statistically significant. We used GAM's to account for potential nonlinearity in the species responses to time since death. We analysed patterns in species composition with unconstrained ordination (non-metric multidimensional scaling; NMDS). NMDS was performed in three dimensions using a distance matrix based on Jaccard dissimilarity. Only snags with a minimum of five recorded species were included in the ordination.

Results

We recorded 135 lichen species including 33 obligate lignicoles from the 331 dated snags (Supporting information). Snag type associations were assigned for 63 lichen species including 19 obligate lignicoles (Fig. 1), i.e. 47% of all recorded species. Nine species were assigned as generalists, and

thus most species were associated with either fresh, intermediate or long-standing snags. The occurrence of most species was concentrated on relatively long-standing snags; 29 species were associated with long-standing snags, and for 49 out of 63 species, the median time since death of the snags with a presence was higher than the median time since death of all surveyed snags. The ratio of sexually and asexually reproducing species was similar among species associated with fresh, intermediate and long-standing snags (Supporting information). Microlichens, as opposed to macrolichens, were most prevalent among species associated with long-standing snags, and least prevalent among those associated with fresh snags. Generalist species mostly consisted of asexually reproducing macrolichens. Time since death explained, on average, 22% of variation in the presence–absence of the 63 species for which snag type associations were assigned based on R^2 values of binomial GAM's (Supporting information).

Lichen community composition on the surveyed snags was closely related to time since death as shown by its relationship with the first and second dimensions of the NMDS ordination (Fig. 2a, Supporting information; NMDS stress 0.155). Compositional change continued throughout the chronosequence. Lichen species richness increased with time since death but reached a high point at an average of 25 when time since death was 90 (Fig. 3a). Thus, compositional change from there on was due to species replacement, but ongoing species replacement also earlier in the chronosequence was evident (Fig. 1). Other explanatory variables (snag size, plot-level tree species composition, study landscape) also affected lichen communities, but the effects were much weaker than that of time since death (Supporting information). Species richness increased weakly with snag size and was slightly higher in pine-dominated plots than in spruce–pine-mixtures. The third dimension of NMDS was related to study landscape (Fig. 2b).

Eleven obligate lignicoles were associated with long-standing snags and thus were identified as specialists of those substrates (Fig. 1). The occurrence of these species reached its highest point at a time since death of about 200 years (Fig. 3b). Additionally, one, four and three obligate lignicoles were assigned as generalists, as associated with fresh snags, or intermediate snags, respectively. The species richness of obligate lignicoles increased in the early part of the chronosequence, but was almost unchanged at values of time since death higher than 50 years (Supporting information).

Discussion

Community dynamics of lignicolous lichens on snags

In accordance with our hypotheses, the 275-year chronosequence in time since tree death was characterized by a continuous replacement of species, paired with increasing species richness, which stabilized at about 90 years since tree death. The chronosequence indicated that over the time that a snag remains standing, there is continuous colonization by and extinction of lichen species within the habitat patch provided

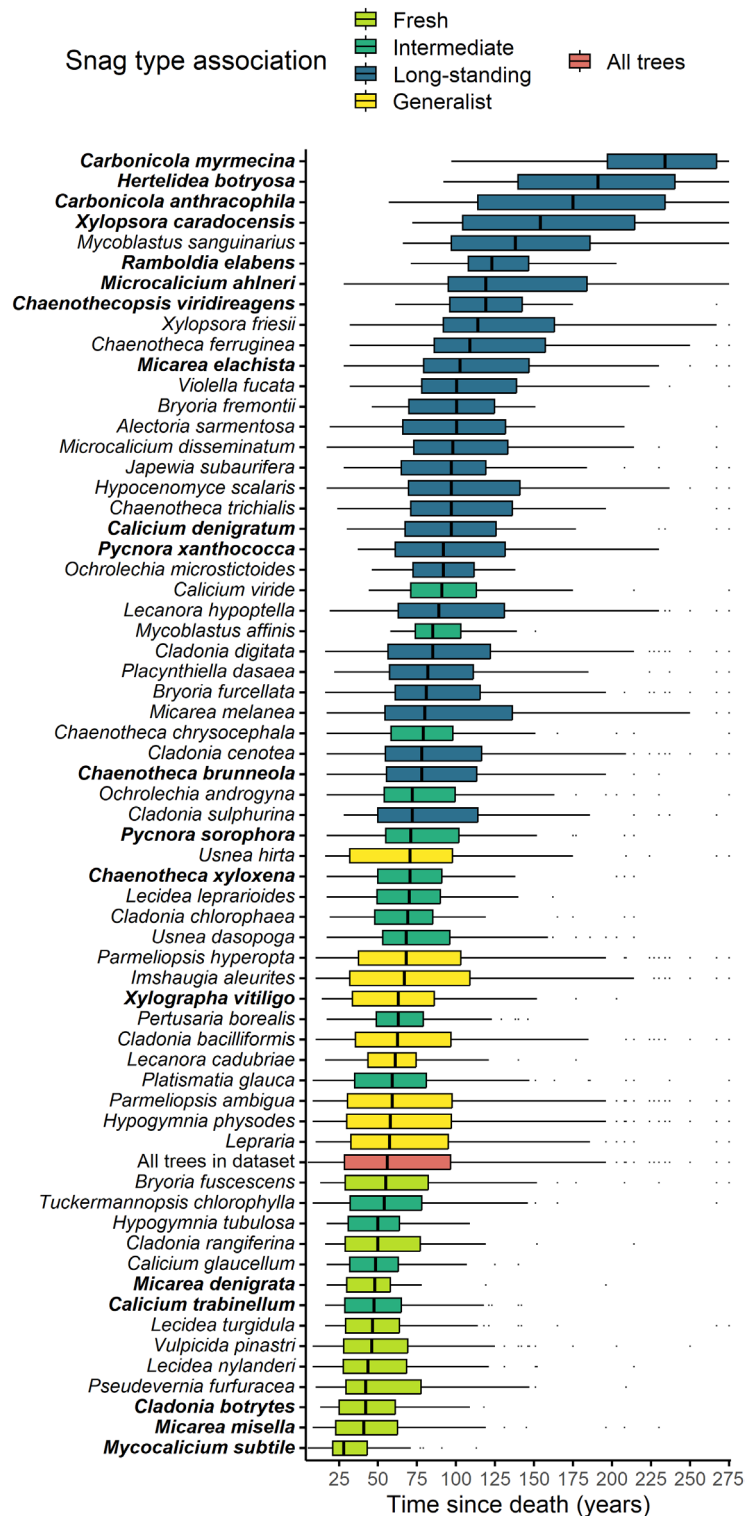


Figure 1. The time since death distribution of snags where the given lichen species was present. Species ordered by the median time since death of the snags with a presence. Includes 63 species for which snag type associations were assigned. Obligate lignicoles in boldface. “All trees in dataset” represents an almost random sample of barkless *P. sylvestris* snags in the study landscapes. Box = interquartile range, whiskers = up to 1.5 times IQR.

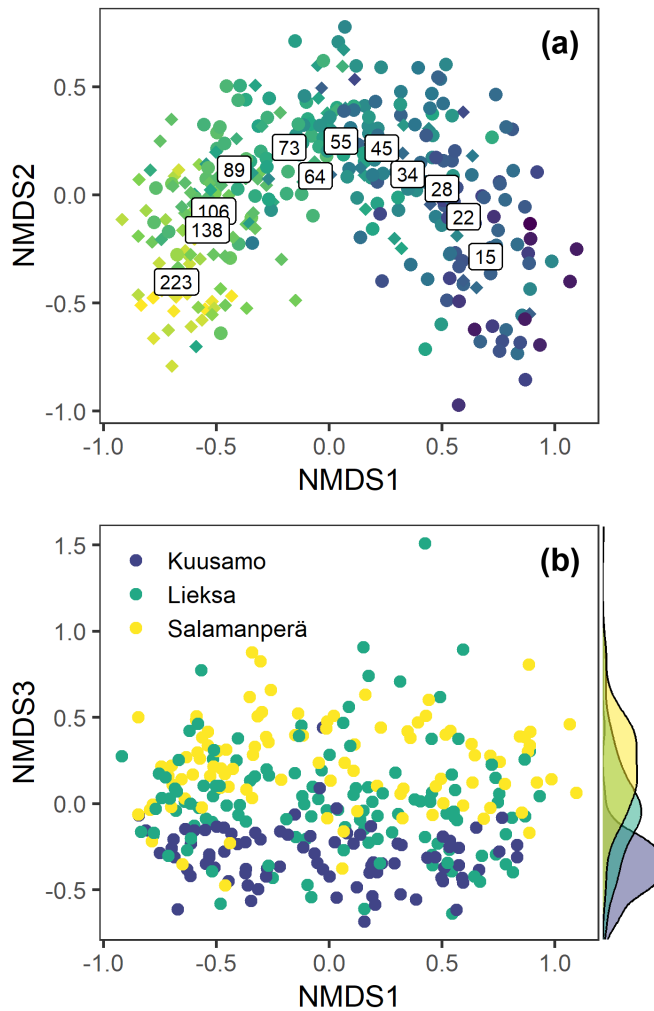


Figure 2. Three-dimensional NMDS ordination of the lignicolous lichen communities. Stress = 0.155. (a) First and second dimensions. The color of the dots is related to time since death. For visualization, the snags were ordered by time since death and divided into twelve bins of equal size. The labels indicate the mean time since death and the mean location in the ordination space of the snags in the bins. Circles denote trees for which year of death was determined from the last formed tree ring, diamonds denote trees for which the sapwood-heartwood model was used. (b) First and third dimensions, with trees in different study landscapes highlighted with coloration.

by the snag. Our assumption is that these colonization-extinction dynamics are largely driven by gradually changing patch quality resulting from the weathering and decomposition of the wood surface changing its physicochemical properties (Supporting information). Each species is able to occupy the patch during the window in which substrate properties match its niche. Aside from a few generalist species with wide niches, most species had distinguishable niches within the chronosequence, agreeing with studies showing the significance of physicochemical gradients to epiphytes (Fritz et al. 2009, Zarate-García et al. 2020, Tatsumi et al. 2023).

Studies on patch-tracking metapopulations have examined their dynamics over periods of a few years and focused

on a few model species (Snäll et al. 2005, Jönsson et al. 2008, Caruso et al. 2010, Johansson et al. 2012). Our community-level chronosequence approach indicated that the dynamics described in those studies do not concern only certain species of interest, but instead, by and large the whole community, and that they may continue for an extensive period in long-lasting, slowly changing habitat patches. Metapopulation studies on epiphytes tend to have focused on species associated with old trees and thus have concluded extinctions to be almost exclusively caused by tree fall (Snäll et al. 2005, Johansson et al. 2012). Evidently, extinctions of species associated with young snags are caused by changes in patch quality in long-standing snags and not just snag fall. When extinctions are caused by the habitat patch becoming unsuitable due to predictable processes such as wood decomposition (Jönsson et al. 2008) or changing bark properties in aging trees (Löbel et al. 2006), the extinctions should be considered deterministic, matching the concept of patch-tracking metapopulations (Snäll et al. 2003). Dead trees continue to be inhabited by lignicolous vegetation also after snag fall, but the communities developing onto fallen deadwood are very different in composition (Nirhamo et al. 2024), usually becoming dominated by bryophytes (Kushnevskaia et al. 2007). Thus, snag fall should be considered patch destruction for lignicolous communities characteristic to snags. Lastly, dispersal processes have an integral role in metapopulation theory, with colonization rates in patch-tracking metapopulations thought to be restricted by dispersal capacities of species (Snäll et al. 2003, 2005, Jönsson et al. 2008, Johansson et al. 2012). Thus, patch occupancy by a given species was most likely affected by both dispersal and patch dynamics, but we could not address the relative importance of these processes.

Chronosequence studies of corticolous lichen communities, although not explicitly applying the perspective of trees as dynamic habitat patches, have shown community patterns that have many similarities to our findings (Johansson et al. 2007, Fritz et al. 2008, Nascimbene et al. 2009, Marmor et al. 2011). This suggests that many of the patterns we describe are widespread in epiphyte communities, and that the dynamics of corticolous communities on living trees and lignicolous communities on snags can be similar. Importantly, epiphyte community dynamics may appear as different when observing entire trees versus observing only a delimited part of them (Woods 2017). We surveyed epiphytes only on the lowest part of the stem, however, the wood surface transformation is probably rather uniform across the length of the snag. If so, epiphyte community dynamics are likely to be similar throughout snags.

Since the surface transformation in snags is slow and subtle, the possibility arises that it remains a weak driver of community dynamics, and species replacement is rather due to autogenic community succession. In epiphytic lichens, it has been proposed that autogenic succession is explained by competition-colonization tradeoffs among species, and manifests as changes in trait composition (Ellis and Coppins 2006, Löbel et al. 2006, Ellis 2012). We did not observe changes in trait composition that might result

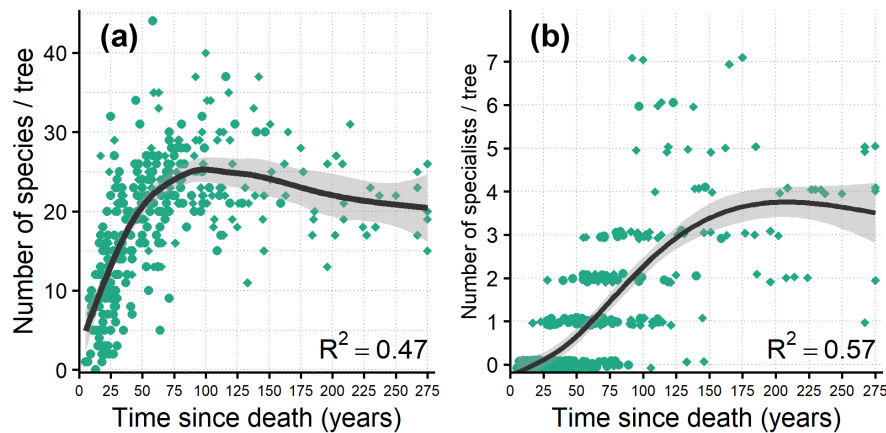


Figure 3. (a) Lichen species richness, and (b) the number of specialist lichens of long-standing snags in relation to time since death with fitted regression curves (GAM) and 95% confidence intervals.

from competition–colonization tradeoffs (Supporting information). Thus, the observed species replacement seems to not have resulted from competition–colonization tradeoffs among species, and it is reasonable to consider the surface transformation as a primary driver of colonization–extinction dynamics.

The centennial time scale of lignicolous lichen community dynamics on snags

Most snags with time since death over 175 years were extensively charred (section ‘Obtaining the time since death of snags’ for definition of extensive charring). Thus, disentangling the effects of extensive charring and very high values of time since death on lichen communities was infeasible. A few species occurred almost exclusively on charred wood, while several others seemed to disfavor charred snags. Therefore, it seems that charring considerably alters patch quality, depending on the degree of charring. Charring had been caused by surface fires which were historically frequent in our study sites but have been absent for at least the last 100 years (Tariyal et al. 2025). The long absence of fire explains the present confounding of time since death and extensive charring. Because of this confoundment, the community changes observed in the final part of the chronosequence can probably not be attributed to the standard process of habitat patch quality change over the time that snags remain standing.

As such, our study is inconclusive about whether lichen communities on snags remain dynamic for the entire duration that snags may remain standing. Yet, focusing on the uncharred snags, they evidently remained dynamic for at least 125–150 years. The previously reported dynamics of deadwood-associated communities usually occur on much shorter time scales than shown here (Kushnevskaya et al. 2007, Ulyshen and Hanula 2010, Lepinay et al. 2022, Lettenmaier et al. 2025). Variation in wood decomposition rates among forest ecosystems (Harmon et al. 2020) can be a major driver of differences in the temporal dynamics of deadwood-associated communities.

Lignicolous lichen communities are intrinsically linked with snag dynamics

Given the influence of time since tree death on lichen communities, lignicolous lichen communities are intrinsically linked with snag dynamics, particularly the longevity or fall rate of snags. Snag fall rates are impacted by climate, especially temperature, and tree traits related to decay resistance through their effects on wood decomposition rate (Oberle et al. 2018, Oettel et al. 2023, Aakala et al. 2024). Thus, snag dynamics vary among forest biomes and focal tree species (Everett et al. 1999, Vanderwel et al. 2006, Aakala et al. 2008, Onodera and Tokuda 2015). Since lignicolous communities begin to form after bark has fallen off, bark loss rate is another aspect of snag dynamics with major significance to lignicolous lichens. Long-standing snags have low recruitment rates because most snags tend to fall relatively quickly, and high longevity is obtained only by a minority (Rouvinen et al. 2002, Vanderwel et al. 2006, Aakala et al. 2008). When long-standing snags do occur, they are likely to be spatiotemporally continuous despite a low recruitment rate because of their long persistence (Rouvinen et al. 2002, Kuuluvainen et al. 2017). Such slow-paced snag dynamics enable high lignicolous lichen diversity.

The value of long-standing snags for lignicolous lichens has so far been addressed only regarding *Pinus sylvestris* in boreal Europe (Santaniello et al. 2017, Nirhamo et al. 2024, this study). However, snags of several other tree species may reach extended longevity (>100 years; Daniels et al. 1997, Everett et al. 1999, Storaunet 2004). Snag longevity is highest in conifers in cold climates (Oberle et al. 2018, Oettel et al. 2023, Aakala et al. 2024). Thus, besides boreal forests, long-standing snags may probably be formed in montane forests, but in some cases, they can emerge also in temperate climates (Daniels et al. 1997). We suggest that the community dynamics of lignicolous lichens that we demonstrated on *P. sylvestris* snags are repeated in snags of several other tree species. Snags of *Larix laricina* (Thor et al. 2024) and *Thuja plicata* (Goward and Arsenault 2018) have been noted to host

specialized lichen species, which is probably linked to high snag longevity.

Specialists of long-standing snags and implications for conservation

The majority of obligate lignicoles were associated with long-standing snags (11 out of 19 species for which snag type associations were assigned). These specialists evidently do not occur on other natural substrates except long-standing snags, although some of them may grow on old human-made wooden structures (Svensson et al. 2005). Additionally, many obligate lignicoles occurred early in the chronosequence. This suggests two frequent and distinct strategies among obligate lignicoles occurring on snags: the use of wood that has undergone several decades of weathering and decomposition, and the use of fresh wood available for a relatively short period after bark loss. In addition, several obligate lignicoles have adopted strategies due to which they occur mainly on fallen deadwood or stumps rather than snags (Svensson et al. 2016).

Human activity has caused lower deadwood quantity in forests in many parts of the world, and crucially, this is often concomitant with a reduction in qualitative variability of deadwood (Thorn et al. 2020). In our study region in boreal Europe, pine snag longevity in managed forests is truncated, and apparently extends above 50 years very rarely, if ever (Mäkinen et al. 2006, Nirhamo et al. 2023). Truncated snag longevity in managed landscapes leads to lower lignicolous lichen diversity, and particularly, very low occurrence or a total absence of specialists of long-standing snags (Larsson Ekström et al. 2023, Nirhamo et al. 2024). Therefore, the specialists are dependent on old-growth forests with intact snag dynamics. We identified 11 species as specialists of long-standing snags, but accounting for species that were rare or absent in our data, the lichen flora of Fennoscandia (Spribille et al. 2008) contains probably at least twice that many such species. It is very likely that specialists of long-standing snags vulnerable to habitat changes from forest management exist also in other regions (Goward and Arsenault 2018, Thor et al. 2024).

To maintain forest biodiversity, deadwood should be restored into managed forests (Thorn et al. 2020). However, studies have shown restored deadwood to support relatively low lignicolous lichen diversity (Hämäläinen et al. 2021, Larsson Ekström et al. 2023, Nirhamo et al. 2024). Evidently, this is because restored deadwood in these studies had formed up to 20 years ago, while high diversity requires much older deadwood. The prerequisites for high snag longevity in *P. sylvestris* are not known properly, making restoration challenging. Yet, even if the restoration of long-standing snags is successful, it is expected to take up to a century until specialists associated with them begin to occur frequently. Moreover, the specialists may fail to reach restored habitats that are located within strongly modified and fragmented landscapes (Moor et al. 2021, Hämäläinen et al. 2023). The significant challenges of restoration highlight the importance of the conservation of remnant old-growth forests with intact snag dynamics.

Conclusions

By applying dendrochronological methods, we were able to address the dynamics of lignicolous lichen communities over a multicentennial chronosequence. The chronosequence indicated that there is a sequence of colonization by and extinction of various lichen species during the persistence of the habitat patches provided by snags. Comparing to previously described cases of deadwood-associated communities, we observed very slow community dynamics, which were shown to be continuous at least for 125–150 years. The slow dynamics are a result of the low decomposition rate of *Pinus sylvestris* snags, which is due to their apparent high decay resistance and the cold climate of our study region. Patterns in the species composition and richness of lignicolous lichens on snags were closely connected to the time that dead trees had remained standing after death. Thus, our study shows a direct link between lignicolous lichens and snag dynamics. The lignicolous lichen diversity of a given forest site is indicated to be strongly influenced by the duration that snags remain standing.

Acknowledgements – We warmly thank Marie Kivits, Romain Bergeret and Alina Kiiskinen for their participation in the field work, and Hanna Tuovila for identifying specimens of non-lichenized calicioid fungi. Open access publishing facilitated by Ita-Suomen yliopisto, as part of the Wiley - FinELib agreement.

Funding – This study was funded by Maj and Tor Nessling Foundation and Kone Foundation.

Conflict of interest – The authors declare no conflict of interest.

Author contributions

Aleksi Nirhamo: Conceptualization (equal); Formal analysis (lead); Funding acquisition (equal); Investigation (lead); Methodology (equal); Writing – original draft (lead). **Pemelyn Santos:** Formal analysis (supporting); Investigation (supporting); Methodology (equal); Writing – review and editing (supporting). **Mariina Günther:** Investigation (supporting); Methodology (equal); Writing – review and editing (supporting). **Jari Kouki:** Conceptualization (equal); Funding acquisition (equal); Methodology (equal); Supervision (equal); Writing – review and editing (equal). **Tuomas Aakala:** Conceptualization (equal); Funding acquisition (equal); Methodology (equal); Supervision (equal); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.5tb2rbpbj> (Nirhamo et al. 2026).

Supporting information

The Supporting information associated with this article is available with the online version.

References

Aakala, T., Kuuluvainen, T., Gauthier, S. and De Grandpré, L. 2008. Standing dead trees and their decay-class dynamics in the

- northeastern boreal old-growth forests of Quebec. – *For. Ecol. Manage.* 255: 410–420.
- Aakala, T., Storaunet, K. O., Jonsson, B. G. and Korhonen, K. T. 2024. Drivers of snag fall rates in Fennoscandian boreal forests. – *J. Appl. Ecol.* 61: 2392–2404.
- Amarasekare, P. and Possingham, H. 2001. Patch dynamics and metapopulation theory: the case of successional species. – *J. Theor. Biol.* 209: 333–344.
- Arpaci, S. S., Tomak, E. D., Ermeýdan, M. A. and Yildirim, I. 2021. Natural weathering of sixteen wood species: changes on surface properties. – *Polym. Degrad. Stab.* 183: 109415.
- Cajander, A. K. 1926. The theory of forest types. – *Acta For. Fenn.* 29: 7193.
- Caruso, A., Thor, G. and Snäll, T. 2010. Colonization–extinction dynamics of epixylic lichens along a decay gradient in a dynamic landscape. – *Oikos* 119: 1947–1953.
- Daniels, L. D., Dobry, J., Klinka, K. and Feller, M. C. 1997. Determining year of death of logs and snags of *Thuja plicata* in southwestern coastal British Columbia. – *Can. J. For. Res.* 27: 1132–1141.
- Ellis, C. J. 2012. Lichen epiphyte diversity: a species, community and trait-based review. – *Perspect. Plant Ecol. Evol. Syst.* 14: 131–152.
- Ellis, C. J. and Coppins, B. J. 2006. Contrasting functional traits maintain lichen epiphyte diversity in response to climate and autogenic succession. – *J. Biogeogr.* 33: 1643–1656.
- Eronen, M. 2002. NOAA/WDS paleoclimatology – Eronen – Lieksa Patvinsuo N – PISY – ITRDB FINL008. – NOAA National Centers for Environmental Information.
- Everett, R., Lehmkuhl, J., Schellhaas, R., Ohlson, P., Keenum, D., Riesterer, H. and Spurbeck, D. 1999. Snag dynamics in a chronosequence of 26 wildfires on the east slope of the Cascade Range in Washington State, USA. – *Int. J. Wildland Fire* 9: 223–234.
- Fritz, Ö., Niklasson, M. and Churski, M. 2008. Tree age is a key factor for the conservation of epiphytic lichens and bryophytes in beech forests. – *Appl. Veg. Sci.* 12: 93–106.
- Fritz, Ö., Brunet, J. and Caldiz, M. 2009. Interacting effects of tree characteristics on the occurrence of rare epiphytes in a Swedish beech forest area. – *Bryologist* 112: 488–505.
- Fukasawa, Y. 2018. Fungal succession and decomposition of *Pinus densiflora* snags. – *Ecol. Res.* 33: 435–444.
- Gärtner, H., Schneider, L. and Cherubini, P. 2024. A new workflow for sampling and digitizing increment cores. – *J. Vis. Exp.* 211: e67098.
- Goward, T. and Arsénault, A. 2018. Calicioid diversity in humid inland British Columbia may increase into the 5th century after stand initiation. – *Lichenologist* 50: 555–569.
- Hämäläinen, A., Ranius, T. and Strengbom, J. 2021. Increasing the amount of dead wood by creation of high stumps has limited value for lichen diversity. – *J. Environ. Manage.* 280: 111646.
- Hämäläinen, A., Fahrig, L., Strengbom, J. and Ranius, T. 2023. Effective management for deadwood-dependent lichen diversity requires landscape-scale habitat protection. – *J. Appl. Ecol.* 60: 1597–1606.
- Haneca, K. 2024. fellingdater: a toolkit to estimate, report and combine felling dates derived from historical tree-ring series. – *J. Open Source Softw.* 9: 6716.
- Harmon, M. E., Fasth, B. G., Yatskov, M., Kastendick, D., Rock, J. and Woodall, C. W. 2020. Release of coarse woody detritus-related carbon: a synthesis across forest biomes. – *Carbon Balance Manage.* 15: 1.
- Holmes, R. L. 1983. Computer-assisted quality control in tree-ring dating and measurement. – *Tree-Ring Bull.* 43: 69–78.
- Johansson, P., Rydin, H. and Thor, G. 2007. Tree age relationships with epiphytic lichen diversity and lichen life history traits on ash in southern Sweden. – *Écoscience* 14: 81–91.
- Jönsson, M. T., Edman, M. and Jonsson, B. G. 2008. Colonization and extinction patterns of wood-decaying fungi in a boreal old-growth *Picea abies* forest. – *J. Ecol.* 96: 1065–1075.
- Johansson, V., Ranius, T. and Snäll, T. 2012. Epiphyte metapopulation dynamics are explained by species traits, connectivity and patch dynamics. – *Ecology* 93: 235–241.
- Kushnevskaya, H., Mirin, D. and Shorohova, E. 2007. Patterns of epixylic vegetation on spruce logs in late-successional boreal forests. – *For. Ecol. Manage.* 250: 25–33.
- Kuuluvainen, T., Aakala, T. and Várkonyi, G. 2017. Dead standing pine trees in a boreal forest landscape in the Kalevala National Park, northern Fennoscandia: amount, population characteristics and spatial pattern. – *For. Ecosyst.* 4: 12.
- Larsson, L.-A. 2005. CDendro & CooRecorder program package, ver. 9.8.1. – <https://www.cybis.se/forfun/dendro>.
- Larsson Ekström, A., Sjögren, J., Djupström, L. B., Thor, G. and Löfroth, T. 2023. Reinventory of permanent plots show that kelo lichens face an extinction debt. – *Biol. Conserv.* 288: 110363.
- Lepinay, C., Tláškal, V., Vrška, T., Brabcová, V. and Baldrian, P. 2022. Successional development of wood-inhabiting fungi associated with dominant tree species in a natural temperate flood-plain forest. – *Fungal Ecol.* 59: 101116.
- Lettenmaier, L., Bäessler, C., Decker, O., Hagge, J., Heibl, C., Mamadashvili, G., Seibold, S., Thorn, S. and Müller, J. 2025. 12 years of assembly patterns in saproxylic beetles suggest early decay wood as ephemeral resource patch. – *J. Anim. Ecol.* 95: 282–295.
- Löbel, S., Snäll, T. and Rydin, H. 2006. Species richness patterns and metapopulation processes/evidence from epiphyte communities in boreo-nemoral forests. – *Ecography* 29: 169–182.
- Mäkinen, H., Hynynen, J., Siitonen, J. and Sievänen, R. 2006. Predicting the decomposition of Scots pine, Norway spruce and birch stems in Finland. – *Ecol. Appl.* 16: 1865–1879.
- Marmor, L., Törra, T., Saag, L. and Randlane, T. 2011. Effects of forest continuity and tree age on epiphytic lichen biota in coniferous forests in Estonia. – *Ecol. Indic.* 11: 1270–1276.
- Meriläinen, J., Lindholm, M., Timonen, M. and Eronen, M. 2004. NOAA/WDS paleoclimatology – eriläinen – Oulanka National Park Kuusamo – PISY – ITRDB FINL046. – NOAA National Centers for Environmental Information.
- Moor, H., Nördén, J., Penttilä, R., Siitonen, J. and Snäll, T. 2021. Long-term effects of colonization–extinction dynamics of generalist versus specialist wood-decaying fungi. – *J. Ecol.* 109: 491–503.
- Nascimbene, J., Marini, L., Motta, R. and Nimis, P. L. 2009. Influence of tree age, tree size and crown structure on lichen communities in mature Alpine spruce forests. – *Biodivers. Conserv.* 18: 1509–1522.
- Nirhamo, A., Hämäläinen, A., Hämäläinen, K. and Kouki, J. 2024. Retention forestry can maintain epiphytic lichens on living pine trees, but provides impoverished habitat for deadwood-associated lichens. – *J. Appl. Ecol.* 61: 2717–2726.
- Nirhamo, A., Hämäläinen, K., Junninen, K. and Kouki, J. 2023. Deadwood on clearcut sites during 20 years after harvests: the effects of tree retention level and prescribed burning. – *For. Ecol. Manage.* 545: 121287.

- Nirhamo, A., Santos, P., Günther, M., Kouki, J. and Aakala, T. 2026. Data from: Community dynamics of lignicolous lichens on standing deadwood in a 275-year chronosequence. – Dryad Digital Repository, <https://doi.org/10.5061/dryad.5tb2rbpjb>.
- Oberle, B., Ogle, K., Zanne, A. E. and Woodall, C. W. 2018. When a tree falls: controls on wood decay predict standing dead tree fall and new risks in changing forests. – PLoS One 13: e0196712.
- Oettel, J., Zolles, A., Gschwantner, T., Lapin, K., Kindermann, G., Schweinzer, K.-M., Gossner, M. M. and Essl, F. 2023. Dynamics of standing deadwood in Austrian forests under varying forest management and climatic conditions. – J. Appl. Ecol. 60: 696–713.
- Onodera, K. and Tokuda, S. 2015. Do larger snags stand longer? Snag longevity in mixed conifer–hardwood forests in Hokkaido, Japan. – Ann. For. Sci. 72: 621–629.
- Pykälä, J., Ahti, T., Jääskeläinen, K., Myllys, L., Vitikainen, O. and Velmala, S. 2024. Lichens. – In: FinBIF 2024. The FinBIF checklist of Finnish species 2023. Finnish Biodiversity Information Facility, Finnish Museum of Natural History, Univ. of Helsinki.
- Ranius, T., Johansson, P., Berg, N. and Niklasson, M. 2008. The influence of tree age and microhabitat quality on the occurrence of crustose lichens associated with old oaks. – J. Veg. Sci. 19: 653–662.
- Rouvinen, S., Kuuluvainen, T. and Siitonen, J. 2002. Tree mortality in a *Pinus sylvestris* dominated boreal forest landscape in Vienansalo wilderness, eastern Fennoscandia. – Silva Fenn. 36: 127–145.
- Santaniello, F., Djupström, L. B., Ranius, T., Weslien, J., Rudolphi, J. and Thor, G. 2017. Large proportion of wood dependent lichens in boreal pine forest are confined to old hard wood. – Biodivers. Conserv. 26: 1295–1310.
- Schweingruber, F. H. 2002. NOAA/WDS paleoclimatology – Schweingruber – Pyhan Hakin National Park – PISY – ITRDB FINL010. – NOAA National Centers for Environmental Information.
- Snäll, T., Ribeiro, J. and Rydin, H. 2003. Spatial occurrence and colonisations in patch-tracking metapopulations: local conditions versus dispersal. – Oikos 103: 566–578.
- Snäll, T., Ehrlén, J. and Rydin, H. 2005. Colonization-extinction dynamics of an epiphyte metapopulation in a dynamic landscape. – Ecology 86: 106–115.
- Spribille, T., Thor, G., Bunnell, F. L., Goward, T. and Björk, C. R. 2008. Lichens on dead wood: species-substrate relationships in the epiphytic lichen floras of the Pacific Northwest and Fennoscandia. – Ecography 31: 741–750.
- Storaunet, K. O. 2004. Models to predict time since death of *Picea abies* snags. – Scand. J. For. Res. 19: 250–260.
- Svensson, M., Johansson, P. and Thor, G. 2005. Lichens of wooden barns and *Pinus sylvestris* snags in Dalarna, Sweden. – Ann. Bot. Fenn. 42: 351–363.
- Svensson, M., Johansson, V., Dahlberg, A., Frisch, A., Thor, G. and Ranius, T. 2016. The relative importance of stand and dead wood types for wood-dependent lichens in managed boreal forests. – Fungal Ecol. 20: 166–174.
- Tariyal, G., Flury, R., Kouki, J. and Aakala, T. 2025. Local and regional factors influencing historical forest fires in eastern Fennoscandia. – Philos. Trans. R. Soc. B 380: 20230452.
- Tatsumi, S., Ohgoue, T., Azuma, W. A. and Nishizawa, K. 2023. Bark traits affect epiphytic bryophyte community assembly in a temperate forest. – Plant Ecol. 224: 1089–1095.
- Thomas, C. D. 1994. Extinction, colonization and metapopulations: environmental tracking by rare species. – Conserv. Biol. 8: 373–378.
- Thor, G., Gockman, O., McMullin, R. T., Selva, S., Goyette, S., Huereca, A. and Spribille, T. 2024. A new lichen and lichenicolous fungus from *Larix Laricina* in patterned fens of boreal North America. – Lichenologist 56: 379–392.
- Thorn, S., Seibold, S., Leverkus, A. B., Michler, T., Müller, J., Noss, R. F., Stork, N., Vogel, S. and Lindenmayer, D. B. 2020. The living dead: acknowledging life after tree death to stop forest degradation. – Front. Ecol. Environ. 18: 505–512.
- Ulyshen, M. D. and Hanula, J. L. 2010. Patterns of saproxylic beetle succession in loblolly pine. – Agric. For. Entomol. 12: 187–194.
- Vanderwel, M. C., Caspersen, J. P. and Woods, M. E. 2006. Snag dynamics in partially harvested and unmanaged northern hardwood forests. – Can. J. For. Res. 36: 2769–2779.
- Woods, C. L. 2017. Primary ecological succession in vascular epiphytes: the species accumulation model. – Biotropica 49: 452–460.
- Yamaguchi, D. K. 1991. A simple method for cross-dating increment cores from living trees. – Can. J. For. Res. 21: 414–416.
- Yatskov, M. A., Harmon, M. E., Fasth, B., Sexton, J., Hoyman, T. L. and Dudoit, C. M. 2022. Decomposition differences between snags and logs in forests of Kenai Peninsula, Alaska. – Can. J. For. Res. 52: 727–742.
- Zarate-García, A. M., Noguera-Savelli, E., Andrade-Canto, S. B., Zavaleta-Mancera, H. A., Gauthier, A. and Alatorre-Cobos, F. 2020. Bark water storage capacity influences epiphytic orchid preference for host trees. – Am. J. Bot. 107: 726–734.